

# AMERICAN JOURNAL OF Botany

---

Abstracts of Papers

Reviewed work(s):

Source: *American Journal of Botany*, Vol. 70, No. 5, Part 2: Program with Abstracts of Papers to be Presented at the Joint Meetings of the Botanical Society of America and the Canadian Botanical Association with Other Affiliated Societies at the University of North Dakota Grand Forks, North Dakota 7-11 August 1983 (May - Jun., 1983), pp. 1-139

Published by: [Botanical Society of America](#)

Stable URL: <http://www.jstor.org/stable/2446518>

Accessed: 04/04/2012 11:54

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*Botanical Society of America* is collaborating with JSTOR to digitize, preserve and extend access to *American Journal of Botany*.

<http://www.jstor.org>

## BRYOLOGICAL AND LICHENOLOGICAL SECTION

### Symposium: Assessing Air Quality with Lichens and Bryophytes – Part I

#### INTRODUCTION - Parts I and II

This symposium will address various methods of using lichens and bryophytes in air quality monitoring. Papers will include the topics of floristic analysis, mapping of sensitive species, statistical analysis of quantitative data, correlating fumigation studies with physiological effects and with field studies, trace element analysis, species variability with respect to air pollution and the ecological importance of lichens and bryophytes. These papers will summarize techniques presently in use and evaluate their reliability and usefulness in assessing air pollution damage. Organized by Clifford Wetmore, University of Minnesota, St. Paul, MN and James Bennett, National Park Service, Denver, CO.

BENNETT, JAMES P. National Park Service, Air Quality Division, Box 25287, Denver, CO 80225.

#### - The air pollution importance of non-vascular plants to the National Park Service.

The National Park Service (NPS) has a mandate to protect the biological resources of the national parks from the effects of air pollution. Under Clean Air Act regulations, the NPS has authority to determine whether or not higher than ambient SO<sub>2</sub> concentrations will cause adverse impacts on lichens and mosses in the parks. The NPS considers non-vascular plants as integral components of natural ecosystems because of their ecological importance as colonizers, nitrogen-fixers, food sources and soil stabilizers. Their position at the base of many food chains makes their role of primary importance.

Lichen sensitivity to SO<sub>2</sub> and heavy metals is well known. Several national parks are currently experiencing elevated SO<sub>2</sub> concentrations, some high enough to cause effects on lichens and mosses. The NPS has initiated six projects on lichens and mosses and air pollution, including floristic studies, sulfur baseline sampling, heavy metal sampling, and ecological community analyses. These studies will enable NPS to determine future adverse impacts on non-vascular plants in the parks.

NASH III, THOMAS H. Department of Botany & Microbiology, Arizona State University, Tempe, AZ 85287 - Correlating fumigation studies with field effects.

Differential tolerance of different lichens to the environment of cities and isolated pollution sources is well established. It is frequently assumed that these patterns reflect differential sensitivity to sulfur dioxide and/or other air pollutants. This assumption may be false or only partially true because lichens may well respond to alteration of other environmental factors. Fumigation studies with controlled levels of air pollutants provides a means for experimentally establishing whether lichens are in fact sensitive to air pollutants. It is important that both realistic exposure

and realistic pollutant concentration levels be employed. Furthermore, exposure conditions must be chosen to reflect conditions characteristic of the environment where the lichens occur naturally. The fumigation literature is critically examined with respect to these caveats and examples are given where the hypothesis that lichens are sensitive to air pollutants is both supported and not supported.

NIEBOER, EVERT\* and KEN A. KERSHAW, Departments of Biochemistry and Biology, McMaster University, Hamilton, Ontario, Canada, L8N 3Z5.

#### - Ecological Implications of Laboratory Toxicity and Related Photosynthetic Studies.

It will be demonstrated that a large proportion of the elemental content of lichens is the result of particulate trapping within the interstitial spaces of the thallus. A strong dependence on surface morphology can be illustrated for this phenomenon. Such accumulation may be expected to be relatively innocuous. Recent studies will be reviewed that show that the largely passive extracellular uptake of metal ions can be either protective or deleterious, depending on the chemical reactivity of the metal cation. Dissection studies are reported that indicate that metal-ion binding occurs to both the algal zone and fungal medulla, and that the uptake capacities of these zones, as well as the total uptake, are strongly lichen species dependent. Work with the uranyl ion further illustrates the importance of chemical speciation. And finally, toxic effects of ion absorption and SO<sub>2</sub> exposure are shown to be ameliorated by the mineral status of the thallus (high Ca<sup>2+</sup>, Mg<sup>2+</sup>, K<sup>+</sup> contents), by uptake inhibition (phosphate competing with arsenate; metal-ion rivalry), and high photosynthetic capacities. In this context, laboratory studies that simulate seasonal variations in photosynthetic capacities are summarized. In addition to species susceptibility, these observations imply a substrate and seasonal dependence of the toxicity to lichens of environmental pollutants. Inferences for the use of lichens as monitors of environmental pollution will be pointed out.

PUCKETT, KEITH.\* J. & SEDIGHEH SANG. Atmospheric Environment Service, Environment Canada, 4905 Dufferin St., Downsview, Ontario, M3H 5T4.

#### -Trace element mapping with lichens and bryophytes.

Since lichens and bryophytes are known to obtain and accumulate metal pollutants as well as their required nutrients from the atmosphere (either from rainfall or by impaction and sedimentation of airborne dust), they have been employed as biological indicators of trace element fallout in a great number of studies. In this paper enhanced levels of elements in lichens and mosses were reviewed and the usefulness of these plants for monitoring and mapping the concentrations of

## 2 Bryological and Lichenological Section

atmospheric pollutants around industrial plants is discussed. The review of the literature suggests that lichens and bryophytes either growing naturally or transplanted near a pollution source absorb and accumulate high concentrations of elements (e.g. Cd, Co, Cr, Cu, F, Fe, Hg, Ni, Pb, S, V, Zn) in their tissues. This accumulation appears to be related to both the distance from the source and prevailing wind conditions. In conclusion, using lichens and mosses as biological indicators of air pollution can prove to be a very reliable, inexpensive and practical method for monitoring the deposition of trace elements from the atmosphere.

SHOWMAN, RAY E. Environmental Engineering Division, AEP Service Corporation, P.O. Box 487, Canton, OH 44701. - Mapping air quality with lichens.

North American lichen - air quality mapping literature is reviewed and discussed. Lichen studies fall into two general categories, distribution and IAP mapping. Distribution mapping is best suited for areas where there is a significant air quality impact. In areas experiencing only slight effects a simplified IAP or other quantitative method is recommended. Care must be taken in interpreting lichen maps. In most areas a quantitative correlation between lichen success and long-term average air quality data is not possible. Never the less, lichen mapping is a valuable tool for obtaining a simple, inexpensive measure of the biological impact of air pollution.

WETMORE, CLIFFORD M. Botany Department, University of Minnesota, St. Paul, Minn. 55108. - Lichen floristics and air pollution.

Lichens are very sensitive to air pollution and many species are killed by low levels of pollutants. Not all species are equally sensitive and some are quite tolerant. By studying the lichen flora of a particular area one can draw certain inferences about the pollutant levels based on presence or absence of different lichens with different sensitivities. In order to use this survey method one must know the lethal levels of the pollutants for as many species as possible and one must have historical or phytogeographical and ecological information about the natural lichen flora. In some areas historical records are available but in others comparisons must be made with nearby clean areas. The distribution of the sensitive species within the study area can also give information about pollution levels. Sub-lethal levels of pollutants can be determined by analysis of lichens for levels of chemical elements. This method of air pollution study is less precise than by using IAP or other quantitative methods but is useful when many or large areas need to be rapidly surveyed for air pollution. The areas showing some reduction in the lichen flora can then be studied in more detail by other more sensitive methods.

WILL-WOLF, SUSAN. Department of Botany, University of Wisconsin, Madison, WI 53706. - Statistical analysis of air pollution indicators.

A survey of published field studies in which air pollution effects were assessed using lichens and/or bryophytes, shows that the most common monitoring approaches in North America since 1973 have been 1) use of lichen species numbers, diversity, or IAP

values, and 2) measuring levels of various elements accumulated in lichens and mosses. Both approaches were generally used to delineate impact zones around moderate to heavy-dose point sources or urban areas. Whenever possible, field studies should be designed to allow data analysis using appropriate parametric statistics, such as ANOVA, multiple regression, or partial correlation. Non-parametric statistics are required whenever percentage data, qualitative evaluations, or indices using ratios are compared. Chi-square tests are appropriate for comparing frequency distributions of all kinds, such as community composition data or cover classes. Complex multivariate analysis techniques such as ordination, classification, or discriminant analysis are best used to provide supporting information rather than directly to document air pollution impact. Useful sample designs and analysis approaches are given for some monitoring situations not extensively treated in the literature: 1) effects of low-dose point source emissions, 2) effects of interactions between pollutants in the field, and 3) effects of regional air pollution.

### Symposium: Assessing Air Quality with Lichens and Bryophytes - Part II

SLACK, NANCY, G. Department of Biology, Russell Sage College, Troy, New York, 12180.

-Ecological importance of lichens and bryophytes: what happens if they disappear?

Quite apart from their importance in assessing air quality, the subject of this Symposium, lichens and bryophytes have recently been shown to play a wide variety of roles in diverse ecosystems. In addition to their traditional role as "pioneers" in soil formation, soil retention, and colonization of difficult habitats not open to other groups, recent research has elucidated their important roles in nitrogen fixation, nutrient cycling, and in the food chain of mammals. Productivity studies have shown the importance of bryophytes as primary producers particularly in arctic and mire ecosystems, with values up to  $800 \text{ g m}^{-2} \text{ year}^{-1}$  reported. High biomass values for both bryophyte and lichen epiphytes have been reported in old growth *Pseudotsuga* forests in Oregon. Cyanophilic lichens, particularly *Lobaria oregana*, have an important role in nitrogen fixation in these forests. The genus *Lobaria* is highly susceptible to air pollution; *Lobaria pulmonaria*, a nitrogen-fixer in deciduous forest, has disappeared from many of its former locations in Britain. Nitrogen fixation by both extra- and intracellular blue-greens association with *Sphagnum* species has been reported in both temperate mires and *Sphagnum* communities in coniferous forest in Sweden, and in mires in Arctic Alaska, Swedish Lapland and Finland. Nutrient cycling in both bryophytes and lichens and the relationship of these nutrient cycles to the utilization of these plants by caribou has been studied in Northern Canada and Arctic Alaska. Whereas lichens are the primary winter food of caribou and reindeer, mosses are also important in the high Arctic, e.g. for reindeer in the Svalbard Archipelago. Mosses and/or lichens are also important in the food chains of such diverse organisms as mites, lemmings, and people.

WIRTH, VOLKMAR. Staatliches Museum für Naturkunde Stuttgart, Arsenalplatz 3, D-7140 Ludwigsburg, Federal Republic of Germany. - Phytosociological approaches to air pollution monitoring with lichens. Phytosociology is an approach to the study of

plant communities that has been extensively employed throughout Europe. Basic principles by which different hierarchical groups of lichens are distinguished, are discussed and examples are given. Epiphytic lichen associations have clearly been modified over the past two hundred years. This can be documented by herbarium records as well as cartographic studies. Even the formerly widely distributed Xanthorion parietinae alliance, that normally prospers in areas adjacent human settlements, has declined markedly. Many of the patterns in lichen community modifications can be correlated with measured SO<sub>2</sub> levels. A number of lichen species have apparently disappeared entirely from the Federal Republic of Germany and about 50% of the lichen flora is considered endangered.

### Poster Session

BASILE, DOMINICK V., MARGARET R. BASILE and ROSS E. KONING. Lehman College of CUNY, Bronx, N.Y. 10468 and Rutgers Univ. Piscataway, N.J. 08854.

- Ethylene production and its possible role in regulating leaf and branch development in *Plagiochila arctica*, a leafy liverwort.

Ethylene production by gametophytes of *Plagiochila arctica* Bryhn & Kaal. in axenic culture was determined by means of gas-liquid chromatography (GLC). Exogenous indole acetic acid (IAA) at approx. 6x 10<sup>-5</sup>M markedly stimulated ethylene synthesis while aminoethoxyvinyl glycine (AVG) at approx. 10<sup>-5</sup>M significantly suppressed it. In these respects ethylene production and its regulation are the same in *P. arctica* as in representatives of the flowering plants (Magnoliophyta). Although these results may have been inferred, they were hitherto unsubstantiated. Furthermore, these data in conjunction with those obtained in previously completed experiments lend support to an hypothesis that auxin-induced ethylene synthesis plays an important role in regulating leaf and branch development in leafy liverworts, particularly those originating from ventral merophytes.

JANSSENS, JAN A. & PAUL H. GLASER. Limnological Research Center, University of Minnesota, Minneapolis, MN 55455.

- Fossil bryophytes and peat stratigraphy in the development of Red Lake Peatland, northern Minnesota.

Ten peat cores, reaching down to the mineral sediment, taken along a transect 7-km long in the center of the vast Red Lake Peatland in northern Minnesota, were analyzed to reconstruct the development of a mire complex consisting of forested ovoid bog islands separated by internal water tracks marked by patterned fens. The reconstruction of past bog, poor-fen, and rich-fen communities is based primarily on the quantitative analysis of fossil bryophyte assemblages;

concentration by weight and volume, accumulation rates, and percentages of identified taxa were calculated. The sharply defined bryophyte zones were stratigraphically correlated among cores by radiocarbon dates, the regional pollen zonation, and buried wood layers. Peat-accumulation rates, calculated from radiocarbon dates, were correlated with measurements of bulk density, humification, and peat ontogeny as based on the local paleoenvironmental reconstruction. The peat stratigraphy indicates that bog vegetation originated about 5000 years ago at the watershed crest and then extended downslope, growing over rich-fen peat in the process. Cores from the internal water tracks contain a striking sequence in fossil assemblages, changing from a basal rich-fen zone to a bog or oligotrophic poor-fen zone and then reverting back to a rich-fen zone towards the top. This stratigraphy supports an earlier hypothesis, based on the study of present-day landforms, that the internal water tracks originated recently within a continuous complex of forested raised bogs, with poor-fen lawn flanks. Conversion of the bog into ovoid islands resulted in the complex landscape.

### Contributed Papers

Allen, Bruce H. Department of Biological Sciences, University of Cincinnati, Cincinnati, Oh 45221.- The protonema of *Drummondia prorepens*.

Spore germination in *D. prorepens* is precocious and endosporic. On sowing of these endosporic protonemata dimorphic protonemal filaments arise: those with long rhomboidal cells having end walls oblique to the long axis, and those with cells more or less square the end walls at right angles to the long axis. By means of anticlinal and periclinal divisions in the latter a massive three-dimensional protonema is formed. Periclinal divisions in the former results in their elongation into the medium. Occasional divisions at right angles to the oblique end walls of the long celled filaments form cells that give rise to three-dimensional cell masses. Leafy gametophytes originate on the primary cell mass within 20 days, and on the secondary cell masses within 59 days. This sporeling type is similar to that reported for some species of *Ptychomitrium*, *Hedwigia* and *Drummondia*. The salient feature of this type is the ability to form, free from the constraint of the spore wall, a primary three-dimensional protonema. Rapid development of leafy gametophytes is considered the principal advantage of this type of sporeling development: minimizing the risk of dessication and of being washed onto an unsuitable substrate.

ANDERSON, DAVID C., LARRY ST. CLAIR 360 Wakara Way Salt Lake City, Utah 84108

-Selection of useful parameters in assessing lichens as biological monitors of air pollution.

The use of lichens as biological monitors of air quality although in its infancy affords an "early warning"

## 4 Bryological and Lichenological Section

system to potential impacts of air pollution on biological activity. Two studies recently conducted in southeastern Wyoming and in eastern Utah evaluated the use of such a system. At permanent plots established at incremental distances from pollution sources the lichen community was characterized and the membrane permeability, a measurement of cell damage, of selected lichen species was determined. The purpose of the studies was to identify parameters most accurately replicated and to characterize the existing lichen community. In southeastern Wyoming, membrane leakage values for Parmelia chlorochroa, a terricolous lichen, was significantly higher at the Dave Johnston plant, a plant on line since 1958, in comparison to the Laramie River plant, in use since 1980. Data from the Dave Johnston plant show significantly higher membrane leakage values, higher lichen selenium content and lower weight per individual at sites nearest the pollution source. On oil shale lands in eastern Utah, the results of a similar study showed that the percentage of total lichen cover, the number of species/quadrat and the sulfur content of the lichen thallus were the least variable parameters measured. The percentage of total cryptogamic cover, the number of lichen species per unit area, membrane leakage and to some extent, elemental analyses of lichen tissue were parameters most replicatable and would, therefore, serve as good indicators of lichen community conditions.

BENNETT, JAMES P. National Park Service, Air Quality Division, Box 25287, Denver, CO 80225.  
- Air pollution studies on lichens in Denver, Colorado.

Denver, Colorado is not known for having very high air quality. The notorious "brown cloud" is easily observed by many visitors. Using the Pollutant Standards Index (PSI) for 1978 to 1980, Denver ranked fourth in the nation for having polluted air. The composition of the pollution is the subject of a continuing controversy, but the presence of SO<sub>2</sub> can not be ruled out. Knowing that lichens are extremely sensitive to low levels of SO<sub>2</sub>, a study was initiated to map lichen frequency on tree trunks. The presence/absence of lichens are noted on a minimum of 100 trees at least 30 cm diameter in size in parks, cemeteries, school yards or other locations containing sufficient number of trees. To date, over 2500 trees have been sampled. Only two species of corticolous lichens are encountered in Denver, the most common being Xanthoria fallax. With over 20 sites sampled so far, a strong relationship has been found between the probability of encountering a lichen on a tree trunk and linear distance from the city center ( $r = 0.73$ ). An objective of the study is to sample a minimum of 50 sites systematically located at selected distances and compass directions from the city center. A model can then be developed relating the probability of lichens occurring on tree trunks to various geographic parameters. With only one SO<sub>2</sub> monitoring station in Denver it will not be possible to relate these effects to air quality, but the observed trend would suggest the need for more monitoring.

DALE, MARK R.T. Botany Dept., University of Alberta, Edmonton, Alberta. T6G 2E1  
The geometry of adjoining lichen thalli in relation to their growth rates  
Models of the growth rates of lichen thalli usually include an initial phase of exponen-

tial radial growth, followed by a phase of linear growth. These models predict that the shape of "true" boundaries between adjoining thalli will have characteristic changes in curvature at points where growth has become linear. Thus a comparison of the shapes predicted from these models with those observed in boundaries between lichen thalli (most easily seen in species like those of Rhizocarpon which have distinct hypothalline margins) permits an evaluation of the models without long term studies. In cases where the models prove to be appropriate, the geometry of the boundaries provides estimates of the size at which growth becomes linear. It is possible that once the growth curves for several species are known, a comparison of inter- and intraspecific boundaries will prove useful in evaluating the relative rates of linear growth in different species.

DEWEY, RICHARD M. Department of Biology, Texas A&M University, College Station, TX 77843  
- Electrophoretic evidence for the recognition of Riccia mcallisteri.

The relationship of the two concepts, Riccia dictyospora M.A. Howe, Bull. Torrey Bot. Club 28:163, 1910., and R. mcallisteri M.A. Howe, The Bryologist 20:35, 1917., is among the most vexing problems in the taxonomy of North American representatives of Riccia subgenus Riccia. An inability to discern reliable critical morphological differences between the two species has prompted some workers to view R. mcallisteri as a taxonomic synonym. Plants representing R. dictyospora, sensu lato, have been collected in several central Texas localities, including the type locality of R. mcallisteri. When surveyed with starch-gel electrophoresis, plants assignable by morphology to either R. dictyospora or R. mcallisteri have exhibited distinctive phenotypes for isozymes of malate dehydrogenase, acid phosphatase, peroxidase and aspartate amino transferase. This preliminary electrophoretic evidence supports the recognition of R. dictyospora and R. mcallisteri as distinct species.

ELIX, JOHN A. Department of Chemistry, Australian National University, P.O. Box 4, Canberra 2600, Australia.

- Lichens in Papua New Guinea

The lichen flora of Papua New Guinea is still poorly known, but even after a cursory investigation the contrast between the flora of the tropical lowland forests and higher altitude montane forests are particularly striking. Corticolous substrates are most important in both environments, but crustose growth forms growing on tree trunks and branches dominate in the coastal forests where lichen cover is high but biomass low. Genera such as Graphis, Arthonia and Anthracothecium are particularly abundant. In the lower montane Castanopsis and Araucaria forests pantropical macrolichen genera such as Parmotrema, Usnea and Leptogium are prominent, while in the higher montane Nothofagus forests the genera Pseudocyphellaria, Sticta, Lobaria and Anzia are preponderant. Interestingly the former two genera and common associates (Menegazzia, Psoroma) are presumably of Gondwanaland origin and also prominent in the Nothofagus forests of Tasmania, New Zealand and Chile, while Lobaria and Anzia appear of Asiatic origin. This dichotomous origin appears to be reflected in much of PNG's lichen flora.

GLIME, JANICE M. Department of Biological Sciences, Michigan Technological University, Houghton, MI 49931. - A photographic study of spore and protonema development in Fontinalis squamosa.

Electron microscopy was used to demonstrate development and arrangement of spores within the capsule. Spore viability, germination, and protonema development are illustrated by light and fluorescence microscopy. The presence of two spore sizes is clearly demonstrated and the reduced viability of the smaller spores is demonstrated by reduced fluorescence. Germination is demonstrated in culture from 5°C-22°C and requires light and moisture, but not submersion. Protonemata branches arise from 1-3 points on the spore, depending upon conditions. Germination and development are slow and depend upon the state of maturation of the spores at the time of culture. Bud development is very slow and the requirements for budding are unclear.

GOWAN, SHARON P. Botany Division, National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario K1A 0M8, Canada - A study of roof-dwelling lichens and the possible effects of a nearby phosphorus plant.

Concern has been expressed by the inhabitants of Long Harbour, Newfoundland, about abundance in their town of roof-dwelling lichens, and the possible relationship of their growth to phosphate- and fluoride-containing substances escaping from a nearby phosphorus plant. In response to this concern, an ecological study was undertaken to compare the roof-dwelling lichen community in Long Harbour with that in nearby towns lacking any significant sources of atmospheric contamination. Results show a concentration of "enrichment species", especially Xanthoria polycarpa and Physcia tenella in Long Harbour, whereas species characteristic of acid bark and rocks, especially Hypogymnia physodes and H. tubulosa predominate in a nearby town. Coverages and effect of lichens on their substrate in the two towns are comparable. It is hypothesized that the abundance of enrichment species in Long Harbour is at least partially a response to high concentrations of air-borne dust rich in phosphates.

GRAHAM, LINDA E. Department of Botany, University of Wisconsin, Madison, WI 53706. - Coleochaete: Advanced green alga or primitive embryophyte?

Ultrastructural studies of reproductive development in Coleochaete have revealed a number of features that do not occur elsewhere in the green algae, but which are characteristic of embryophytes. Filamentous species of Coleochaete produce unicellular antheridia as do other green algae, but the parenchymatous species may produce internal, multicellular antheridia that resemble early developmental stages of land plant gametangia. Following fertilization, the zygote of Coleochaete is retained on the haploid plant, and apparently induces the formation of a layer of covering cells that may produce localized wall ingrowths. These cells resemble gametophytic placental transfer cells of embryophytes in location, time of development, and ultrastructure. Upon germination, the zygote develops into a multichambered, spore-producing structure that is not observed elsewhere among green algae, but which resembles spore mother cells of embryophytes in some important features. Finally, Coleochaete produces more spores per

fertilization event than other freshwater, or haploid, haplobiontic green algae. This last feature is probably related to retention of the zygote, zygote enlargement and storage of photosynthate, and putative nutrient interactions between haploid and diploid phases of the life cycle. These features may thus have been preadaptations of major importance during the transition of plants to land and the origin of embryophytes from charophycean algae.

HOARE, JANET K. Room 429 Hensill Hall, San Francisco State Univ., San Francisco, CA 94132 - Lichen succession and diversity on dated Hawaiian lava flows.

Lichens were collected on lavas of thirty-two ages on the island of Hawaii to determine lichen succession and diversity on a series of lava substrates of known ages. One hundred eighty-six collections were made at sixty sites representing nine geographic locations. Stereocaulon is the most prevalent genus and, with Lepraria, becomes established in less than ten years, followed by foliose genera (largely Parmelias), and Gladonias. Crustose genera appear on lavas at least thirty years old, but are uncommon on lavas younger than a few hundred years. The greatest lichen diversity was found on old lavas at sea level in the south-east portion of the island where rainfall is moderate. The most profuse growth (Stereocaulon) appears on lavas one hundred and fifty years old in the central saddle area where rainfall is heavy.

LAWREY, JAMES D. Department of Biology, George Mason University, Fairfax, VA 22030.

- Lichen herbivore behavior: preference or avoidance?

Field data collected in a saxicolous lichen community in Shenandoah National Park showed that the lichen herbivore Pallifera varia prefers certain lichen species to others. Two hypotheses were developed to explain this preference. The avoidance hypothesis, that preference by slugs actually results from the rejection of unpalatable species, was tested by offering slugs choices of filter paper disks impregnated with secondary products of the avoided and preferred species. The preference hypothesis, that slugs select lichens of highest quality, was tested by measuring the concentration of essential elements in lichens eliciting high and low preference by slugs. Lichens with the highest element contents were assumed to be of highest quality to herbivores. Results showed that the preferred lichens had significantly lower concentrations of N, P, and Ca, and that avoided lichens produced secondary compounds that inhibited P. varia grazing activity. These results suggested that lichens with high concentrations of essential elements are most likely to produce defense compounds, an observation supporting some explanations for chemical defense patterns in vascular plants.

Mankiewicz, Paul S. Harding Laboratory, New York Botanical Garden, Bronx, New York, 10458

-Water conduction by external capillary spaces and the shape of bryophyte colonies.

While the major kinds of bryophyte colonies have been well described in the literature, there have been no empirical studies of the spatial arrangement of plant axes in cushions,

## 6 Bryological and Lichenological Section

wefts, tufts, and canopies of bryophytes. In the present study, two sets of methods have been elaborated: one set of methods permits the external capillary spaces within bryophyte colonies to be visualized by modifications of standard paraffin embedding methods, as well as other novel means using colloidal infusions or polymerization; the other set of methods permit direct laboratory or field measures to be taken of water flow through a bryophyte colony. The results of these methods demonstrate that cushions, wefts, tufts and canopies are: 1) qualitatively distinguishable in terms of the distribution of axes and appendages within the colonies; and, 2) quantitatively distinguishable in terms of the amount of water that the cross-sectional area of a given colony type is capable of transporting.

MATTHES-SEARS\*, UTA and THOMAS H. NASH III.  
Department of Botany and Microbiology, Arizona State University, Tempe, AZ 85287. - Morphological and physiological variations of *Ramalina menziesii* along a coast-inland gradient.

The corticolous lichen *Ramalina menziesii* Tayl. shows marked morphological variation along a coast-inland gradient in western California. Photosynthetic patterns throughout the year were studied at a coastal and an inland site and found to differ markedly as a result of the oceanic influence which modifies the moisture aspect of the climate. Both populations became activated by rainfall and dew during the rainy season; these winter photosynthetic rates were generally higher at the coastal than the inland site. During summer, the inland population was inactive due to drought, whereas the coastal population was regularly activated by coastal fog and high atmospheric humidity. Preliminary data show that the finer, less reticulate coastal morphotype was slightly more efficient in absorbing water vapor from the air and consequently exhibited higher photosynthetic rates under conditions of high atmospheric humidity. This suggests an adaptation of the coastal population to utilization of non-precipitation sources of moisture.

MILLER, HARVEY A. Department of Biological Sciences, University of Central Florida, Orlando, Florida 32816 - Two hepatic genera new to Hawaii and Polynesia.

Among the thousands of unreported collections of Pacific island bryophytes assembled by the author, many specific novelties have been discovered. Two genera found among these collections, *Southbya* and *Aphanolejeunea*, have not been reported previously from Hawaii and Polynesia. *Southbya* is new to all tropical Pacific islands and its presence in Hawaii provides additional evidence for a floristic tie to temperate Asia. *Aphanolejeunea* was reported by Stephani from Norfolk Island but that questionable record until now has been the sole report for the tropical Pacific.

MISHLER, BRENT D.\* and STEVEN P. CHURCHILL. Farlow Herbarium, Harvard University, Cambridge, MA 02138 and Division of Biological Sciences, University of Kansas, Lawrence, KS 66045. - On the application of Hennigian cladistics to the phylogeny of the bryophytes.

The empirical concern of bryophyte systematists with new methods for studying characters has generated important new data bearing on the relationships of these plants. It is important also, however, to pay explicit attention to the theory behind systematics and the study of phylogeny, to the assumptions, justifications, and even procedures that have usually been left implicit. We argue that the application of Hennigian cladistics to bryology can provide a rigorous framework for investigating phylogeny, sound concepts of monophyly, homology, and relationship, and a maximally useful basis for classification. We present the results of a study of the cladistic relationships of the major groups of bryophytes, with respect to the green algae and the tracheophytes. While the embryophytes as a whole do seem to form a monophyletic group, the bryophytes (sensu lato) are paraphyletic. The mosses appear to have shared a more recent common ancestor with the tracheophytes than either has with the liverworts or hornworts. The phylogenetic placement of the hornworts is more problematical, but on the basis of current information, they seem to have shared a more recent common ancestor with the moss-tracheophyte lineage, than with the liverworts. Hennig's central phylogenetic insight, that only shared, derived characters are evidence of relationship, can provide a focus for further research to test and refine the preliminary cladogram presented here.

MISHLER, BRENT D.\* and DANIEL C. SCHEIRER. Farlow Herbarium, Harvard University, Cambridge, MA 02138 and Department of Biology, Northeastern University, Boston, MA 02115. - Development of the leaf of *Tortula obtusissima*: systematic and ecological implications.

The development of leaves of field-collected and cultured plants of *Tortula obtusissima* (C. Muell.) Mitt. has been studied with light microscopy, SEM, and TEM. Leaves of young gametophores produced from spores show a characteristic juvenile morphology, differing from adult leaves in shape, curvature of the leaf margin, and the merely apiculate apex. The hollow papillae are initially simple, on 3-5 regions of both surfaces of the leaf cell, and develop by enlarging and bifurcating twice, finally becoming antleroid. Leaf ontogeny is of potential phylogenetic importance when compared to other species of *Tortula* with mature leaf morphologies similar to the juvenile morphology of *Tortula obtusissima*, and in which the same type of papilla is elaborated to a lesser or greater extent. Mature leaves of *Tortula obtusissima* are keeled, with recurved margins and a long-excurrent, hyaline, serrate awn. The basal leaf cells are hyaline, rectangular, often with both surface walls resorbed and standing open wet or dry. The upper leaf cells are strongly mamillate, in addition to bearing the characteristic papillae, and have a cuticle. The leaf morphology appears to have several ecological functions. The perforated basal cells and sheathing leaf bases serve for external water transport. The greatly amplified cell membrane in the hollow papillae implies transport processes--an external analogy to the transfer cells at the foot of moss sporophytes. The papillae, which with the mamillate cell walls form channels for capillary movement of water over the leaf surface, may also serve to facilitate gas exchange during active photosynthesis.

NEUMANN, ALAN J. and DALE M. J. MUELLER\*. Department of Biology, Texas A&M University, College Station, TX 77843. - Structure and function of the peristome in *Leucodon julaceus* (Musci).

The sporophyte of *Leucodon julaceus* (Hedw.) Sull. has a peristome consisting of a reduced endostome and an exostome of sixteen stout, pale teeth that are ornamented with papillae on the upper two-thirds of the teeth. The endostome is composed of cellulosic primary cell walls of the inner (IPL) and primary (PPL) peristome layers, plus heavy secondary wall thickenings on the IPL which appear to be of carbohydrate and lipid composition. The exostome is composed of portions of adjacent periclinal cell walls of the PPL and outer (OPL) peristome layers and a common middle lamella. The middle lamella is composed of pectinaceous and lipoidal compounds. The adjacent primary walls of the PPL and OPL are composed of densely packed cellulosic microfibrils. The primary walls are highly birefringent and the main axis of microfibril orientation is parallel to the longitudinal axis of the tooth. Secondary wall thickenings are heaviest along the PPL and consist of cellulosic microfibrils embedded in a matrix of other carbohydrate and lipoidal compounds. The basal one-third of the exostome exhibits the heaviest secondary thickenings on the inner lamellae. The peristome functions in the regulation of spore release and is classified as hydrocastique because spore release is favored during periods of high humidity). The secondary wall thickenings at the base of the inner lamellae of the exostome swell upon hydration, causing the teeth to reflex to an erect position, thus allowing unhindered release of spores from the urn. Upon dehydration, these thickenings of the inner lamellae shrink causing the teeth to inflex over the mouth of the urn.

OLAFSEN, ASTRID G.\* and THOMAS H. NASH III.  
Department of Botany and Microbiology, Arizona  
State University, Tempe AZ 85287.

- Patterns in carbon and nitrogen fixation in two lichens from arctic habitats.

*Peltigera canina* and *Stereocaulon tomentosum*, two disparate nitrogen-fixing species, were monitored diurnally in situ throughout the summer at Anaktuvuk Pass, Alaska. Nitrogen fixation showed greater responses to changes in thallus water content (%oven dry weight) than did carbon fixation. At thallus water less than 250% (*P. canina*) and 160% (*S. tomentosum*), nitrogen fixation declined, almost ceasing at 100%, in contrast to carbon fixation, which began dropping rapidly at 100% for both species. Above 250% and 160%, nitrogen fixation increased gradually, peaking at 300% and 200% for *P. canina* and *S. tomentosum*, respectively. Carbon fixation plateaued at water greater than 100% for both species, with no decline at high water contents, which never exceeded 520% for *P. canina* nor 350% for *S. tomentosum*. Nitrogen fixation increased with temperature, both species having their highest activity (15 nmoles  $C_2H_4$   $mg^{-1}hr^{-1}$  (*P. c.*) and 4.2 nmoles  $C_2H_4$   $mg^{-1}hr^{-1}$  (*S. t.*)) recorded at 19-21° C, while any photosynthetic increase with temperature was indistinguishable from the light effect. Gross photosynthesis saturated at 260-320  $\mu E$  (.28 cal  $cm^{-2}min^{-1}$ ) for *P. canina*, and 100  $\mu E$  higher for *S. tomentosum*, with nighttime fixation 5-10% of daytime levels; nighttime nitrogen fixation continued on par with daytime levels, showing no increase with increased light. Since 90% of the observed light levels and 80% of the observed temperatures of physiologically active samples were at or below these optima, both species were light limited for photosynthesis and temperature limited for nitrogen fixation through most of the season.

RUSHING, ANN E.\*, ZANE B. CAROTHERS AND JEFFREY G. DUCKETT. Department of Botany, University of Illinois, Urbana, IL 61801 and School of Biological Sciences, Queen Mary College, Mile End Road, London E1 4NS. U.K. Some aspects of spermatid micro-anatomy in the Jungermanniales.

A comparative study of the locomotory apparatus and cytoskeleton of *Cephalozia lunulifolia* and *Chiloscyphus pallescens* (Jungermanniales) has revealed numerous similarities between these two species and notable differences from previously investigated hepatics. In both species, the spermatid mother cells undergo ovalization prior to the final mitotic division, and the multilayered structure (MLS) shows the typical 4-layered morphology. In *Cephalozia*, the anterior portion of the lamellar strip (LS) is wider on both sides than the narrow anterior portion of the spline but is equal in width to the spline at its maximum. Similar lateral extensions of the LS were not observed in *Chiloscyphus*. At its widest, the spline of *Cephalozia* comprises 17 microtubules while that of *Chiloscyphus* comprises 25. The spline narrows gradually to form a shank usually made up of 6 long tubules. The anterior basal body (ABB) occupies a subapical position; the triplet extensions of the posterior basal body (PBB) extend forward and overlap with the ABB. The anterior mitochondrion (AM) follows closely the outline of the LS and may extend posteriorly beyond the LS where it then underlies the spline. The posterior mitochondrion, in certain sections, is seen to nearly ensheath the spherical, starch-containing plastid, a condition more commonly seen in mosses. The starch grains show a clumped arrangement. In contrast, the spermatids of *Marsupella*, the only other jungermannialian genus to be studied in detail, show no overlap of the ABB and the PBB or their extensions and the starch grains are linearly arranged in the plastid.

SCHAFFER, KAREN L. Department of Botany,  
University of Iowa, Iowa City, IA 52242.  
- Development of papillae on stem leaves of  
*Thuidium delicatulum* (Hedw.) BSG.

The development of papillae on upper cells of stem leaves of *Thuidium delicatulum* was investigated with light, scanning and transmission electron microscopy. Initially, through a combination of cell wall deposition and expansion, a small protuberance forms in the central portion of the cell wall. At this point the cell wall is very thin, but inner and outer layers are differentiated. The protoplast extends into the lumen of the developing papilla. As a result of further deposition of inner cell wall material, the papilla continues to enlarge and there is a progressive thickening of the entire cell wall. Associated with this stage is the occurrence of tubular vesicles that originate inside the protoplast and possibly contain wall precursor material. These vesicles are closely associated with the plasmalemma. Also, microfibril formation has been observed on the side of the plasmalemma adjacent to the cell wall. Ultimately, the papillae are more-or-less solid structures that are composed primarily of inner wall material. Although the papillae that occur on mature stem leaf cells of *Thuidium delicatulum* are simple, the developmental stages are fundamentally the same as those that have been established previously for the branched papillae that characterize upper leaf cells of *Anomodon attenuatus* (Hedw.) Hüb.

## 8 Bryological and Lichenological Section

SHAW, A. JONATHAN. Herbarium, University of Michigan, Ann Arbor, MI 48109 - Peristome Morphology and Homology in Mielichhoferia.

The peristome of M. mielichhoferi has traditionally been considered single and endostomial. However, new observations provide evidence that it is double, consisting of more or less well-developed exostome teeth and a rudimentary, endostomial basal membrane. Other Mielichhoferia species whose peristomes have been incorrectly interpreted as single and endostomial include M. himalayana, M. macrocarpa, and M. lahulensis. Many tropical Mielichhoferias do have peristomes consisting of endostome only, but there is much variation in structural detail. Observations on Mielichhoferia, as well as selected other diplolepidous taxa, support Philibert's contention that the endostome is two layered, consisting of inner and outer cell wall plates.

SIGAL, LORENE L. Oak Ridge National Laboratory, P.O. Box X, Oak Ridge, TN 37830.<sup>1</sup> - Lichen research and regulatory decisions.

During recent years, in response to an increased awareness of the adverse consequences of air pollution, the government has enacted legislation that is of interest to lichenologists. This report discusses the role that lichen research has had in the development of this legislation or in decisions made as a result of the legislation. The major acts of interest are the National Environmental Policy Act of 1969 and the Clean Air Act Amendments of 1970 and 1977. Under the Clean Air Act, the Environmental Protection Agency established the National Ambient Air Quality Standards, the Prevention of Significant Deterioration class I, II, III areas, and the "adverse impact" determination for class I areas. In order to make enlightened decisions on environmental issues related to these regulations, data are needed that define: 1) terminology such as "adverse impact," acceptability, significance, reversibility, etc.; 2) dose-response functions, including chronic effects and effects of pollutant combinations; 3) differential sensitivities of species; 4) abundance of natural populations; 5) understanding of inter- and intra-specific relations; and 6) the role of the organism in the structure and function of ecosystems. Lichen research has addressed some of the preceding points, but the necessary data for others are lacking. Evaluation of existing research has identified information gaps and suggested avenues of future research not only for lichenologists interested in air pollution but also for those interested in ecology, population biology, and physiology.

<sup>1</sup>Operated by Union Carbide Corporation under contract W-7405-eng-26 with the U.S. Department of Energy.

SMITH, CLIFFORD W.\* & WILLIAM J. HOE. Department of Botany, University of Hawaii at Manoa, 3190 Maile Way, Honolulu, HI 96822, and Herbarium Pacificum, Bishop Museum, P.O. Box 19000-A, Honolulu, HI 96819. - Bryophytes and lichens atop Mauna Kea, Hawaii.

Mauna Kea above 13,000 ft. is a bleak area which had remained relatively unaffected by modern civilization until it became the site of several astronomical observatories. It is an ideal site for such studies because of its general aridity and unpolluted atmosphere. A survey conducted to provide baseline information for an environmental impact statement

for further development of the area demonstrated the presence of 11 mosses (including one new species) and 22 lichens. No liverworts were found. Six species were new records to the Hawaiian Islands. Most species are found in highly protected areas though Umbilicaria hawaiiensis and Pseudephebe pubescens are found on rock faces fully exposed to the prevailing winds. The cinder cones were poor habitat except in spatter ramparts. The lava flows supported the richest flora particularly on west-facing aspects. Lake Waiau, a permanent lake at 13,000 ft. on the south side of the mountain, had a very poor flora even though the area is immersed in late afternoon fog particularly in the summertime. The absence of fruticose species in this situation may be the result of freezing temperatures every night of the year.

STARK, LLOYD R. Department of Biology, 202 Buckhout Laboratory, The Pennsylvania State University, University Park, PA 16802. - Life history studies on *Forsstroemia trichomitria* (Hedw.) Lindb. (Cryphaeaceae).

Populations of Forsstroemia trichomitria in central Virginia initiate perigonia and perichaetia along same stems during June. Inflorescences are produced on current cycle stems only, and maturation of inflorescences is acropetal. In most cases, the arrangement of inflorescences is gonioautoicous. The interval of fertilization extends from mid-August through September, with young embryos first observed in September. These embryos are hyaline for several weeks and exhibit very slow development. Near the onset of winter, the embryos cease growing and become chlorophyllose. Both stem and sporophyte elongation are apparently negligible during the winter months. Resumption of growth in the spring entails renewed embryonic and stem elongation. The embryonic phase is broken near the end of July, as setae elongate. Capsule expansion begins shortly thereafter, extending through September. Spore development is slow, and opercula do not fall until February of the ensuing winter. Thus while a set of gametangia is initiated and matured in the same growing season, sporophyte maturation takes approximately 17 months. Hence, during the months of September-February, two sporophyte generations occur simultaneously on the same stem.

THOMAS, R. J.\* and JAMES G. ELLIS. Department of Biology, Bates College, Lewiston, ME 04240.

- Phototropic curvature of *Pellia* sporophytes. Positive phototropic curvature of elongating liverwort sporophytes was described by Askenasy as early as 1874, but has only been studied sporadically since that time. The response is of interest in that: (1) it is rapid (occurring within 20-60 minutes after exposure to unilateral illumination); (2) it is sensitive (blue wavelengths of light being the most effective); and (3) it is not possible to separate the response from the site of perception. Removal of apical spore capsules from *Pellia epiphylla* sporophytes, for example, has little effect on the phototropic responses of sporophyte stalks. Localized unilateral illumination of sporophyte stalks results in curvature at the point of illumination only, with no transmission of the stimulus. Acid efflux, as determined by agar-dye techniques (Mulkey and Evans, 1981 - Science), is also associated with localized regions of curvature. Owing to (1) the simulation of curvature using localized application of indole-3-acidic acid in lanolin paste, and (2) a presumed relation-

ship between auxin concentration and  $H^+$  efflux (Rayle, 1973 - *Planta*), we postulate a mechanism for phototropism based on change in relative hormone concentrations between opposite sides of these structures.

WEBSTER, HAROLD J. Biology Department, DuBois Campus, The Pennsylvania State University, DuBois, PA 15801 - Elemental Analyses of Splachnaceae and Their Substrates.

The elemental analyses of field-collected plants and their substrates and of laboratory-cultured plants of the Splachnaceae provided evidence in reference to the nitrophile hypothesis. The Splachnaceae exhibit strong affinities for substrates of animal origin, which has been suggested as a requirement for nitrogen. Owl pellets and dung with and without plants of the Splachnaceae had relatively high levels of N, P, and Ca. Field-collected taxa had slightly higher elemental percentages than other cold-region bryophytes. The higher Ca and P levels reflect substrate contents. *Tetraplodon mnioides* plants had higher Ca, P, and N percentages than did the more hydric *Aplodon wormskjoldii* plants. Analysis of cultured plants shows no major differences among taxa or among media used, although deficiency levels were indicated for plants grown on media with low levels of Ca, N, and Mg. Comparison of field and culture analyses suggests field plants may be nitrogen deficient despite the high nitrogen content of their substrates.

WHITTIER, H. O., H. PRINGLE, H. A. MILLER & B. A. WHITTIER. Department of Biological Sciences, University of Central Florida, Orlando, FL 32816 - Matrix analysis for Pacific insular bryogeography.

Electronic data files established during production of the *Prodromus Florae Muscorum Polynesiae* (1978) and the *Prodromus Florae Hepaticarum Polynesiae* (in press) provide a data base containing nomenclatural and distributional records for 174 genera and 1,760 hepatic species, and 254 genera and 1,627 moss species, reported on 114 tropical Pacific islands and as shared with 49 circum-Pacific and other world areas approximating those of *Index Muscorum* (Wijk et al., 1959-1967). Files kept current on key-punched cards for security may be accessed directly by entry onto Harris 800 disk files. FORTRAN programs enable production of matrices as large as 200 X 200 geographic areas. Recoding permits organization into smaller condensed geographic groups or regions. These matrices display numbers of species reported for an island or its archipelago on the diagonal, and at matrix intersections in the upper triangle, numbers shared by two areas. A lower triangle contains indices of similarity. A taxonomic recoding option permits similar matrix production for genera. Subprograms list (1) families (either alphabetically or phylogenetically) with their genera and species, or (2) genera and species alone, for any single island, group, or for all islands and groups, and can identify and enumerate reported endemics and their percentage of the known bryoflora. Various cluster analysis routines can be applied within the program system. Program construction design is such that application requires minimal computer experience, and permits use of other taxonomic and biogeographic data sets (up to 9,999 taxa and 200 geographic areas). Conversion to a microcomputer program system is planned.

## DEVELOPMENTAL AND STRUCTURAL SECTION

### Symposium: A Developmental and Structural Perspective on Phenotypic Plasticity: A Contribution to its Delineation

#### INTRODUCTION

When the concept of phenotypic plasticity is invoked, it is usually in reference to the impact of external environments on plant form. There are two possible ways to view phenotypic plasticity. One is that it represents an additional set of developmental events induced by the external environment and, in that context, represents something added to the normal developmental processes in a plant. The other is that it is a manifestation of the normal developmental events seen in the ontogeny of any plant. It is the purpose of this symposium to present information on plant development, including that of phenotypically plastic systems, to assess which of the two views presented above, or any others, are most appropriate for understanding phenotypic plasticity. An understanding of the underlying basis for phenotypic plasticity is of significance in attempting to explain the evolutionary and developmental consequences of its existence. Organized by Jack Maze, University of British Columbia, Vancouver, BC.

FISHER, JACK B. Fairchild Tropical Garden, Miami, FL 33156. - Branching patterns and simulations of trees: deterministic vs. stochastic models.

Published attempts at computer modeling of the geometry of tree crowns and rhizomes are reviewed. Deterministic and stochastic (probabilistic) models are contrasted, and the problems associated with each method of simulating complex biological patterns are noted. Small changes in the elemental parameters of branching geometry (branch angles, branch unit length) can have major effects on overall crown shape after many orders of branching. While stochastic simulations produce "realistic" trees, they may not be meaningful for ecological or adaptational studies since they obscure local specific phenotypic responses to environmental or age-dependent conditions, e.g. sun-shade effects, architectural reiteration.

KAPLAN, DONALD R. Department of Botany, University of California, Berkeley, CA 94720 - Heteroblastic development and phenotypic plasticity in higher plants.

Any effort to study environmentally induced changes in plant structure (phenotypic plasticity) must be done against the background of the normal develop-

## 10 Developmental and Structural Section

mental changes expressed during the ontogeny of the plant. The term "heteroblastic development" has been used to refer to such regular ontogenetic changes in plant form. Using recent research on the developmental basis of the heteroblastic change in leaf form in *Acacia*, it will be shown that the change involves: 1) a regular ontogenetic change in proportion of blade to petiole; and 2) a change in the type of blade morphology (from pinnate to simple) which is independent of its position in the shoot and hence a plasticity response. Once a clear delineation of the involvement of these two components in this heterophylly is made, it can be shown that the original distinction between homoblastic and heteroblastic development was falsely defined because it was based on the phenotypically plastic component. From an analysis of attempts to induce juvenile types of foliage in adult plants, using hormones such as gibberellic acid, it is suggested that many of the responses may be examples of phenotypic plasticity and not a true reversal of the developmental phase. The significance of these conclusions for the evaluation of hormone roles in phase changes in plants will be discussed.

PAOLILLO, D. J., JR. AND GAIL RUBIN. Section of Plant Biology, Cornell University, Ithaca, NY 14853. - Environmental plasticity of sexual phenotypes in *Onoclea sensibilis*.

Young *Onoclea* gametophytes become male in abundance when grown on their native soil but are inhibited from expressing maleness when grown in axenic cultures on agar. Classical experiments designed to test the action of antheridiogens using agar-grown *Onoclea* gametophytes are logically restricted to the explanation of laboratory anomalies because the control plants do not resemble field-grown organisms. Most soil-grown plants become male, without the intervention of antheridiogens, after attaining their meristems and becoming small hearts. On agar, femaleness is more prominent but some heart-shaped gametophytes become male at the same time their cohorts become female. Thus, the concept that a meristem is antithetic to maleness is also related to laboratory artifacts. On agar, dark-grown gametophytes become male at the same time as light-grown gametophytes. Male plants in the dark are small filaments. Thus, neither the meristem nor the morphological state of the organism appears to bear a direct, causal relationship to maleness. Likewise, there is no basis for the concept that the action of antheridiogens in *Onoclea* is to overcome a light-induced block to maleness. It remains possible, however, that the action of applied antheridiogen is antagonized by light in *Onoclea*. However, these and all other conclusions based on agar cultures must be interpreted with a fuller knowledge of the limits of phenotypic plasticity when *Onoclea* is the test organism.

Richards, J.H. Dept. of Biol., Fla. International U., Miami, FL 33199. Developmental basis of leaf plasticity in *Eichhornia crassipes* Solms. (Pontederiaceae).

In 1965 A.D. Bradshaw defined plasticity as the "amount by which the expression of individual characteristics of a genotype are changed by different environments." Such change requires some change in development of that characteristic. Leaf development was studied

in a clonal mat of water hyacinth in order to quantify parameters which show variability and to document the developmental basis of divergence in form. The mat environment varies from the mat edge to center. Leaves on plants inside the mat differ in petiole length, lamina length, petiole width and lamina width from leaves on the mat edge. Differences are not a function of plant age alone. Leaf shape parameters have different variances between the two environments--petiole measurements display more variability than lamina. When development of the two leaf types is compared, they show parallel relative growth rates for leaves less than 2.5 mm. Divergence in form results from differences between leaf types in 1) how long growth continues and/or 2) late-developing differences in relative growth rates. The earliest divergences in relative growth rates occur in leaves app. 8 mm long.

Developmental divergences between these plastic leaf types contrasts with developmental divergences between invariant leaf types. In *E. crassipes* prophylls and foliage leaves are always different in form, regardless of environment. These differences, however, are present soon after leaf initiation.

### Symposium: Developmental Physiology of Flowering

#### INTRODUCTION

The process of flowering can be divided into at least five sequential phases; our speakers will review the subjects of flower induction, flower differentiation, flower opening, pollination, and flower senescence.

Organized by Ross E. Koning, Rutgers University, Piscataway, NJ.

GREYSON, RICHARD I. Department of Plant Sciences, University of Western Ontario, London, Ontario. N6A 5B7. - Flower primordia - a challenge to plant developmentalists.

The following phenomena, all described from traditional morphological and anatomical viewpoints still represent a profound challenge to developmentalists. A) Primordia initiation: The relative contributions and orientations of cell division and enlargement to the setting and establishment of a primordium. B) Determination and differentiation: A number of different models have been described. Some exhibit delayed canalization while others are less easily modified. C) Organ growth: From the few analyses that do exist, primarily on stamens, one should expect considerable variety in the regulatory stimuli and the type of cellular response which leads to common structures. This variety of mechanism points toward considerable parallelism in the evolution of the final developmental events. D) Sexual differentiation: The exploration of the developmental basis of sexual differentiation has proceeded at a plant of levels. Perhaps the most popular studies implicate plant hormones as causal factors. In reviewing these studies we conclude that while in some flowers regulation may sharply correlate with endogenous levels and activities of hormones, more frequently such parallels cannot be identified.

Certainly, no single hormone-based model can be presented at present to account for sexual differentiation. Studies of protein patterns and other gene-product analyses are rare and at present inconclusive.

HALEVY, ABRAHAM H. Department of Environmental Horticulture, The University of California, Davis. (on leave from The Hebrew University, Rehovot, Israel).

- Regulation of petal senescence.

The main growth regulator controlling petal senescence of some flowers (e.g., carnations) is ethylene. Other flowers (e.g., roses) are much less sensitive to ethylene. The most effective inhibitor of senescence and abscission in ethylene-sensitive flowers is Ag<sup>+</sup>, applied as Ag-thiosulfate. Cytokinins delay petal senescence by inhibiting ethylene biosynthesis. Pollination promotes petal senescence. There seems to be a multi-stage pollination-induced senescence signal. The first one being 1-aminocyclopropane-1-carboxylic acid (ACC), diffused from the pollen. Wound-ethylene and auxin may participate in later stages. In both ethylene sensitive and ethylene non-sensitive flowers, a decrease in membrane fluidity was observed during aging. Environmental or chemical agents modifying the rate of senescence, correspondingly also altered the rate of change in petal membranes fluidity. The decrease in fluidity corresponding to an increase in the ratio of free sterols to phospholipids, due to a decrease in the content of membrane phospholipids. The activity of petal ATPase and of sucrose uptake by the petals is correlated with membrane fluidity. These processes may regulate the reduction in water and dry weight content of fading petals.

KEVAN, PETER G. Department of Environmental Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada.

- Floral characteristics for pollinators.

Floral attractants appeal to the senses of pollinators and should be investigated with those in mind. Attractants may be visual, as colors, color patterns, sizes, outline shapes, and arrangement of floral parts. Depth effects, as in tube- and funnel-shaped flowers are also involved. Olfactory cues function in long- and short-distance attraction of, and in flower discrimination by pollinators. Guide patterns on flowers may be visual, chemical, and structural and aid pollinators in foraging and pollinating. Microsculptural features on flowers are distinguished by insects which may use them as guides and in plant species recognition. Some floral structures benefit pollinators by providing shelter and/or warmth. Color, form, presentation, and sporophyll placement indicate the various pollination syndromes. Correlated with those are features of pollen and the chemical nature and amounts of floral rewards for pollinators.

KONING, ROSS E. Department of Biological Sciences-Botany, Rutgers University, Piscataway, NJ 08854.

- Plant hormones and growth of flower parts during flower opening.

There is no simple understanding of the roles of plant hormones in control of flower part growth since, until recently, no species had been examined for the

roles of all of the plant hormones, both applied and endogenous, in growth of all of the flower parts. Such an analysis was recently completed for *Gaillardia grandiflora*. Three types of measurements were made: 1) growth of the flower parts under natural conditions, 2) growth of isolated flower parts in response to hormones applied in vitro, and 3) the endogenous hormone levels. These measurements were correlated with each other to determine the roles of the various plant growth substances. In *Gaillardia*, corolla elongation occurs by gibberellin control, filament and style elongation occur by auxin control, and stigma unfolding occurs by ethylene control. The ray flower corolla must be fully expanded to attract pollinators before the fertile disc flowers open, thus explaining need for separate controls. The growth of the filaments and the style can be controlled by a single hormone; the sequential events are timed by the position of the two organs with respect to the auxin source: the pollen. As pollen develops, auxin is first transported to the filament; only after the pollen is shed directly onto the stigma, is the auxin transported to the style. The level of auxin in the stigma is then high enough to promote the production of ethylene and cause stigma unfolding. The tidy control mechanism elucidated in *Gaillardia* probably applies only to members of a small subset of Asteraceae species, since in the literature, unrelated plants have different methods of developmental control. Future complete studies will provide a basis for sorting the seemingly contradictory findings into a more systematic understanding of flower part growth.

LANG, ANTON. MSU-DOE Plant Research Laboratory, Michigan State University, East Lansing, MI 48824 - Flower induction: endogenous hormone-like factors.

Evidence for a hormone-like inducer of flower formation ("florigen"), which is formed in the leaves while acting in the apical shoot meristems, exists for about 50 years. Most of it is based on grafting experiments between photoperiodic plants maintained in the noninductive daylength ("receptors") on one hand and similar plants exposed to the inductive daylength or dayneutral (DN) plants ("donors") on the other. Experiments of this kind have been done in eight plant families. It has also been shown that long-day (LD) receptors can be induced to form flowers by LD, short-day (SD) and DN donors; SD receptors can be induced by SD, LD and DN donors; and flower in DN receptors can be hastened by LD and SD donors. Donors and receptors can belong to the same species, to different species of the same genus, and to different genera. Thus, florigen appears to be ubiquitous and to be nonspecific in both the taxonomic sense and with respect to the physiological response type. For about 5 years we also have evidence for a graft-transmissible inhibitor of flower formation ("antiflorigen"), so far in two LD plants. Antiflorigen inhibits flower induction in DN and SD plants of the same or a different genus; like florigen it is evidently nonspecific both taxonomically and physiologically. Flower induction thus appears to involve both promotive and inhibitory, endogenous hormone-like factors: florigen which in LD and SD is formed only in LD and SD respectively, while in DN plants it is formed independent of daylength; and antiflorigen which is formed at least in some LD plants under SD conditions. This situation will be briefly discussed in relation to other aspects of flower induction.

### Symposium: Homology in Modular Organisms – Concepts and Consequences

#### INTRODUCTION

It is proposed that the concept of homology as it applies to modular organisms (specifically higher plants) be the subject of this symposium. The discussion will be timely as the recognition of homologous structures is foundational to the application of cladistic methods. If the basic assumptions of cladistic analysis can be shown to be well-founded, its methodology is strengthened; if it is not, then the methodology is likely to lead to erroneous conclusions. Clearly also the basic concepts of evolutionary morphology of higher plants deserves a careful scrutiny independent of any influence derived from the study of organisms with unitary construction. Organized by P.B. Tomlinson, Harvard University, Petersham, MA.

KAPLAN, DONALD R. Department of Botany, University of California, Berkeley, CA 94720  
- The problem of serial homology in higher plants: a case study.

When two different organ forms are produced along the higher plant shoot, intermediates between the two types typically are formed at the intervening nodes. Such transitional forms have been a principal source of evidence in determining the structural correspondences (serial homology) between the two leaf types. Typically most morphologists in the past were content to determine such structural relationships from the comparison of fully-developed organs rather than study their development. In a recent study of the developmental basis for the classic case of heterophylly in *Acacia* it was shown that such deductions of serial homology based on mature leaf forms led to erroneous conclusions of phyllode morphology and developmental divergence. The difficulty arose because the nature of the change in blade form masked the true change in proportion between petiole and blade, forcing investigators to rely on blade form as an indication of the length of the petiole. Underlying much of the erroneous judgement of phyllode morphology was the assumption that the developmental change proceeded by Goebel's metamorphosis concept. Actual comparative developmental analysis of serial appendages in seedlings of phyllodineous species of *Acacia* have not only negated the metamorphic concept but have underscored the necessity of truly comparative developmental data for a correct assessment of organ homologies.

SATTLER, ROLF. Biology Department, McGill University, Montreal, Quebec H3A 1B1  
- Homology - a continuing challenge.

According to Sneath and Sokal (1973) morphological correspondence and common ancestry are the two basic ideas at the root of the many different homology concepts which have been proposed. Definitions of homology in terms of common ancestry have been criticized by many authors for a variety of reasons. The other idea of homology which refers to morphological correspondence may be based on a philosophy of essentialism. Accordingly, two structures are homologous whenever they are essentially similar. Remane (1952) specified three main criteria and a number of auxiliary criteria which determine what is meant by essential

similarity or morphological correspondence. Although many structures can be easily homologized according to these criteria, difficulties arise when different criteria lead to contradictory homologizations. A resolution of such difficulties is achieved by distinguishing different kinds of homology. Other difficulties are resolved by the application of a semiquantitative or quantitative homology concept which leads to the recognition of partial homologies (or partial correspondences) in contrast to total homologies (1:1 correspondences).

STEVENS, Peter F. Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138 - Homology and plant systematics.

I discuss aspects of similarity, homology, and the relationship between them. (1) The operations by which we decide that characters are similar (potentially homologous) and so useful in phylogenetic analysis are little discussed in recent taxonomic literature; we face similar problems irrespective of our taxonomic school. These problems include the evaluation of conflicting criteria of similarity; the reification of terms which may then lead to untested assumptions about similarity; and the criteria used in the delimitation of character states. (2) The translation of assessments of simple similarity to hypotheses of homology, similarity as a result of common ancestry, are crucial. The translation involves cladistic analysis of all similar characters; those derived characters that are congruent with the best-supported cladogram may be hypothesized to be homologies; such hypotheses are tested both against new data and more detailed studies of the original similarities. In cladistic analysis, homology and synapomorphy are synonymous and neither can be partial. (3) The relationships between organisms, criteria for assessing similarity in structure of different organisms, and theories concerning the relationships between organisms that is decided by some estimate of similarity, are considered. Emphasis is placed on the process of reciprocal illumination in an attempt to evaluate the claims of some morphologists and systematists as to the historical and/or epistemological priority of certain parts of the systematic process.

TOMLINSON, PHILIP B. Harvard University, Harvard Forest, Petersham, MA 01366.  
- Homology : An empirical view.

Comparative morphology in plants is presented as an empirical discipline into which "homology" (a set of theoretical concepts) is often inserted as an impediment to analysis. Problems arise because homology is defined and homologous structures are established in a variety of ways. A priori rules applied in morphological analysis can result in circular reasoning. Observation can be relegated to a lower order of scientific endeavour, at the expense of theoretical analysis. Modular organisms, like the higher plants with extended heteroblastic ontogenetic sequences and indeterminate addition of parts, offer abundant opportunity for misinterpretation, as compared with organisms with unitary construction. Their adaptive organization depends on a high degree of plasticity. Evolutionary development of plant form is a process of "fixing" this plasticity and regenerating it in novel ways. A particular confusion is that between "structural similarity" which is a direct result of the organization of the individual, and is inherent

in the concept of "serial homology", and the more concise notion of strict homology which (by definition) is due to descent. A historical perspective is particularly illuminating, especially as the basic principles of comparative morphology are largely conceived in a pre-evolutionary environment. Emphasis will be placed on developmental analysis in comparative morphology as a basic process in the generation of the modular organism. Knowledge of development can frequently illuminate comparative analysis. Examples will be cited where the organizational plasticity almost defeats the possibility of evolutionary morphological analysis in modular organisms.

W. H. WAGNER, JR., Department of Botany, University of Michigan, Ann Arbor, Michigan 48109. - Homology and the early diversification of vascular plants.

Primitive vascular plants are the ones that first appeared in the fossil record, that possess simple life cycles, and are most similar to the outside group, the bryophytes. Because of their diversity, homology of even major organs has been controversial. Theories like the Stelar Theory or the Telome Theory try to fit the morphics of plants into preconceived molds. Objectivity is best accomplished by using classical tests of position, ontogeny, mature structure, and absence of intermediates. Evidence of early diversification of vascular plants comes from cladistic analysis of living groups, psilotopsids, lycopsids, equisetopsids, and polypodiopsids, together with the fossil remains of trimerophytes, zosterophytes, and rhyniophytes, a motley assemblage. Our problem is to connect different organs in different groups, because there are such large gaps, and intermediate stages or trends are lacking. How teratology fits into this is a question. In addition to various tissue types, the major organs are discussed: stem, root, leaf, sporangium, spore, gametophyte, gametangia, gametes, embryo, and foot. Because of homoplasy, homology is, by itself, not necessarily a criterion of relationship. At the tissue level, the stele provides a challenge; at the organ level, the foliar appendages. Parsimony suggests that at least in the case of the leaf, all of the appendages were originally emergences. The position of sporangia, so fundamental, apparently, in the early differentiation of vascular plants, is a good example, of the absence of intermediates, suggesting abrupt, rapid changes. There is a spectrum of degrees of homology of the organs of early vascular plants -- from very obvious to very questionable.

## Poster Session

BASILE, DOMINICK V. and MARGARET R. BASILE  
Department of Biological Sciences, H. H. Lehman College of CUNY, Bronx, N.Y. 10468.  
- Auxin antagonist-induced desuppression of leaf primordia of *Plagiochila arctica* (Hepaticae): Possible integration of auxin, ethylene and hydroxyproline-alterable proteins in correlative control of cellular suppression.

Two inhibitors of auxin transport, triiodobenzoic acid (TIBA) and N-1-naphthylphthalamic acid (NPA), and an inhibitor of auxin action,  $\alpha$ -(p-chlorophenoxy)isobutyric acid (PCIB), induced the same kind of pheno-

variation in *Plagiochila arctica* Bryhn & Kaal. (Hepaticae) as do antagonists of ethylene synthesis/action and antagonists of hydroxyproline-protein (hyp-protein) synthesis. This indicates that the two phytohormones and a cell surface protein sensitive to antagonists of hyp-protein synthesis play an integrated role in the correlative control of cellular suppression - primordium development. Auxin-induced ethylene synthesis and ethylene-induced cell surface hydroxyproline protein deposition correlated with suppressed development have been reported by others, previously. This, however, is the first experimental evidence to implicate all three molecules, two phytohormones and a cell surface glycoprotein, in the same morphoregulatory system. This correlative control system conceivably plays an important role in other, if not all, groups of land plants (Embryophyta).

CAESAR, J. C. AND A. D. MACDONALD\*. Department of Biology, Lakehead University, Thunder Bay, Ontario. P7B 5E1.

- Comparison of early growth of vegetative and reproductive short shoots of *Betula papyrifera*.

This study shows the cost to short shoot growth of female inflorescence development. Expanding and flushing short shoot buds were collected from mature trees from April-June 1982. Quantitative analyses were made on fresh and FAA-fixed material for relative growth rates (RGR) of leaves and buds, specific leaf area (SLA), leaf area ratio (LAR), leaf area (LA) and number of leaf side nerve pairs (SNP). Material was partially dissected to determine whether the bud was reproductive or vegetative. Short shoot buds may be vegetative or may bear a female inflorescence; these buds may be proximal on a long shoot or terminal on a short shoot. Axillary short shoot buds flush later than 2-4 year old short shoot terminal buds, which flush later than 5-10 year old shoots. Mean RGR of 5-10 year old short shoot buds is greater than that of younger short-shoot buds. It is suggested that older short shoot buds are relatively autonomous and that the flushing long shoot exhibits an inhibitory influence on the proximal axillary buds and possibly on young short shoot terminal buds. Reproductive short shoots differ from vegetative short shoots in that they have lower LAR's and leaf RGR's, higher SLA's, smaller LA's, fewer SNP's and they seem to grow more in length than in width. These findings are related to reproductive cost. The developing inflorescences act as preferred 'sinks' for resource allocation.

CECICH, ROBERT A. Forestry Sciences Laboratory, P.O. Box 898, Rhinelander, WI 54501 -  
Histochemical and ultrastructural changes in microsporangia of jack pine during the winter.  
The development of jack pine (*Pinus banksiana* Lamb.) microsporangia from October to April was investigated. DNA, RNA, and protein content of sporogenous cells was measured with a microdensitometer at monthly intervals. DNA was unreplicated (2c) until March when DNA synthesis was first noted, coinciding with a loss of condensed chromatin. Protein staining increased in April. RNA staining increased in December, followed by a loss of staining in January.

## 14 Developmental and Structural Section

Numerous stacks of rough endoplasmic reticulum (RER) and lipid bodies first appeared in the sporogenous cells in December and may be related to the increase in RNA. The RER stacks were only occasionally seen in the March collection. Lipid bodies were abundant in the tapetal and primary wall cells throughout the period of study. The apparent incorporation of lipids into the plasmalemma of those two cell types was noted in November. An unidentified cytoplasmic structure, without a bounding membrane, was abundant from November through March. Golgi bodies, abundant in October, were rarely seen again until March. Microbodies were abundant in March when starch was first noted in the plastids. Observations substantiate reports that winter is not a time for cessation of development.

DOBBINS, DAVID R. & HARRY ALDEN. Biology Dept., Millersville University, Millersville, PA 17551, & Dept. of Botany, University of California, Davis, CA 95616. - Development of the shoot system in *Marcgravia rectifolia* L.

*Marcgravia rectifolia* L. is a dimorphic vine having distinct juvenile and adult shoots. The juvenile shoot is a climber characterized by an orthotropic growth habit. Its stem is very flattened and has numerous adventitious roots along the stem edges. In contrast, the adult shoot has a plagiotropic growth habit, a cylindrical stem and no adventitious roots. Both phases have distichous phyllotaxy, but the plastochron is shorter for the adult phase than for the juvenile phase. The mature leaf of the juvenile shoot is ovate while that of the adult shoot is lanceolate.

Developmentally, the flattened stem of the juvenile results from differential production of cells primarily in the pith region. Internodes of the adult phase are longer than those of the juvenile. The longer internodes are a result of more cell production rather than greater cell expansion. The juvenile phase can change into the adult phase and the adult phase can revert to the juvenile phase with equal frequency.

GREEN-PENNINGTON, J.K.\*, P.E. RICHARDSON AND R.L. BURTON. Department of Botany and Microbiology, and Department of Entomology and USDA, Oklahoma State University, Stillwater, OK 74074 - Evaluation of silicon levels surrounding the penetration site of two biotypes of aphid in the leaves of a susceptible and resistant strain of barley.

Silicon deposits are naturally occurring in the node, internode and leaves of barley. Deposition has been found in epidermal cells, sclerenchyma, mesophyll and xylem elements. Silicon may be found in impregnations of the secondary wall or in opaline silica deposits filling the entire lumen of the cell. Preliminary study indicates an increase in the level of silicon surrounding the penetration sites of the aphid. Two biotypes (C and E) of the aphid *Schizaphis graminum* (Rondani) were studied on a susceptible (Rogers) and a resistant (Will) strain of *Hordeum vulgare*. Aphids were allowed to feed for approximately one hour. Samples were taken at time intervals and prepared for study under the light microscope, SEM, and electron probe x-ray microanalyser.

MACDONALD, A.D.\* AND D. H. MOTHERSILL. Department of Biology, Lakehead University, Thunder Bay, Ontario P7B 5E1.

- Short shoot organogenesis in *Betula papyrifera*. This study describes the sequence and chronology of inception and development of structures associated with various short shoot buds, which include: 1. axillary short shoot buds (proximal axillary buds on long shoots), 2. terminal vegetative bud, 3. terminal reproductive bud, 4. short shoot axillary bud (forms on a flowering short shoot). Developing and expanding buds were collected from mature trees from April to September in 1980-1982, fixed in FAA, dissected, stained with fast green and photographed with an epi-microscope. Drawings of long and short shoots were made from photocopied fresh material. Silhouette drawing of bud parts were prepared with a camera lucida. An axillary short shoot apex forms in year n, appendages are initiated in n + 1, flushing occurs in n + 2. This apex forms a terminal bud after bud burst. Floral induction may occur in late June, year n + 1, or any subsequent year. All buds possess 1-3 embryonic foliage leaves, initiated in May-June and a fixed number of rudimentary leaves which arise in late June-July. Stipules of the latter form bud scales of the succeeding bud. Pattern of foliage leaf formation followed by inception of 3 rudimentary leaves may repeat for several years for the successive development of terminal buds. Flowering breaks the repetitive sequence and an axillary bud forms in the axil of a foliage leaf. Buds are determined as incipient long or short shoots during bud development, in early July, but this may be altered at flushing.

SEKHAR, K.N. CHANDRA\* and VIPEN K. SAWHNEY. Department of Biology, University of Saskatchewan, Saskatoon, Sask., S7N 0W0, Canada. - Comparative studies of vegetative shoot apices of the sclanifolium mutant and normal plants of tomato.

We are using single gene mutants to investigate the factors which regulate the genetic expression in the leaf and flower development. In the mutant *Solanifolium* (sf/sf), the development of both leaves and flowers is affected. The leaves produced had entire margins in contrast to the dentate margins of the normal plants and the mutant flowers had free sepals, petals, stamens and split carpels as opposed to the partly fused sepals and petals and united anthers and carpels of normal plants. In order to establish the stage at which the differences between the two genotypes appear, vegetative shoot apices of both types of plants were studied with the LM, SEM and TEM. The LM and SEM studies showed differences in the time of initiation of leaflet primordia; in the normal plants leaflet primordia were initiated on the P<sub>3</sub> leaf primordia while in the mutant plants leaflet primordia were initiated on P<sub>4</sub>. TEM studies of the apical meristems showed the following features common to both types of plants: meristems with a two layered tunica; cells of T<sub>1</sub> with large distal vacuoles containing electron dense structures and cells of T<sub>1</sub> and differentiating cells containing chloroplasts with proteinaceous bodies - the prethylakoidal bodies. The only significant difference observed between the two genotypes was the presence of microbodies near the axils of the leaf primordia of mutant plants. These studies show that morphological and some fine structural differences are detectable early in the ontogeny of leaves of the two genotypes.

## Contributed Papers

ALLEN, RANDY D.\*, DAVID A. PRIER AND LOUIS H. BRAGG. Department of Biology, Texas A&M University, College Station, TX 77843 and Department of Biology, University of Texas at Arlington, Arlington, TX 76019.

-Ultrastructure of *Prosopis glandulosa* cotyledon cells during storage mobilization.

Cotyledon cells of *Prosopis* contain numerous large protein bodies which are closely surrounded by a single layer of minute lipid bodies. Lipid bodies also line the inner face of the plasmalemma. After germination, the protein body matrix first develops a granular appearance. Later, electron transparent regions form, usually at the protein body periphery. These areas are membrane bound and have been termed "Protein body vacuoles." These areas swell and may become much larger than the original protein bodies. Electron dense protein body fragments remain within the protein body vacuoles. Fusion of protein body vacuole areas eventually results in the formation of a large main cell vacuole which still contains spherical fragments of undigested storage protein. Lipid bodies enlarge slightly but retain their position around protein bodies until enlargement of the protein body vacuole. Some evidence of lipid body fusion is seen and fewer, larger lipid bodies are observed in cells at later stages of development.

ALMOUSAWI, A.H., P.E. RICHARDSON,\* R.L. BURTON. Department of Entomology and Botany, Oklahoma State University, Stillwater, OK 74078 - The Ultrastructure of Greenbug Feeding Damage in Susceptible and Resistant Wheat Cultivars.

Cell and tissue differences resulted when biotype C greenbugs *Schizaphis graminum* (Rondani) fed on susceptible as opposed to resistant wheat cultivars. There were two different types of cell damage in the susceptible cultivar (TAM W-101). Adjacent to aphid feeding tracks in vascular bundles there was extensive and rapid damage to a few phloem cells and their contents. In a second type of damaged area there was slower degeneration of organelles of mesophyll parenchyma cells in areas traversed by the tracks. Chloroplasts lost all membrane structure. Later, vesicles appeared in mitochondrial cristae and in the nuclear envelope. Dense sheath material was located in many feeding sites. Resistant wheat (Amigo x TAM W-101) was symptomless at 10 days post-infestation. At two days there were a few patches of scattered collapsed dried mesophyll cells surrounded by many unaffected cells. Salivary sheath material was found at 2 days post-infestation but not later. Feeding tracks in susceptible wheat are mostly intercellular with feeding in the phloem. Feeding damage to the resistant variety was mainly to mesophyll, was slight, and appeared to result in little persistent damage. There were no physical structural differences between varieties, and differences in extent and types of feeding tracks and damaged cells appeared to reflect genetic, physiological, and biochemical differences.

ANDERSON, LORAN C. Department of Biological Science, Florida State University, Tallahassee, FL 32306. --Neotenic expression in *Gordonia stomata*.

The Loblolly Bay, *G. lasianthus* (Theaceae), is a medium-sized evergreen tree. Large buttressed peristomatal rims characterize the stomata. Extensive

survey for stomatal variation throughout the species' range found that a few trees had a strikingly different cuticular pattern around the stomata (concentric rings of striae rather than buttressed cups). Seeds were germinated from plants having the standard buttressed cup cuticles. Stomata of cotyledons lack cuticular relief; seedling leaves are sequentially more elaborate in cuticular build-up until eventually they achieve the striate pattern seen rarely on older (neotenic) trees. Root sprouts, on mature "standard pattern" trees, have the juvenile cuticular pattern as well. The general tree age for switching to cuticles with buttressed peristomatal cups has not been determined.

ARMSTRONG, JOSEPH E. Department of Biological Sciences, Illinois State University, Normal, IL 61761. - The comparative floral anatomy of the Solanaceae.

There have been relatively few studies of floral anatomy in the Solanaceae and none of the broad, comprehensive studies necessary for comparative study of the systematics and phylogeny of this family. A preliminary survey of floral anatomy in the Solanaceae was recently undertaken to provide a basis for further studies. The vascular anatomy and histology of the floral organs provided numerous characters and character states of potential systematic usefulness. Preliminary observations support the recognition of two subfamilies, Solanoideae and Cestroideae, and also supports their proposed relative level of phylogenetic specialization. Anatomical characters support the recognition of the endemic Australian genera as the tribe Anthocercideae. The Lyceae and Nicotianeae are similarly distinct tribes based on anatomical characters. Floral anatomy does not support the recognition of the Nolanaceae as a separate family.

ARNOTT, HOWARD J.\* and MARY ALICE WEBB. Department of Biology, The University of Texas at Arlington, Arlington, TX 76019-0498. - Calcium oxalate crystal development in a fungus found in pine beetle mines in the cambial zone of *Pinus ponderosa* logs.

The production of calcium oxalate crystals by fungal hyphae has been established for almost a century (De Bary, 1887), but up to now only a few examples have been studied with electron microscopy. In the present case we have studied a fungus found growing in association with a pine beetle that bored through the cambial region of *Pinus ponderosa* logs collected in Pagosa Springs, Colorado. The fungus produces clamp connections and is therefore a basidiomycete, but is otherwise not yet identified. The fungus produces a white mat in the beetle mines, both in association with the bark and the beetle excrement. In many areas the white mat is many hyphal layers thick. Calcium oxalate dihydrate (Weddellite) is produced by the hyphae in three ways. 1) Single bipyramidal crystals develop along the surface of the hyphae. 2) An encrustation of many small interpenetrant twins is produced along segments of hyphae. 3) Druse-like multiple interpenetrant twins are also found. Many of these druse-like bodies are produced as terminations of main hyphae or terminations of short lateral hyphal branches. Occasionally the druse-like bodies are produced on one side of a hypha similar to those reported by Arnott (1983). TEM and SEM observations on the development of these three forms of calcification will be presented and discussed. De Bary, A. 1887. Comparative Morphology and Biology of Fungi, Mycetozoa and Bacteria. Clarendon Press, Oxford; Arnott, H. J. Calcium oxalate (Weddellite) crystals in forest litter. Scanning Elect. Microsc., 1983. III: 1141-1149.

## 16 Developmental and Structural Section

BARKER, W. GEORGE. Department of Botany and Genetics, University of Guelph, Guelph, ON N1G 2W1.

- Further observations on the regenerative pattern of *Impatiens balsamini* L. seedlings following mutilations.

In continued studies on regenerative behaviour of seedlings of *Impatiens balsamini* L., garden balsam, additional patterns have been identified. The seeds now available exhibit after germination the same developmental sequences as those discussed (Annals of Botany 47:661, 1981) but the events occur more rapidly than reported. Additionally, a series of further experiments discloses other behaviours of this plant following mutilations. The ability to form a regenerated collet is minimized and lost as the seedling ages. The tendency to form roots in the area basipetal to the excised collet persists as seedlings mature but without the encircling collet swelling and without associated hairs. Single roots become more common than the four earlier noted. In seedlings of ca. 6.0 cm in total length the rooting after mutilation is quite distinctive if the excising cut is made immediately behind the collet, midway between collet and cotyledon and adjacent to cotyledons.

It is quite apparent that the control leading to the regeneration of the collet-root complex is diminished with physiological age.

BARKER,\* W. GEORGE, and HUSSEY, D. BLAINE. Department of Botany and Genetics, University of Guelph, Guelph, ON N1G 2W1.

- The initiation of lateral root primordia during the early development of seeds in *Impatiens balsamina* L.

*Impatiens balsamina* L. seedlings produce a swollen encircling ring, the collet basipetal to the root apical meristem. From this four lateral roots emerge promptly after germination. As recently reported (Annals of Botany 47-661, 1951), mutilation of seedling by excision of the collet-radical-lateral root apparatus will result in the regeneration of a basal encircling swelling from which four lateral roots and root hairs will emerge (regenerated collet). Present evidence suggests that this regeneration requires the presence of cotyledonary tissue.

It was considered central to further work on lateral root development in garden balsam to establish the normal pattern of development of the collet-lateral root complex. To this end plants were grown in the greenhouse and sections were made of developmental stages subsequent to fertilization and including the visual appearance of the collet subsequent to germination. It is apparent that the essence of the collet complex was present very early in the development of the embryo.

BENDA, G. T. A. U.S. Sugarcane Field Laboratory, Box 470, Houma, LA 70361. -Leaf-base overlap in subtending leaves and bud scales of a sugarcane clone.

The sequence of direction of overlap of leaf bases was determined for groups of four leaves, each group consisting of the subtending leaf and the three oldest scale leaves of the main bud in its axil. A total of 380 nodes was examined from 10 greenhouse-grown shoots, 15 to 18 months of age, of a sugarcane clone (*Saccharum* interspecific hybrid, CP 68-413) selected because of the frequent occurrence of one or

two supernumerary buds per node. The sequence was identified unequivocally for 244 groups. The subtending leaves ( $lv$ ) had 120 of an expected 122 leaf bases which overlapped to the left, the oldest scale leaves ( $s_1$ ), 117, the second-oldest scale leaves ( $s_2$ ), 112, and the third-oldest scale leaves ( $s_3$ ), 132. The direction of overlap was the same for  $lv$  and  $s_1$  in 65% of the groups, for  $s_1$  and  $s_2$  in 56%, and for  $s_2$  and  $s_3$  in 39%. When the groups were classified according to the sequence of direction of overlap from  $lv$  to  $s_3$ , all classes corresponding to the 16 permutations had some groups, but the distribution among classes was not uniform. When these classes were assigned to five combinations, the number of groups in each were as follows: all left (14), three left-one right (61), two left-two right (89), one left-three right (64), all right (16). These results agree with those predicted from the binomial formula for equal probability of overlap in either direction. When the direction of overlap of  $s_1$  was compared for the main and supernumerary bud of 98 two-budded nodes, the results showed that it was the same for 50 and opposite for 48 pairs. These results demonstrate that the sequence of direction of overlap in this clone does not follow a standard pattern of development such as a sequential alternation of direction.

BRAGG, LOUIS H. Biology Department, University of Texas at Arlington, Arlington, TX 76019.

- The testa, hilum, and tracheoids of selected *Lupinus* seeds.

Seeds of *Lupinus texensis* Hook., *L. subcarnosus* Hook., and *L. havardii* S. Wats. were examined with scanning electron microscopy for characters that would separate them at the species level. Variations of the basic simple-foveolate pattern of the testa were distinctively different for each species with minor exceptions. This basic pattern has been unreported for the genus. The hila shapes are species characteristic as well. The tracheid bar is the most common type found in the subfamily but possesses tracheoid variations between these species. Usefulness of the testa and the hilum as taxonomic characters is suggested.

BROWN, ROY C. and BETTY E. LEMMON. Department of Biology, University of Southwestern Louisiana, Lafayette, LA 70504 - Microtubule organization and morphogenesis in young spores of the moss *Tetraphis pellucida* Hedw.

Microtubule systems appear sequentially at the distal and proximal poles of tetrad members during mid-sporogenesis in the moss *Tetraphis pellucida* Hedw. The distal microtubule system, which appears immediately after cytokinesis, emanates from a microtubule organizing center (MTOC) located between the single plastid and the nucleus. Whereas the distal system is ephemeral, the proximal microtubule system, which appears slightly later than the distal system, is a more stable component of mid-sporogenesis. The proximal MTOC is an irregularly lobed, patelliform aggregation of electron-dense granules located beneath the plasma membrane at the proximal spore pole. Several bundles of microtubules radiate from the proximal MTOC and traverse the cell, enclosing the nucleus in a cone of microtubules. The proximal microtubule system is thought to function in aperture development and organelle migration. The nucleus migrates to the proximal pole early in the tetrad stage and maintains

its acentric position throughout later stages of sporogenesis. The plastid migrates later in the tetrad stage from its meiotic position parallel to the distal surface to a position perpendicular to the distal surface with one tip in close proximity to the proximal MTOC. The proximal microtubule system reaches its maximum development by the end of the tetrad stage and all micrographic evidence of it is lost in the maturation stages of late sporogenesis.

BRUCK, DAVID K.\* and DAN B. WALKER. Department of Biology, UCLA, Los Angeles, CA 90024

- Epidermal commitment in the Citrus embryo.

At the 30-60 celled globular stage of embryogenesis in the rough lemon (*Citrus jambhiri*), a central core of cells dividing in random planes is surrounded by cells whose anticlinal walls predominantly radiate out from the core. Not until a globular stage containing 150-200 cells, however, are periclinal divisions in the peripheral cells eliminated. Thereafter the convoluted surface becomes smooth as the protodermal cells are layered and tabular. The thick cuticle of the mature lemon epidermis is not observable during embryogenesis under conventional histological stains. Whether the layering of the surface cells is truly a reflection of commitment to epidermal ontogeny is one subject of our investigations. Our experimental evidence to date indicates that once the epidermis is determined, except for rare or specialized circumstances, the subepidermal tissue lacks the competence to redifferentiate as epidermal even if put in the position and environment of an epidermal cell. Removal of epidermal cells in various organs (stems, leaves, floral organs) at various developmental stages has resulted in a replacement of the epidermis with wound callus or periderm rather than epidermal regeneration by subepidermal tissue. To test if embryos at sufficiently early stages of tissue commitment can be induced to regenerate a protoderm from subsurface cells, we have surgically removed the protoderm from intact embryos. Surgical procedures and subsequent growth of embryos required the development of an in vitro culture system where the lemon embryos were grown in nurse ovules of citron (*Citrus medica*).

BUNTMAN, D.J.\* and H.T. HORNER. Department of Botany, Iowa State University, Ames, IA 50011.

- Microsporogenesis of normal and ms<sub>3</sub> mutant soybean (*Glycine max*).

The ms<sub>3</sub> genetic male sterile soybean anther is compared with its normal line by using light, scanning, and transmission electron microscopy. Floral development, with the exception of androecium development, is similar between normal and ms<sub>3</sub> lines. The first difference between normal and ms<sub>3</sub> anther development is observed in the tapetum. At the early meicyte stage ms<sub>3</sub> mitochondria appear abnormal. The ms<sub>3</sub> tapetum then becomes more disorganized and breaks down prematurely. Tetrads are not released and subsequently abort. These events are accompanied by the accumulation of large amounts of an unidentified refractive material interior to the parietal cells.

CALVIN,\* CLYDE L. and M. CAROL ALOSI. Department of Biology, Portland State University, Portland, OR 97207 and Department of Botany, University of California, Berkeley, CA 94720 - Developmental

anatomy of the epidermis of the dwarf mistletoe, *Arceuthobium tsugense*.

The developmental anatomy of the epidermis of *Arceuthobium tsugense* (Rosendahl) G.N. Jones was studied using both light and scanning electron microscopy. Aerial shoots of the dwarf mistletoe may reach a height of 10 cm or more, but most are somewhat shorter. In recently emerged shoots the decussately arranged leaves of adjacent nodes overlap, concealing the stem. As internodal elongation continues, stem segments gradually become visible. The leaf pairs, which are joined at their bases, stop their development early. In mature stems they appear as small boat-shaped structures surrounding the nodes. No trichomes were present on the shoots examined at any stage of development. Stomates are present on stems and leaves. On the latter, they are most abundant on the keeled midregions of abaxial leaf surfaces. The longitudinal axes of stomates are oriented perpendicular to the stem axis. Guard cells are partially covered by over-arching subsidiary cells, producing a small antechamber just above the stomatal aperture. Substomatal chambers are small to absent and contiguous tissues have a paucity of intercellular spaces. As development continues, the epidermis is covered by a very thick cuticular layer and stomates become occluded. Subsequently, subepidermal cells also secrete cuticular material, isolating sections of epidermal tissue that become necrotic. The changes outline constitute the formation of a cuticular epithelium much like that described for *Phoradendron*. The generally xerophytic features displayed by *Arceuthobium* seem inconsistent with known physiology of the parasite.

P.C. CHENG\*, TAN K.H., MCGOWAN J.Wm. and FEDER R. Dept. of Anatomy, Univ. of Illinois, Chicago, IL; Canadian Synchrotron Radiation Facility (CSRF), Physical Sci. Lab., Univ. of Wisconsin, WI; Dept. of Physics, Univ. of Western Ontario, Canada; IBM T.J. Watson Res. Ctr., NY. - Recent developments in soft x-ray spectroscopy and contact microscopy.

Feder et al (1981) reported that the x-ray image of blood platelets is different from the electron image, which they believe is due to differences in the x-ray absorption and electron scattering properties of P in cytoplasmic phosphate compounds. We have also reported some preliminary attempts on imaging plant tissues by x-rays. A better understanding of the absorption spectra of various biological compounds is important for future interpretation of x-ray microscopic images. Due to the availability of a synchrotron source, only low (20-280 eV) x-ray spectra were used in this study. Three biological samples, ADP (Na salt), l-methionine and crude corn leaf extract (1:1 methanol/chloroform) and two polyamino acids (homopolymers), poly-l-methionine and poly-cysteine, were used in the study. The samples were either dissolved in water or EtOH and coated on a thin Formvar film, or incorporated in the Formvar film (i.e. leaf extract). Absorption measurement was done on a beam line of Tantalus storage ring with a Mark IV Grasshopper monochromator (CSRF). The results show a P L absorption edge in the ADP sample and a S L edge in the l-methionine, poly-l-methionine and poly-cysteine samples. The S L absorption edge of methionine shows a few eV shift from the atomic state. Corn leaf extract shows a P edge which could be contributed by membrane phospholipids.

X-ray contact microscopy of various corn tissues were conducted with synchrotron radiation and x-rays generated by a stationary target source (C and V targets). X-ray contact images were formed on a PMMA x-ray resist back supported by a Si<sub>3</sub>N<sub>4</sub> window, then the contact image magnified by a TEM.

## 18 Developmental and Structural Section

CONTRERAS, LUZ., and NELS R. LERSTEN.\* Department of Botany, Iowa State University, Ames, IA 50011.

### -Foliar nectaries in Ebenaceae: Morphology, anatomy, and distribution.

The Ebenaceae is variously interpreted as having 2-6 genera. The approximately 450 species are trees or shrubs of mostly tropical distribution, although a few extend to temperate regions. Foliar nectaries are widespread in the family but they have mostly been reported as "glands" without any detailed descriptions. A morphological survey was made, largely from herbarium specimens, of about 160 species from the four major genera and most sections of Diospyros, the largest genus. One or more leaves from all species examined were cleared. Nectary-bearing portions of leaves from about 25 representative species were then processed for paraffin sectioning, and samples from a few living plants were processed for paraffin and resin sectioning, and for scanning electron microscopy. Foliar nectaries were found on all species except for a few in Euclea. There may be few to many nectaries per leaf. They are all abaxial, occurring both in the proximal and distal halves. All nectaries are discoid or oval and embedded, usually flush with the surface, but they can be divided into two categories. The A-type is small and lacks direct connections to vascular bundles, which remain separated by 2-3 layers of parenchyma sheath. A-type occurs mostly in North American and Asian species. B-type nectaries are mainly larger, with connections to veins which end just below the nectariferous tissue. B-type nectaries occur mostly in species from Africa and Central and South America. Nectariferous tissue in both consists of small, more-or-less isodiametric cells. Both types secrete abundant nectar containing fructose, glucose, maltose, and sucrose in about equal proportions.

COOK, ROBERT EDWARD Population Biology/Physiological Ecology, NSF, Washington, D.C. 20550

### - Ideal and real growth in Mediola.

Recent theoretical and field studies of clonal growth and reproduction in herbaceous plants have emphasized the importance of "rules of growth" controlling modular proliferation and generating geometric patterns of space occupation. Mediola virginiana is a clonal herb whose rhizomatous pattern of growth theoretically tessellates the space of the forest floor. In the study reported here, the real patterns of growth are analysed from a 3 x 4 meter map of a Mediola population. The "rules of growth" of Mediola rhizomes are much more variable than previously recognized and the occupation of space is stochastic in nature. Comparison of the real patterns with the ideal geometries of theory reveals significant aggregation in populations, and the adaptive benefits of tessellation are questioned.

CURTIS, JOHN D. Biology Department, University of Wisconsin-SP, Stevens Point, WI 54481.

### Hydathode anatomy in marsh cinquefoil (Potentilla palustris Rosaceae).

Guttating leaves of Potentilla palustris were collected in Bayfield Co., Wisconsin, and processed for thick plastic sections, clearings and scanning electron microscopy. Each attenuated leaf tooth is terminated by an elongated pad of 50 to 60 sunken water pores which are positioned directly above the terminus of two or usually three large vascular bundles. On fully enlarged leaves, the water pore

guard cells are the same size as those of normal abaxial stomates and the pore is usually open. The rest of the hydathode epidermal pad is composed primarily of protoxylem and seem to lack a well defined bundle sheath. Epithem cells have few chloroplasts and few if any intercellular spaces.

DEMASON, DARLEEN A.\* and PAMELA K. DIGGLE. Botany and Plant Sciences, University of California, Riverside, 92521. - Histochemical and autoradiographic analysis of the relationship of the PTM and the STM in Yucca whipplei.

Observations were made of RNA and protein-staining on plants ranging from embryos to three-month-old plants of Yucca whipplei Torr. var. percursa Haines. One-, two-, and three-month-old plants were labelled with tritiated thymidine, fixed in FAA, sectioned, stained with the Feulgen reaction, and prepared for autoradiography. The serial transverse sections were outlined with a camera lucida recording all labelled nuclei on a graphics tablet. Computer-assisted reconstructions were made in three dimensions to observe the locations of labelled nuclei. The two techniques collaborate each other. The PTM is broad near the top of the stem and occupies narrower bands at successively basipetal levels of the stem, and finally disappears below the level of recent root initiation. There are no gaps in staining or labelling, and there are no changes in staining or labelling that would distinguish between activities of the PTM and the STM. They are continuous at all stages of development in the young vegetative stem. The STM is interpreted as a developmental continuation of the PTM.

DENGLER, NANCY G. Department of Botany, University of Toronto, Toronto, Ontario M5S 1A1. - Comparison of leaf development in normal (+/+), entire (e/e) and lanceolate (La/+) plants of tomato, Lycopersicon esculentum cv. Ailsa Craig

The developmental processes which result in the morphological and histological differences between the compound leaves of normal (+/+) Lycopersicon esculentum and those of the mutants entire (e/e) and lanceolate (La/+) are described. Despite considerable differences in mature leaf size and form, dimensions of the shoot apical meristem, arrangement of young leaves in the bud and pattern of leaf expansion are similar in the three genotypes. In normal leaves lateral leaflet formation begins earlier and is of longer duration, resulting in a greater number of leaflet pairs. In the entire genotype growth of the lamina of the terminal leaflet is initiated earlier and expansion proceeds at a greater rate than in normal leaves. In lanceolate leaves lateral leaflets are usually absent and, while the lamina is initiated at the same stage as in entire leaves, extension occurs more slowly than in either of the other two genotypes, resulting in a narrow leaf blade. Detectable cell enlargement in the adaxial protoderm begins earlier and proceeds at a great rate in lanceolate leaves, resulting in greater cell area at maturity.

<sup>1</sup>DENGLER, RONALD E. \*, <sup>1</sup>NANCY G. DENGLER and

<sup>2</sup>PAUL W. HATTERSLEY. <sup>1</sup>Department of Botany, University of Toronto, Toronto, Ontario M5S 1A1, <sup>2</sup>Research School of Biological Sciences, The

Australian National University, Canberra, A.C.T. 2601. - Differing ontogenetic origin of PCR ("Kranz") sheaths in leaf blades of C<sub>4</sub> grasses (Poaceae)

The origin and development of ground meristem and provascular tissue have been examined in leaf blades of eight C<sub>4</sub> grasses, representing different taxonomic groups and the three recognized biochemical C<sub>4</sub> types (NADP-ME, NAD-ME and PCK types). Comparisons were made with the C<sub>3</sub> species, Festuca arundinacea (poid). In NAD-ME (Panicum effusum, eupanicoid; Eleusine coracana, chloridoid) and PCK (Sporobolus elongatus, chloridoid) species, the provascular tissue of primary veins gives rise to xylem, phloem and a mestome sheath; associated ground meristem differentiates as PCA ("C<sub>4</sub> mesophyll") and the PCR ("Kranz") sheath. This parallels development in the C<sub>3</sub> grass, except that associated ground meristem differentiates into mesophyll and a parenchymatous bundle sheath. By contrast, the provascular tissue of NADP-ME C<sub>4</sub> species (Panicum bulbosum and Digitaria brownii, eupanicoid; Cymbopogon exaltatus, andropogonoid) differentiates into xylem, phloem and a PCR sheath; associated ground meristem giving rise only to PCA tissue. Findings support W.V. Brown's hypothesis that the PCR sheaths of NAD-ME and PCK-type C<sub>4</sub> grasses are homologous with the parenchymatous bundle sheaths of C<sub>3</sub> grasses, whereas in NAD-ME C<sub>4</sub> grasses, they are homologous with mestome sheaths. Aristida biglandulosa and Arundinella nepalensis have unusual C<sub>4</sub> leaf anatomy of special interest to this hypothesis.

DERSTINE, KITTIE S.\* and SHIRLEY C. TUCKER. Department of Botany, Louisiana State University, Baton Rouge, LA 70803  
-Comparative floral ontogeny of Parkinsonia aculeata (Caesalpinioideae), Lupinus havardii (Papilionoideae) and Acacia baileyana (Mimosoideae).

The three subfamilies of Fabaceae are distinguished on the basis of floral symmetry, aestivation of petals in bud (valvate or imbricate), degree of fusion in calyx and corolla, and morphology of seeds and leaves. The first three characteristics will be addressed, using SEM primarily. Ontogenetic studies of a representative taxon in each subfamily are intended to determine when during development these diagnostic features first become evident. In each taxon, order of initiation of sepals and petals is used to establish first evidence of symmetry. Middle developmental stages elucidate first indications of aestivation and/or apparent fusion among sepals, petals and filaments. Final flower form is seen in later developmental stages with petal expansion into divergent forms and cell differentiation as well as degree of filament fusion and further apparent petal fusion.

DICKISON, WILLIAM C. Department of Biology, University of North Carolina, Chapel Hill, NC 27514. - Fruits and seeds of the Cunoniaceae.

Cunoniaceae fruit morphology varies from ventrally dehiscent follicles, and dry, septically dehiscent capsules, to dry, indehiscent capsules, fleshy drupes, berries, and winged fruit types. The foliular fruit is the primitive condition in the family from which dehiscent capsules and indehiscent forms evolved. The majority of species produce fruit in which the pericarp is differentiated into exocarp, mesocarp, and lignified, fibrous endocarp.

Major shifts in dispersal strategy resulted in more advanced taxa in which the entire fruit is modified for seed dispersal and protection. Most dehiscent-fruited genera produce seeds with dispersal appendages in the form of wings or hairs. Hairs are generally apically comate, less commonly distributed in other patterns. Genera with indehiscent fruits possess a variety of seed morphologies but all are devoid of wings or hairs. Seed coats are exotegmic in construction, that is, the outer epidermis of the inner integument differentiates into the mechanical layer. Two distinct trends are recognized in seed coat structure: (1) reduction in seed coat thickness, including loss of a mechanical layer, and (2) amplification of the seed coat by secondary divisions of integumentary cells in the post-fertilization ovule. The diversity of seed surface patterns will be described and illustrated.

DIGGLE, PAMELA K.\* and DARLEEN A. DEMASON. Botany and Plant Sciences, University of California, Riverside, 92521. - Developmental relationship between the PTM and the STM in Yucca whipplei. Histological and anatomical observations were made on plants ranging from embryos to three-year-old plants of Yucca whipplei Torr. var. percursa Haines. Our objective was to determine the time and position of origin, ontogenetic relationship, and function of the primary thickening meristem (PTM) and the secondary thickening meristem (STM) during development of the vegetative axis. The PTM arises in the stem periphery during germination. It is longitudinally continuous from beneath the youngest leaf primordia to the primary root, and functions in the production of primary vascular bundles and ground tissue. The STM arises ontogenetically from the PTM in the base of two- to three-month seedlings and produces secondary vascular bundles and ground tissue. Parenchyma in the ground tissue is arranged in anticlinal cell files continuous from beneath the leaf bases, through the cortex and central cylinder to the pith. Individual vascular bundles in the primary body are collateral. The parenchyma cells of the ground tissue of the secondary body are also arranged in files continuous with those of the primary parenchyma. Secondary vascular bundles are amphivasal and have an undulating path with frequent anastomoses. The PTM and STM, primary and secondary vascular bundles, and files of primary and secondary ground tissue are continuous at all developmental stages studied. Development of the primary body is histologically and quantitatively similar to development in monocotyledons which possess only a PTM; and secondary growth is interpreted as a developmental continuation of the process of primary thickening.

DUTE, ROLAND R. Department of Botany, Plant Pathology, and Microbiology, Auburn University, Auburn, AL 36849.  
- Features of sieve-element ontogeny in Ginkgo biloba.

In an effort to enhance our knowledge of the phloem of gymnosperms, an ultrastructural investigation was conducted into the development of petiolar sieve elements of Ginkgo biloba. As in the sieve elements of other species, there is a stage of ER stacking which precedes cytoplasmic lysis. In some cases the ER forms concentric layers enclosing portions of ribosome-rich cytoplasm. These concentric layers are held together by bridges of 7 nm in length which

## 20 Developmental and Structural Section

traverse the intercosternal spaces. In newly-matured sieve elements whose lumina are otherwise devoid of ribosomes, the concentric layers may retain ribosome-rich centers.

During the process of lysis, those structures not destroyed become localized along the plasmalemma. The process of localization in *Ginkgo* is associated with attachment of organelles to bundles of microfilaments. The peripheral position of structures in the mature sieve element is maintained by minute bridges observed between plasmalemma and ER, and by association between ER and mitochondria. Due to the overall similarity of sieve-element ontogeny in different vascular plants, it is hypothesized that similar structures and associations will be observed elsewhere.

EL-GHAZALY, GAMAL AND WILLIAM A. JENSEN\*. Botany Department, University of Alexandria, Egypt, and Botany Department, University of California, Berkeley, CA 94720. - Ontogeny of pollen wall of *Triticum aestivum*.

Pollen of *Triticum aestivum* was studied at a series of developmental stages. Observations were made on the ultrastructural level and the light microscope level. Cytochemical tests were made to determine, where possible, the chemical nature of the developing wall. In the late tetrad a thin fibrillar matrix formed around each microspore between the callosic special cell envelope and the plasma membrane. Bacules are initiated as dense stained patches distributed in the fibrillar matrix. On release of the microspores from the tetrad the bacules are differentiated into a cylindrical rod with a conical head which extends beyond the distal surface of the fibrillar matrix. The fibrillar matrix is elevated from the plasma membrane and has a reticulate pattern. The tectum is formed as a result of deposition of material on the fibrillar matrix. The foot layer is established on both sides of a white line centered lamellation formed on the surface of the plasma membrane of the free microspores. There are sites on both tectum and foot layer where material was not deposited and consequently channels in the exine are formed. The plasma membrane becomes undulated and a compact fibrillar layer which designates the endexine is formed on the plasma membrane distal surface. A thick intine, containing cytoplasmic strands, forms at the proximal surface of the endexine. Detailed analysis of the development of the aperture has been investigated.

EVERT, RAY F., C.E.J. BOTHA and ROBERT J. MIERZWA\*. Departments of Botany and Plant Pathology, University of Wisconsin, Madison, WI 53706; Department of Botany, Fort Hare University, Republic of Ciskei, South Africa. - The use of free-space markers in the study of water movement in the leaf of *Zea mays* L.

Two techniques were used for the study of water movement in the xylem and leaf apoplast of *Zea mays*, the Prussian blue technique and one utilizing lanthanum nitrate. Prussian blue crystals and deposits of lanthanum were found within the lumina of the vessels and the apoplast, or cell wall continuum, of the vascular tissues and bundle-sheath cells. Although numerous Prussian blue crystals and lanthanum deposits were found in the outer tangential and radial walls of the bundle-sheath cells, few or none were found in the walls of mesophyll cells

contiguous to the bundle sheath. This pattern of deposition indicates that the suberin lamellae in the outer tangential walls of the bundle-sheath cells effectively inhibited the apoplastic movement of water between the bundle sheath-mesophyll cell interface.

EVERT, RAY F.\*, WALTER ESCHRICH and ROBERT J. MIERZWA. Departments of Botany and Plant Pathology University of Wisconsin, Madison, WI 53706; Forstbotanisches Institut der Universität Göttingen, Büsgenweg 2, D3400 Göttingen, Federal Republic of Germany. - Cytochemical localization of ATPase activity in the leaf of *Zea mays* L.

Standard lead precipitation procedures were used to study the localization of ATPase activity in the mature leaf of *Zea mays*. ATPase activity was most consistently localized on the outer surface of the plasmalemma of the vascular parenchyma cells contiguous to both vessels and thick-walled sieve tubes. (The thick-walled sieve tubes typically have numerous pore-plasmodesma connections with the vascular parenchyma cells.) The plasmalemma of the thick-walled sieve tubes exhibited relatively light deposits of reaction product. By contrast, in the same vascular bundles, the plasmalemmas of the thin-walled sieve tubes commonly contained very heavy deposits on both their surfaces. Reaction product also was associated with the sparse, parietal endoplasmic reticulum of the thin-walled sieve tubes. The plasmalemmas of the companion cells often contained less enzyme activity than those of their associated thin-walled sieve tubes. The plasmalemmas of the bundle-sheath cells and mesophyll cells often contained little or no reaction product. Little or no enzyme activity could be detected in association with the plasmodesmata between the various cell types. Together with previously obtained information on the maize leaf, the results of this study indicate that the plasmalemma of vascular parenchyma cells, companion cells, and thin-walled sieve tubes are involved in the active transport of sucrose into these cells, while little active transport occurs across the plasmalemma of the thick-walled sieve tubes.

EWERS, FRANK W.\* and MARTIN H. ZIMMERMANN. Harvard University, Harvard Forest, Petersham, MA 01366 - The hydraulic architecture of two conifers.

Trees of *Abies balsamea* and *Tsuga canadensis* were studied to determine from both a structural and functional point of view how well these species conform to the "pipe model" theory, where the plant is regarded as an assemblage of "unit pipe systems", each of which support a unit of leaves. This model predicts a constant Huber value (cross-sectional xylem area per dry weight of supplied leaves) throughout the plant. However, in both species the Huber value rose sharply in going up the tree, e.g., for a 5 m tall tree of *Abies* from .035 at the base to 11.6 cm<sup>2</sup>/g near the tip. In terms of water conduction, measurements of leaf-specific conductivity (LSC-conductivity in  $\mu\text{l}$  per hour at gravity gradient divided by dry weight of supplied leaves) are more informative than Huber values. LSC's decreased in going up the plant in the above tree from 277 at the base to 96 near the tip. The greater LSC values toward the base are apparently due to larger tracheids ( $X = 41 \mu\text{m}$  diameter at base vs.  $18 \mu\text{m}$  near tip). Superimposed on the above trends the trunk portions had greater LSC and Huber values than branches of comparable diameter. The differences between trunks and branches were much greater in *Abies balsamea* than in

*Tsuga canadensis*, which may be a reflection of the stronger apical dominance in the former species. The pipe model would have to be modified to account for the above data, such that each unit pipe system had many more but smaller tracheids near the top than the bottom of the tree, and such that the trunk component of a unit pipe had more and wider tracheids than the lateral branch component. A more useful morphogenetic model involves hormonal gradients that control tracheid size and number in the plant. Hydraulically the architecture of these species favors the trunk over lateral branches and may thus help the upper leaves on the tree to compete with lower leaves for water and minerals.

FAGERBERG, WAYNE, R. Dept. of Biology, Southern Methodist University, Dallas, TX 75275.- A morphometric analysis of the homogeneity of palisade cell structure in leaves of *Helianthus annuus*. L.

Leaves were divided into four quadrants and random samples taken from each quadrant. The ratio descriptors,  $V_v$  and  $S_v$  were calculated to describe the relationship between organelle compartment and cell size for the chloroplast, mitochondria, vacuole, microbody, oil, starch, and mitochondrial - chloroplast membrane compartments. Since ratio values do not often reflect changes in mean cell volume, cell volumes and actual compartment sizes were also determined. In mature fully expanded leaves statistically significant variations were found between quadrants in  $V_v$  ratio of the chloroplast, vacuolar and starch compartments and in the  $S_v$  ratios of the granal membranes. The granal membrane compartment was the most variable, between sampled quadrants. The starch compartment was significantly smaller in the bottom 1/2 of the leaf suggesting that starch may be more rapidly mobilized from the lower half of the leaf. This study suggests that palisade cells are not homogeneous throughout the whole leaf due to variation in organelle compartments involved with photosynthesis. These results will be compared to similar data derived from developing leaves.

FLORES, EUGENIA M. Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica, América Central. - Cauline glands of *Gunnera insignis*. Cauline glands of *Gunnera insignis* were studied with light and scanning electron microscopy. Two types are recognized: (1) stellate glandular trichomes secreting mucous material and (2) whitish lobulated bodies covered by stomata which release water. The glandular trichomes develop around the leaf primordia and between the numerous squamules. These organs, as well as the shoot apex, are immersed in the mucous secretion. Many filaments of *Nostoc* and other organisms (algae, fungi, nematodes, insect larvae) are observed living in the mucilage. *Nostoc* is also recognized inside the trichomes and cauline tissues. Eventually, these trichomes degenerate and form brownish spots associated with *Nostoc*. The structures which release water develop later and occupy the spaces left by the glandular trichomes. They cease functioning, turn green and extend longitudinally when the leaf which they surround

reaches maturity. The interaction *Gunnera* - *Nostoc* represents the only known symbiosis between an angiosperm and a nitrogen-fixing bluegreen alga. This relationship is still not well known. Apparently in *Gunnera* the alga *Nostoc* penetrates through the glandular trichomes. It seems pertinent to study the role of these glands in relation with *Nostoc* penetration and the nitrogen fixing mechanism.

FOLSOM, MICHAEL W. Dept. of Botany, Univ. of Alberta, Edmonton, Alberta, CANADA T6G 2E9. - Structural aspects of the central cell of Soybean, *Glycine max* (L.) Merr. with respect to fixation technique.

Ultrastructure of the eight nucleate embryo sac of soybean *Glycine max* (L.) Merr. demonstrates an unusual sequence of events in the central cell. Metabolites enter the embryo sac, are polymerized into starch grains, and are degraded mostly disappearing from the central cell before fertilization. These starch grains are organized into groups that have been referred to as "packets" by previous workers. Unlike starch grains reported in most plant cells these packets do not appear to be membrane bound. The absence of a membrane is most likely not caused by fixation problems since other membrane bound organelles of the central cell exhibit normal membranes. The addition of Alcian Blue 8GX (AB) to the fixation process shows that rather than being naked or bound by a plastid membrane, these packets are at least partially enclosed in a layer of amorphous material, a mucopolysaccharide, deposited some time after the starch grains begin to form. Coomassie Brilliant Blue has shown that the material surrounding the starch packets has a protein component. The role of Alcian Blue acting as stabilizing agent for this glycoprotein and the preservation of cellular components by various fixation techniques (e.g. GA/OsO<sub>4</sub>, GA + AB/OsO<sub>4</sub>, GA/OsO<sub>4</sub>/TA/OsO<sub>4</sub>, and freeze substitution) will be discussed with respect to the starch packets and associated glycoprotein in the central cell.

FREEMAN,\* THOMAS P., MURRAY E. DUYSEN AND THOMAS J. GULYA. Departments of Botany and Plant Pathology, North Dakota State University and U.S.D.A. Agricultural Research Service, Fargo, N.D. 58105. - Ultrastructural changes in sunflower chloroplasts caused by *Pseudomonas syringae* pv. *tagetis*.

Severe chlorosis and ultrastructural modifications of chloroplasts occur in sunflowers in response to infections of *Pseudomonas syringae* pv. *tagetis*. Chlorosis became apparent within two days after the cotyledons of ten day old sunflower seedlings were inoculated with the bacteria. The first symptoms generally appeared in the center of leaves at the second node above the cotyledons. During the next few days the chlorosis progressed to include leaves at several nodes. Despite the fact that some of these leaves lost essentially all of their pigmentation they remained turgid and continued to expand. The loss of pigmentation is directly related to ultrastructural changes within the chloroplast. Grana thylakoids became dilated and separated from the granal stacks. These thylakoid membranes were not altered as in the cases of chromoplast formation or normal senescence. Both grana and stroma thylakoid membranes coalesced to form a large membrane sheet in the center of the plastid. Starch and plastid ribosomes were lost early in the chlorotic cycle. Other cellular organelles do not appear to be altered by the bacterial infection.

## 22 Developmental and Structural Section

FRENCH, J.C. Department of Biological Sciences, Mississippi State University, Mississippi State, MS 39762-5759. - Preliminary observations on the anatomy and systematic occurrence of secretory structures in Araceae.

A preliminary survey was made of the structure and systematic occurrence of extrafloral nectaries, wax glands, resin canals and laticifers in Araceae. Extrafloral nectaries were found in only two subfamilies, Philodendroideae and Lasioideae; extrafloral nectaries from both taxa have a similar anatomical organization. Wax glands were found on the undersides of leaves at the juncture of certain primary veins and the midvein of several species of Alocasia and Xenophya. A wax gland comprises a palisade layer of epidermal cells that excretes a thick outer plaque of wax. Resin canals have been found in roots, stems and leaves of certain genera of Lasioideae and Philodendroideae. Resin canals in roots of Philodendron, Cercestis and Culcasia have a sclerenchyma sheath surrounding the epithelium. Resin canals in some species of Culcasia lack both an epithelium and intercellular space, and have only sclerenchyma. Laticifers of Colocasioideae were found to contain a variety of particles in their latex, including osmiophilic bodies about 8  $\mu$ m in length. Two types of these large particles have been found, one typical of latex from Old World genera, e.g. Colocasia, and a second type typical of New World genera, e.g. Syngonium. Laticifers from roots of Colocasioideae examined thus far differ from those in the shoot in lacking the large osmiophilic particles in latex, and in lacking anastomoses.

FRENCH, J.C. and P.B. TOMLINSON. Department of Biological Sciences, Mississippi State University, Mississippi State, MS 39762-5759 and Harvard Forest, Petersham, MA 01766. - A summary comparison of vascular bundle organization in Araceae, Cyclanthaceae and Pandanaceae.

In previous, separate studies compound vascular bundles have been investigated in three families of monocotyledons: Araceae, Cyclanthaceae and Pandanaceae. These results are brought together in the form of a summary comparison. Compound bundles from different taxa may appear to have a similar construction when comparisons are based on single transverse stem sections. However, when the three-dimensional course of bundles is compared from representatives of Araceae, Cyclanthaceae, and Pandanaceae, distinctly different patterns of construction are found. These results confirm the usefulness of cinematographic methods in comparative studies of the anatomy of monocotyledons. The results also support the view that these families probably have no close phylogenetic affinity. In addition, the concept of the compound vascular bundle has been broadened to include: 1) forms which intergrade with amphivasal bundles, a common feature of some Araceae, e.g. Dieffenbachia, Philodendron and 2) bipolar or multipolar bundles resulting from long-delayed fusion between a leaf trace and axial bundle(s), which is a consistent feature of Cyclanthaceae.

FRENCH, J.C. and P.B. TOMLINSON. Department of Biological Sciences, Mississippi State, MS 39762 and Harvard Forest, Petersham, MA 01766. - Cinematic analysis of stem vasculature in Philodendron (Araceae).

A survey of stem vasculature in Philodendron has been made using cinematic analysis of series of transverse sections. Philodendron exhibits the most diverse vascular organization in the Araceae, with respect to

both the arrangement of xylem and phloem in vascular bundles and the three-dimensional course of the bundles. In a few species (P. scandens) simple collateral bundles are present in the central cylinder, and when leaf traces are followed basipetally each trace fuses with an axial bundle. In other species bipolar, or tri- to multipolar bundles predominate in the central cylinder, and exhibit a complex pattern involving unpredictable fusion and/or anastomosis of components in compound bundles. In some species with compound bundles each collateral component is completely surrounded by a sclerenchyma sheath, while in other species little or no sclerenchyma is present, and compound bundles appear to intergrade with amphivasal bundles. In addition to intermediate types, well-defined amphivasal bundles are present in some species, which have a solid core of phloem and a continuous cylinder of xylem. In some species of Philodendron with amphivasal bundles some of the tracheary elements do not develop in a typical fashion. Even in mature stems secondary cell walls of some elements remain thin and un lignified or are absent, and cell diameters are reduced. When this condition occurs, it is typically found in many bundles in a stem, and has been found in 17 species (e.g., P. smithii, imbe, hastatum, longilaminatum) thus far.

GRAYBOSCH, ROBERT A.\* and PALMER, REID G. Genetics Department, Iowa State University, Ames, IA. 50011.

- Cytological studies on a male-sterile mutant (ms2) in soybean (Glycine max).

All known male-sterility mutations in soybeans are of the genetic type; to date, six such recessive nuclear mutations have been described. The ms2 mutant was discovered in 1975, but no cytological studies aimed at elucidating exact causes of male sterility have been undertaken. This report presents results of preliminary studies on cytological events associated with the ms2 mutant, accomplished via comparative studies of anther and pollen development in male-sterile and male-fertile plants. Squash preparations reveal that chromosome pairing and segregation is normal in microspore mother cells of developing sterile anthers. Microsporogenesis proceeds normally until tetrad stage, at which time premature abortion usually occurs; on rare occasions separation of microspores from tetrads occurs, but release of microspores from callose was not observed. Abnormalities in the tapetal layer are associated with tetrad degeneration. These are manifested in the form of vacuoles or inclusions, first observed during first meiotic division of microspore mother cells. They progressively enlarge during anther ontogeny. Tapetal development resembles that occurring in plants homozygous for either the ms3 or msp (partial male sterile) mutations. Anther morphology is normal during early developmental stages, but a progressive degeneration of external tissues is noted.

GRIMSON, MARK J.\* and HOWARD J. ARNOTT, Department of Biology, The University of Texas at Arlington, Arlington, TX 76019-0498. - Electron microscopy of druse crystals in the abscission zone of Phyllanthus niruri L.

Abscission plays an important role in the development and survival of plants. In Phyllanthus niruri L. (Euphorbiaceae), masses of druse crystals are found proximal to the abscission zone of the leaf and flower as well as

in the septa between the carpels. Although crystal sand can be found in cells of the ovary and prismatic crystals in leaf idioblasts, only druses are found in the zones associated with abscission or dehiscence. The druses are found in the abscission zones at relatively early stages long before abscission is to occur. The druses (a multiple array of twin crystals arranged in a spherical space) develop within the vacuole of the crystal idioblasts. The druses vary somewhat in size and morphology and in the structure of the individual crystals which make up the druse. In some cases crystals are sharply pointed, in other cases they are less pointed or even rounded. As the crystals of the druse develop some appear to press through the cytoplasm and grow near the cell wall. Later in development a cell wall-like sheath grows around the crystal. Whether this is a response to the crystal penetrating the cytoplasm and appressing the cell wall is not yet clear. The cell wall-like sheath can easily be seen by electron microscopy and appears similar to the primary wall. Isolated crystals may still be encased by this sheath. Once the sheath is complete the crystal is sealed off from the remainder of the still living cell. After the organ has abscised the crystal remains just below the scar left by abscission. The concentration of crystals at this point suggests a possible protective role for the crystals. Obviously this may be a secondary "function" in that the crystals may play a more meaningful role in calcium metabolism prior and during the formation of the abscission layer.

JENSEN, WILLIAM A.\*, MARIE MIZELLE, RAVINDER SETHI and MARY ASHTON. Department of Botany, University of California, Berkeley, CA 94720. - Pollen development in wheat treated with a chemical hybridizing agent.

Triticum aestivum seedlings were treated with a chemical hybridizing agent developed by Rohm and Haas Chemical Company known as RH0007. It caused the pollen to abort without markedly affecting the fertility of the ovule. Ultrastructural and histochemical studies revealed the compound specifically inhibited the formation of sporopollenin. This inhibition was not complete but the pollen in treated plants laid down a wall only 1/3 as thick as that found in the control. Histochemical studies indicate that it is not the synthesis of the carotene subunits but the polymerization step that is inhibited.

JENSEN, WILLIAM A.\*, MARIE MIZELLE, RAVINDER SETHI and MARY ASHTON. Department of Botany, University of California, Berkeley, CA 94720. - Ultrastructural study of pollen development in wheat.

A study of pollen development in Triticum aestivum was made using the electron microscope. The study began with the microspore mother cell and continued to the mature pollen. Stress was placed on the changes in the cytoplasm during the various developmental stages, as well as on the wall. Marked changes in ribosome number, plastid size and shape, and amounts of ER were noted at various stages. The quantity of wall deposited was also studied in detail. This study forms the foundation for the data presented in the subsequent work on a chemical hybridizing agent.

KANE, MICHAEL E.\* and LUKE S. ALBERT. Department of Botany, University of Rhode Island, Kingston, RI 02881. - Effects of ABA on heterophylly and stomatal development on submerged juvenile shoots of Myriophyllum heterophyllum Michx.

In the heterophyllous aquatic angiosperm M. hetero-

phyllum, submerged juvenile shoot apices develop dissected astomatous leaves that are composed of filiform divisions consisting of a compact mesophyll. In contrast, aerial juvenile apices develop smaller and thickened pinnatisect leaves which bear adaxial stomata in a cutinized epidermis and lacunae within the mesophyll. Results of recent investigations on the physiological control of submerged and emergent forms in two other heterophyllous aquatics suggest a role for water-stress induced formation of abscisic acid (ABA) in the development of aerial leaf morphologies. To determine whether ABA also plays a role in the development of the aerial juvenile phase of M. heterophyllum, axenic cultures of the submerged juvenile phase were grown in a liquid medium consisting of Murashige and Skoog salts, vitamins, and 3% sucrose with or without ABA ( $10^{-9}$  to  $10^{-4}$ M) at 25 C in a 16 hr photoperiod (PAR; 200  $\mu$ E  $m^{-2}s^{-1}$ ) for 10 days. Control plants produced astomatous leaves typical of the submerged growth phase while exposure to  $10^{-6}$ ,  $10^{-5}$ , or  $10^{-4}$  M ABA induced the formation of leaves morphologically and anatomically similar to those on aerial juvenile shoots. The influence of ABA on adaxial stomatal development was evident by observed increases in stomatal densities with hormone concentration (23, 100, 150, and 154 stomates/ $mm^2$  for plants exposed to  $10^{-7}$ ,  $10^{-6}$ ,  $10^{-5}$  and  $10^{-4}$  M ABA, respectively.) The hormone ABA therefore appears to play an important role in the control of heterophylly and stomatal development in an increasing number of aquatic angiosperms.

KAUL, ROBERT B. School of Life Sciences, University of Nebraska, Lincoln NE 68588. - Inflorescence architecture and evolution in Asiatic Fagaceae.

More than 200 Far Eastern species of Castanea, Castanopsis, Lithocarpus, and Quercus have been examined. Flowers are borne on spikes that are axillary to leaves and bracts of the current and previous seasons' stems. The spikes are often unisexual and male spikes greatly outnumber females on a tree. Some spikes, however, are androgynous, gynecandrous, or androgynecandrous, and all three conditions can occur on a single tree. Various degrees of separation of the sexes and of aggregation of spikes into reproductive short-shoots exist. Some short-shoots have abortive apices and others produce monopodial continuation growth. Sometimes both kinds occur on the same individual, in which cases the determinate short-shoots are below the indeterminates and ordinarily bear only male flowers; the determinates usually bear a few female flowers in their distal spikes. More or less paralleling these phenomena is reduction from foliage leaves to bracteoles on the short-shoots. The most extreme condition occurs in Quercus, where the short-shoots are always unisexual, determinate, and only bracteolate, and male flowers are borne on pendulous spikes (catkins).

KAUSCH, A.P.\* and H.T. HORNER. Department of Botany, Iowa State University, Ames, IA 50011. - Increased nuclear DNA content during raphide crystal idioblast development in Vanilla planifolia L.

Files of calcium oxalate raphide crystal idioblasts are formed in the cortex of adventitious roots of Vanilla planifolia L. Idioblast initials are first recognized by intense fluorescence of the cytoplasm with the acridine orange method. Nuclear and nucleol-

## 24 Developmental and Structural Section

lar enlargement ensue and continue during development; these cells do not undergo mitosis. Two-wavelength Feulgen microspectrophotometry was accomplished on root cortical preparations to determine the DNA content of idioblast nuclei during their development. Telophase nuclei (measured individually) and anaphase nuclei (measured together) served as internal standards (2C:4C) for relative DNA content of cortical parenchyma cells. Chicken erythrocytes were used as an internal quantitative standard (2.62 pg DNA/nucleus). DNA content of developing crystal idioblasts averaged 5.9 times that of telophase cortical parenchyma cells and ranged from 4C to 32C. Light and electron microscopy provides structural evidence of polyteny in idioblast nuclei. Heterochromatic regions are larger and slightly more numerous compared to interphase nuclei of cortical parenchyma cells. Frequency distribution of idioblast DNA contents indicates endopolyploidy, probably via endoreduplication, to an octaploid condition followed by less strict DNA replication within the idioblast genome.

LERSTEN, NELS R.\*, AND GLENN W. TURNER. Department of Botany, Iowa State University, Ames, IA 50011.

### - Foliar nectaries in *Ardisia* (Myrsinaceae).

*Ardisia* is the largest genus of the Myrsinaceae (35 genera, 1000 species), with about 400 species of mostly tropical shrubs and small trees. We investigated the anatomy of extrafloral nectaries that occur on the leaves of some species using light and scanning electron microscopy. We also studied the distribution of these nectaries with a dissecting microscope on herbarium specimens of 60 species representing 13 of the 14 subgenera usually recognized. This is the first report on the occurrence and structure of an extrafloral nectary for any member of the Order Primulales. Nectary structure varies from isolated, short, capitate trichomes to large discs with a palisade epidermis on a broad base of large isodiametric cells. Both types are sunken in epidermal depressions, so that in each the upper surface of the nectary is nearly flush with the surrounding epidermis. Copious nectar secretion was observed from large nectaries on greenhouse grown plants of *A. polycephala* and small amounts from the capitate trichomes of *A. crenata*. Intermediate forms were observed on herbarium material and the two types appear to be homologous. *Ardisia* extrafloral nectaries fit into Zimmerman's (1932) category of Schuppennektarien ('scalelike nectaries'). Such nectaries have been reported to be derived from trichomes in certain other groups of plants. Nectary distribution in *Ardisia* correlates somewhat with geography and this may be of some use as a taxonomic character.

MACDONALD, JOANNE E. Department of Forest Resources, University of New Brunswick, Fredericton, N.B., Canada, E3B 6C2.

### - Effect of date of cut on length, winter-readiness and winter-survival of first-year stump sprouts of sugar maple (*Acer saccharum* Marsh.).

The study was conducted on a clearcut area of the Nashwaak Experimental Watershed Project in the west central uplands of New Brunswick, Canada. Thirty residual trees (6 to 10 cm dbh) were cut during the overwintering dormant period and the subsequent growing period. Elongation of dominant and co-

dominant sprouts on stumps of these trees was monitored weekly during the subsequent or the remaining part of the growing period. Sprouts were examined in late October for indications of winter-readiness, and in the following June to assess winter-survival. Vigour of elongation, sprout length, and degree of winter-readiness decreased with each successive date of cut. In late October, most leaves had abscised and most internodes were woody on sprouts arising from dormant-period cuts. Leaves were brown and rigid on sprouts arising from June and early July cuts, and straw-coloured and limp on sprouts arising from late July cuts. The proportion of hardened internodes decreased with each successive date of cut on sprouts arising from June and July cuts. Frost damaged distal leaves and internodes on sprouts arising from late July cuts, and all leaves and internodes on sprouts arising from August cuts. Damage ranged from isolated black blotches on tissue to fully blackened, hardened tissue. In June, after overwintering, terminal buds and distal and proximal lateral buds burst on some sprouts, and only distal and proximal lateral buds burst on other sprouts arising from dormant-period and June cuts. Only proximal lateral buds burst on sprouts arising from July cuts. Sprouts arising from August cuts did not survive the winter.

MACDONALD, S. ELLEN\*, DAVID M. REID and C.C. CHINNAPPA. Department of Biology, University of Calgary, Calgary, Alberta, Canada. T2N 1N4 - Studies on phenotypic plasticity in the *Stellaria longipes* complex (Caryophyllaceae): Stem elongation.

The *Stellaria longipes* complex is known to be a plastic group with respect to: number of flowers, length of stem, leaf shape, pigmentation and cuticular wax. It has been shown that thermoperiod has a greater effect than photoperiod in inducing stem elongation. Stem elongation and subsequent flowering are further investigated here. Evidence is presented for a winter cold requirement to achieve maximum stem elongation and for flowering. A cumulative temperature effect operates in inducing stem elongation, while light appears to have a synergistic effect. Temperature is shown to override the effect of hormones (GA and AbA) on stem elongation. Induction of stem elongation in response to red:far red ratio will be discussed.

MAHLBERG, PAUL G.\*, AND JOANNA PLESZCZYNSKA. Department of Biology, Indiana University, Bloomington, IN. 47405. - Evolution of succulent *Euphorbia* as interpreted from latex composition.

The morphology of starch grains and the gas-liquid chromatographic profile of triterpenes derived from latex of the nonarticulated laticifer of succulent African *Euphorbia* were examined for their applicability to interpret phylogenetic relationships of this genus. Several trends in starch grain morphology and triterpene composition were evident in the 38 examined taxa. Rod shaped grains, interpreted to be conservative, occurred in only a few taxa in several dwarf groups. Grains of osteoid shape prevailed in most taxa. Highly osteoid grains possessing lobed ends represented the most complex form and were present in some taxa endemic to Madagascar. Triterpene profiles which contained from 2 to 14 or more compounds were derived from all taxa. Each taxon possessed a

characteristic profile, or identifying fingerprint. The composition of the profile differed quantitatively and qualitatively among taxa. Taxa with few triterpenes, tentatively interpreted as primitive, occurred in dwarf forms, whereas Madagascan taxa tended to possess high numbers of triterpenes reflective of specialization. This study supports the interpretation that laticifer starch grain morphology and triterpene composition, both gene mediated stable markers, can be employed to determine and correlate phylogenetic relationships between taxa of this complex genus.

MAKSYMOWYCH, ROMAN\* Department of Biology Villanova University, Villanova, PA 19085.  
MYRON C. LEDBETTER, Biology Department, Brookhaven National Laboratory, Upton, NY 11973.

- Fine Structure of Secretory Canals in *Xanthium pennsylvanicum* Petioles.

Secretory canals, lined with an epithelium, occur in many families, e.g. Umbelliferae, Compositae. These canals extend continuously through the root and shoot systems and are known, in some cases, to secrete resins, essential oils, etc. In *Xanthium* the canals initials. Subsequent divisions lead to a ring of 7-12 epithelial cells surrounding a central cavity. During maturation the epithelium becomes crushed and obliterated. Canals were examined in petioles of *Xanthium pennsylvanicum* (Cocklebur) plants grown under long day illumination to maintain vegetative growth. The fine structure of the canal and its epithelium was studied by electron microscopy of thin sections cut transverse to the principal axis of petioles from leaves in an early stage of development. The canal proper is delimited by walls of epithelial cells which protrude into a scallop shaped cavity. In comparison to the surrounding parenchyma, the epithelial cells are smaller, cytoplasmically more dense, and less vacuolate. The epithelium contains pleomorphic starch-free plastids with planar thylakoids frequently stacked into granna; thus, the plastids are presumed photosynthetically active. Mitochondria are abundant and often dense. The cytoplasm is rich in free polysomes, and smooth endoplasmic reticulum predominates

LELAND C. MARSH AND JAMES L. SEAGO, JR.\* Department of Biology, State University of New York, Oswego, NY 13126.

- Adventitious rooting in *Typha glauca* under experimental conditions.

Overwintering sterile plants from a single clone of *T. glauca* were grown in nutrient solution with last year's sterile stalk either submerged or emerged to determine the effect on adventitious rooting. The following results were observed: 1) Plants with sterile stalks above the solution showed earliest rooting (within 4 days). These plants produced 35-60 lateral roots per cm over the basal 10 cm of the adventitious roots. 2) Plants with submerged sterile stalks delayed rooting until 10 days, and then only after new stalks with developed aerenchyma had elongated 30 cm above the water surface. These plants had fewer adventitious roots with less lateral roots, except in the basal 1 cm. It was concluded

that root development is related to the presence of an air pathway from above the water surface to the rooting zone at the base of the developing buds.

MAUSETH, JAMES D. Dept. of Botany, University of Texas, Austin, TX 78712. - Development and anatomy of the parasite *Tristerix aphyllus* (Loranthaceae) infecting *Trichocereus chilensis* (Cactaceae).

Many of the large columnar cacti *Trichocereus chilensis* near Santiago are infected by *Tristerix* (= *Phrygilanthus*) *aphyllus*. This is one of the most highly reduced plants known: it is an endoparasite, the flowers being the only parts of the plant ever to emerge from the host, all the rest existing as an endophytic haustorial system; roots, stems and leaves are not produced. After infection, the parasite spreads in all directions through the thick cortex of the host, eventually reaching the vascular cambium and conducting tissues. The parasite in this invasive stage occurs as a "mycelium" of uniseriate filaments that grow between host cells, deforming them, but only rarely entering them. Later growth is by apparently random cell division that produces irregular parenchymatous strands. Ultimately xylem and phloem are produced in these strands; the phloem is normal but the xylem is almost pure parenchyma, with only occasional idioblastic tracheary elements. Strands close to the epidermis of the host are able to produce adventitious flower buds that emerge through either soft regions in the epidermis (the areoles) or through accidental breaks in it. The flower stalk may persist, forming a small perennial inflorescence that has normal wood, phloem and bark but is without leaves or chlorophyll. The portions of the endophyte that produce these exophytic inflorescences do not develop normal anatomy, but persist as irregular parenchymatous strands with small amounts of xylem and phloem. Host cells appear healthy and normal, with no sign of damage caused by the presence of the parasite.

MAZE, JACK. Department of Botany, University of British Columbia, Vancouver, B. C. V6T 2B1, Canada. - Explanations for leaf development. The explanations offered for leaf development are usually causal. The most common one is that leaf development is the result of ontogenetic events that are under genetic control, the cause in this case being genetic. As well, kinetics, surface area thermodynamics, and natural laws pertaining to increasing disorder have been implicated in ontogeny and may be presented as explanations of leaf development. It is also possible to apply teleological explanations to leaf development since the most general form of a functional explanation for leaf development is the same as the most general form for the explanation for a vertebrate predator's hunting behaviour, an undoubted teleological system. It would thus appear that both teleological and causal explanations may be applied to leaf development. Of the causal explanations proposed, all would seem to be based in natural laws. However, causal explanations involving genetic control of ontogeny, using natural laws pertaining to chemical bonds, would not allow one to deduce increasing complexity with development. To do so, one must use natural laws pertaining to kinetics, thermodynamics or increasing disorder.

## 26 Developmental and Structural Section

McCAULEY, MICHELE\* and JUDITH CROXDALE. Dept. of Botany, Univ. of Wisconsin, Madison, WI 53706.

-Establishment of a plastochron index for *Dianthus chinensis*  
*Dianthus chinensis* was grown under greenhouse (100 plants) and growth chamber (25 plants) conditions to determine if this plant meets the three assumptions required for use of the plastochron index (P.I.): its leaves must grow exponentially in their early stages, grow at the same rate during the exponential phase, and be initiated at equal intervals. In both studies, one leaf of each expanded pair was measured on a regular basis for two months. To test the first two assumptions, the mean lengths of all expanded leaves were calculated for each day of measurement and linear regressions performed over the leaves' exponential growth. The coefficients of determination ( $r^2$  values) for these lines ranged from 0.96 to 1; the slopes of the lines varied from 0.05 to 0.16 for the greenhouse plants and 0.11 to 0.26 for the growth chamber plants. To determine if this variation was a result of the averaging of leaf lengths, linear regressions were calculated and averaged for each leaf of each growth chamber plant; these slopes ranged from 0.11 to 0.27. A one-way ANOVA showed that the change in slopes was significant. The third assumption was tested by calculating a plastochron age for each plant for each day of measurement, determining the mean plastochron age, and regressing this against time. The high  $r^2$  values for the regression lines of leaf length vs. time indicate that in their early stages, leaves grow in an exponential manner. The slope values indicate that the P.I. can only be used for certain leaves. High  $r^2$  values for the regression lines of mean plastochron age vs. time show that the leaves are initiated at equal intervals. The mean duration of a plastochron was 4.55 and 4.35 days under greenhouse and growth chamber conditions. The value of the P.I. in predicting the plastochron stage of the apex will be discussed.

TERPILL, EDWARD E. Department of Botany, University of California, Berkeley, CA 94720 -  
Heteroblastic seedlings of *Fraxinus pennsylvanica*: a system to compare simple and compound leaf development.

Seedlings of *Fraxinus pennsylvanica* grown under constant conditions produce pairs of simple and compound leaves in a predictable sequence. In a sample population of 36 seedlings, all leaves were simple through node 4. From nodes 5 to 7 progressively fewer simple leaves were formed, and at node 8 all leaves were compound, 65% having 5 leaflets. Since successive leaf pairs are initiated and grow exponentially at the same rate, the plastochron index and leaf plastochron index of Erikson and Michelini (1957) can be used to predict developmental events of leaf primordia still in the terminal bud. Simple leaves (node 4) and compound leaves (node 8) are both initiated approximately 3.5 plastochron intervals before reaching an index length of 35 mm. Within half a plastochron interval after initiation, primordia of simple leaves show indications of lamina development and primordia of compound leaves show localized outgrowths which will become leaflets. This system is being used to characterize differences in marginal activity which may be associated with the development of different leaf forms (simple and compound). Cell lineage, histological differentiation (i.e. cell expansion, cytoplasmic density and histochemistry) and cell division activity are being investigated.

MIKESELL, JAN. Department of Biology, Gettysburg College, Gettysburg, PA 17325.

-Ovule development in *Phytolacca americana* L.  
Several populations of *Phytolacca americana* (pokeweed) were collected along the Maryland-Pennsylvania border. Pokeweed is a common roadside plant, and occurs frequently in recently disturbed areas. Approximately 6 shoots differentiate adventitiously from the top of the underground tap root. An average of 34 racemes develop from each shoot, and each raceme has about 50 fruits. Thus, a fully developed plant can have 10,000 or more fruits differentiating from the above-ground shoots. Young fruits are green, but older fruits are purple measuring 7-8 mm in diameter. Fruits are usually composed of 10 carpels and 10 locules. Each locule contains 1 ovule. Older ovules and seeds are laterally compressed, being vertically positioned within a locule. Ovules are bitegmic, crassinucellar, and they exhibit axile placentation. Measurements of the length, width, and breadth of ovules and locules, as well as the number and size of cells in ovules, were calculated at different stages of fruit development. The width of pokeweed ovules, early in ontogeny, is their smallest dimension, but ovule width eventually becomes the greatest measurement followed by ovule length. Measurements of length, width, and breadth for young and old ovules are  $23\mu\text{m} \times 15\mu\text{m} \times 23\mu\text{m}$  and  $205\mu\text{m} \times 237\mu\text{m} \times 86\mu\text{m}$  respectively. Reorientation of the ovule is another conspicuous change in ovule development. The ovule becomes curved to such an extent, during its development, that the nucellus and integuments are considerably displaced. Correlated with reorientation is a change in the position of the micropyle, which was initially directed toward the ovary wall, and is directed later toward the centrally positioned placenta--a change of 180 degrees.

MOGENSEN, H. LLOYD. Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011 - Double fertilization in barley and the embryological basis for the formation of haploid embryos, embryoless caryopses and ovule abortion.

The progeny of an induced barley mutant has recently been shown to produce a relatively high percentage of caryopses containing haploid embryos. In addition, some caryopses have a full complement of endosperm but lack an embryo, and still other ovules abort at an early stage. This study was initiated to investigate the embryological explanation for these unusual phenomena. Since the majority of the ovules studied showed normal double fertilization, a built-in control was provided and, therefore, this process is also described. The pollen tube delivers the two male gametes to the embryo sac by first growing through the micropyle then between nucellar cells before discharging into the degenerate synergid. Double fertilization is effected after the sperm cells exit the degenerate synergid and enter the intercellular space between the egg apparatus and the central cell. Haploid embryos arise from the unfertilized egg. In these ovules, triple fusion occurs normally, but the other sperm fails to enter the egg even though it reaches the intercellular space just outside the female gamete. Embryoless caryopses appear to result from a similar condition; i.e., the lack of syngamy accompanied by triploid endosperm formation. However, in this case, the egg does not continue to develop into an embryo. The absence of polar nuclei or the failure of triple fusion even though the egg may be fertilized, results in the ultimate abortion of some ovules.

MOSELEY, MAYNARD F. Department of Biological Sciences, University of California, Santa Barbara, CA., 93106. Aspects of vegetative structure in Cabomba.

The plant of *Cabomba*, as revealed by *C. caroliniana*, consists of a principal axis, which is a short-shoot with decussate phyllotaxy. It bears axillary, decussate rhizomes and flowering shoots. A rhizome may give rise to axillary flowering shoots or bend upwards to form a short shoot. Flowering shoots are proximally decussate or ternate, but distally, where flowers are borne, the phyllotaxy changes. In all but *C. piahyensis*, phyllotaxy becomes 1/3 helical, and floral positions vary from axillary to extra-axillary. The shoots may become sympodial in *C. aquatica* and *C. palaeformis*. In *C. piahyensis*, the proximal ternate phyllotaxy is essentially retained, but as flowers appear, one at a node, the flowers become extra-axillary and a larger than normal space occurs between the flower and its closest leaf other than the one it is associated with. The four positions, those of the three leaves and one peduncle, or at least of the peduncle, shift dextrorsely 60° from one node to the next. The unoccupied space between two organs also shifts relative to the other organs. Vasculature of the vegetative axes and floral shoots of all but *C. piahyensis* consists of two pairs of collateral bundles, each bundle rotated about 45° so that its xylem partially faces that of its mate. A canal, possibly a common protoxylem canal, lies between the bundles of each pair, and somewhat centripetally. Leaves have one pair of bundles; peduncles have three. In *C. piahyensis* (short shoot and rhizome are unknown), the flowering shoot axes have three pairs of bundles. At each node of all categories of axes, an elliptical, more or less continuous ellipse of vascular tissue links the bundles proximal to it, and from it bundles to the internode above and organ traces are supplied.

MOSELEY, MAYNARD F.<sup>1</sup>, INDIRA J. MEHTA<sup>2</sup>, PAULA S. WILLIAMSON<sup>2</sup> and HATSUME KOSAKAI<sup>1</sup>. <sup>1</sup>Department of Biological Sciences, University of California, Santa Barbara, CA, 93106 and Department of Developmental and Cell Biology, University of California, Irvine, CA, 92717. - The floral anatomy of Cabomba. Six vascular bundles in 3 pairs supply the peduncle of the flower. Each pair is associated with a common protoxylary canal. A short, cylindrical complex of vascular tissue is formed in the receptacle and this complex is extended into a slightly distal mound, cylinder or arc of tissue. The basal vascular complex gives rise to traces for sepals, petals and stamens. The bases of the 3 sepals and 3 petals are arranged in a single whorl and may or may not be basally connate into a single tube. Distally, the members separate; petals bend centripetally and sepals centrifugally. Each sepal and petal receives 3 to 5 vascular traces which are branches of a single, basal principal trace. Principal traces separate from the complex at about the same level. In 3-stamen flowers, each stamen stands opposite and distal to a petal and the petal principal trace and associated staminal trace may be basally connate. In 6-stamen flowers, stamens are aligned with the intervals between petals and sepals; connation of staminal and perianth principal traces are not frequent. The number of carpels varies most commonly from 1 to 3. Each carpel receives 1 principal trace, from the extension of the receptacular complex, which divides proximally to, or within, the carpellary base into the conventional 3, typically oriented veins, basally 120° from one another. Usually, the 2 ventral veins meet in the center of the distal, ventral ovarian region. Positions of the anatropous,

ovular attachments may be to the interior wall over 1 or more of the veins, or any position between 2 veins including a central position over the union of the ventral veins. Ovular vascular supplies are very variable, but appropriate.

MUELLER, RICHARD J. Department of Biology, Utah State University, Logan, UT 84322 - Architecture and development of sylleptic branching in *Alstonia scholaris* (Apocynaceae).

The tropical tree *Alstonia scholaris* exhibits modular branching and belongs to Prevost's model in the Halle and Oldemann architectural classification. The tree consists of a main trunk and plagiotropic, sympodial lateral branches. Each lateral branch module consists of a long basal internode, two whorls of 6-10 foliage leaves and a distal whorl of four scale leaves. The shoot apex of each branch becomes parenchymatous or produces a terminal inflorescence to end the growth of each module. During vegetative growth, a new branch arises in the axil of each of the scale leaves. The initiation and development of these branches was investigated. The diameter of the shoot apex reaches a larger maximum size during successive plastochrons of the lateral branch module. Therefore the smallest leaves (scale type) are initiated from the largest shoot apical meristem. The occurrence of this unusual phenomenon is related to the nearly simultaneous initiation of the large buds of the sylleptic branches in the axils of the scale leaves. The formation of these buds consumes most of the tissue of the broadened apex. The initiation of the scale leaves, the formation of their axillary buds, and the parenchymatization of the central region of the original shoot apex are closely associated temporally and morphologically.

NIKLAS, KARL J. Section of Plant Biology, Division of Biological Sciences, Cornell University, Ithaca, NY 14853. - Morphological consequences of the efficient display of photosynthetic tissues: implications on early land plant evolution.

Conventionally, the evolution of increased plant stature has been related to the selective advantages of discharging spores at greater heights and of displaying photosynthetic surfaces above adjacent vegetation. The consequent changes in photosynthetic efficiency (I), resulting from alterations in plant geometry, are assessed by means of computer simulations and a model relating I to the projected surface area to total surface area (Ap/A) of a plant's photosynthetic tissues. The evolutionary appearance of orthotropically growing cylindrical and bifurcating axes is demonstrated to be one developmental response capable of optimizing I. In addition, a trade off between I and the mechanical stability of high order branching systems (defined by the total moment arm, M) is shown to result in the appearance of overtopped, tree-like morphologies. Multidimensional plots of I, M, and geometric features of branching result in three-dimensional topologies with "peaks" corresponding to  $I_{max}$  and  $M_{min}$ . Self-crowding and self-shading of higher order branches can be resolved by compartmentalizing supporting (branches) and photosynthetic (leaves) organs. This results in computer simulations analogous in structure to the morphologies of various fossil and extant plants.

## 28 Developmental and Structural Section

OKATAN, YENER and OLGUN, GÖKSEL. Department of Biology, University of Istanbul, Turkey. Department of Biology, University of Trakya, Turkey.  
- Hormonal relations between vegetative and reproductive structures in monocarpic plants. I. The pattern of senescence in *Digitalis purpurea* L. and some developmental changes brought about by parthenocarpy.

In this study, the effects of parthenocarpy on senescence and on the other aspects of development of *Digitalis purpurea* L. were investigated. Unpollinated flowers of the plant were treated with gibberellin after emasculation. With this method, 100% parthenocarpic fruits were obtained. The number of flowers per plant was observed to increase by 109% the period of flowering by 131% and the growth of flower stalk by 107% in plants with parthenocarpic fruits. Similar observations were made on plants deflowered before pollination. On the other hand, in untreated plants with normal fruits, flowering was found to cease with the mature of the fruits. These observations suggest that senescence occurs as apical senescence in the plant *D. purpurea* and that this is induced by the development of the seeds.

OLGUN, GÖKSEL and OKATAN, YENER. Department of Biology, University of Trakya, Turkey. Department of Biology, University of Istanbul, Turkey.  
- Some ultrastructural changes in the mesophyll chloroplasts of the podded and the deflowered soybean plants.

During the vegetative growth or pod-fill period, no destruction occurs in the thylakoid membranes. Cessation of the vegetative growth in deflowered plants or maturation of the seed on the podded plants lead to accumulation of starch granules in the chloroplasts of the young leaves. Thylakoid membranes look like intact but squeezed by starch granules. As the senescence starts in the podded plants, thylakoid membranes are destructed, osmiophilic bodies appear, starch granules disappear. Regular senescence dose not occur in deflowered plants. Thylakoid membranes remain intact. But, neither osmiophilic bodies nor starch granules are seen as dense as to be expected.

ORR, ALAN R.,\* W. BRADFORD, and L. LOVE.  
Department of Biology, University of Northern Iowa, Cedar Falls, IA 50614.  
- Cytochrome oxidase activity in the shoot apical meristem of *Brassica campestris* L. during transition to flowering.

Histochemical studies on fresh-frozen, cryostat sections of evoked shoot apices of *Brassica campestris* showed there was an increase in cytochrome oxidase activity within the first 24 hr after plants were transferred from short days (8 hr light) to long days (16 hr light). Cytochrome oxidase activity was observed in the central, peripheral and pith-rib meristem zones of the meristem at the transition stage. Activity in the late transition stage was localized in areas of the peripheral zone where floral bud primordia would be formed. These observations support an interpretation of floral evocation in a transforming meristem of *Brassica* as consisting, at least partially, of a higher respiratory rate than the vegetative meristem of *Brassica*. Results are discussed in relation to other histochemical and cytological events which are known to occur in the meristem of *Brassica*.

JOHN. N. OWENS. Biology Department, University of Victoria, Victoria, B.C. V8W 2Y2. - Cone bud development and shoot growth in Douglas-fir under GA<sub>4/7</sub> and root pruning treatments.

The time and method of cone initiation has been determined for many conifers. Cone induction has been accomplished using gibberellin A<sub>4/7</sub> (GA<sub>4/7</sub>) in 16 members of the Pinaceae. Cone induction in the Pinaceae appears to be most successful when GA<sub>4/7</sub> is used in conjunction with cultural treatments such as root pruning. This paper reports on the development of vegetative and potential cone buds under control, GA<sub>4/7</sub>, root pruned and GA<sub>4/7</sub> plus root pruned conditions in juvenile Douglas-fir. Trees with a flowering history and trees with no flowering history were assigned to each of the four treatments. One group of 80 trees was used for analysis of the general coning response, at the end of the growing season. In a second group of 16 trees, shoot elongation was measured weekly, other shoots were collected weekly, and developing terminal and axillary buds were sampled for anatomical study. This paper describes axillary bud development as it relates to shoot elongation and cone bud differentiation. Flowering was significantly increased by the GA<sub>4/7</sub> and root pruning treatments. The magnitude of this response was mediated by the trees flowering history. Shoot growth was reduced by root pruning regardless of flowering history and was increased by GA<sub>4/7</sub> only in trees having a poor flowering history. Terminal and axillary bud development had the same phenology and time of cone bud differentiation as in mature trees growing under natural conditions. Root pruning with and without GA<sub>4/7</sub> reduced mitotic activity in distal potential vegetative and potential cone-bud apices. The possible relationship between treatment, shoot elongation, apical development and cone bud differentiation will be discussed.

PALSER, BARBARA F. Department of Biological Sciences, Rutgers University, Piscataway, NJ 08854 - Floral anatomical and embryological evidence bearing on the segregation of *Harrimanella* from *Cassiope* (Ericaceae).

Two species of *Cassiope*, *stelleriana* and *hypnoides*, have been segregated as species of *Harrimanella* on the basis of gross morphology and leaf anatomy. Eleven taxa, including these two, have been studied and compared for several floral characteristics. All are pentamerous, pentacyclic, actinomorphic, sympetalous, and hypogynous, the appendaged anthers inverting to introrse rather late in development. More or less variation, however, is found in other features: vascular anatomy, peduncle hairs, sepal anatomy and stomata, corolla shape at base, anther shape and dehiscence, nectary shape and stomata, style shape, ovary stomata--particularly internal, ovule size and number megagametophyte development and mature structure. In most of these characters *stelleriana* differs from all the others except *hypnoides*, thus supporting its segregation in a separate genus. The case is less clear for *hypnoides*. This species agrees with *stelleriana* in several characteristics, the most significant being a Polygonum type of megagametophyte development in contrast to the Allium type found in all other species. It agrees with the nine other taxa in a few characteristics and is intermediate in several others, such as the mode of anther dehiscence (collapse vs. resorption tissue/*Harrimanella* vs. *Cassiope*). On the whole, *hypnoides* appears to have enough characters in common with *stelleriana* to be included with it in *Harrimanella*.

PETERSON, CURT M.\* and MICHAEL W. FOLSOM. Department of Botany, Plant Pathology, and Microbiology and the Alabama Agricultural Experiment Station, Auburn University, AL 36849, and Department of Botany, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.

- The effect of a cytokinin on flower and pod abscission of soybean, *Glycine max* (L.) Merr.

Abscission of flowers and immature pods accounts for most of the reduction in yield potential of soybean (*Glycine max* (L.) Merr). Terminal racemes of 'Bragg' soybean plants were sprayed with  $10^{-7}$ ,  $10^{-5}$  or  $10^{-3}$ M 6-benzylaminopurine (BAP) to determine the influence of a cytokinin on flower and pod abscission. A significant reduction in abscission occurred only when  $10^{-3}$ M BAP was applied. A significant increase in the total number of seeds per plant also was observed for the  $10^{-3}$ M BAP treatment. This was due entirely to an increased number of pods per raceme, because there was no difference in the mean number of seeds per pod. Most abscissions within each treatment occurred during the first 14 days of the treatment period. The effect of BAP in reducing abscission was observable within 10 days after spraying. All mature pods of control plants were located at the first seven (proximal) nodes on terminal racemes. Compared to other treatments the increased number of mature pods following  $10^{-3}$ M BAP treatment was due to a significantly higher number of mature pods at nodes distal to node 7. Changes in distal shoot morphology were observed on some treated plants suggesting that BAP may alter reproductive development to favor increased pod set in soybean.

PITPOLY, JOHN J.\* New York Botanical Garden, Bronx, NY 10458 and DENNIS W. STEVENSON, Barnard College of Columbia University, NY 10027. - Phyllotaxis, stelar morphology and shoot apical organization of *Lyconodium anpressum* (Lyconodiaceae).

Phyllotaxis consists of a system of alternating pseudowhorls with a 2/19 phyllotactic spiral which corresponds to a 9+9 contact parastial system with 18 orthostichies. Each of the six stelar lobes is a sympodium of the leaf traces of three orthostichies and is composed of three protoxylem poles. At the very least, the outer region of the stele is composed of leaf traces and is therefore not completely autonomous. The shoot apex consists of four zones which may be recognized both cytologically and histochemically, as follows: surface initials, subsurface initials, rib meristem, and peripheral meristem. The differentiation of the procambium and protoxylem appear to be bi-directional with respect to the ontogeny of the leaf traces.

POSLUSZNY, U. and R.E. SUBDEN. Department of Botany and Genetics, University of Guelph, Guelph, Ontario, Canada N1G 2W1

- Development of the vegetative and floral shoots of the hybrid grape cultivar Ventura.

Although grapes are amongst the oldest cultivated crops, very little critical scientific work has been done on the development of the vegetative and floral shoots. As in other plants with a vine-like habit the branching in the grape shoot is highly unorthodox. The axillary buds (usually 2-6 in each axil) are formed early in the summer of the year preceding bud break. The bud possesses partially developed embryonic structures of next year's flowers, tendrils and shoots. All three of these structures

can develop from a common primordium referred to as an anlage. What determines the kind of structure (flower, tendril or shoot) the anlage will form and the sequence on the stem is unknown. Within the overwintering bud numerous hair-like outgrowths develop, surrounding the meristematic tissue. The development and possible function of these hair-like outgrowths is currently being investigated.

RANSOM, J. STEVEN\* and RANDY MOORE. Biology Department, Baylor University, Waco, TX 76798.

- A morphometric analysis of the ultrastructure of columella cells of primary and lateral roots of *Phaseolus vulgaris*.

A morphometric analysis of the ultrastructures of columella cells of primary and lateral roots of *Phaseolus vulgaris* was performed in order to determine the precise location of cellular organelles in these cells of graviresponsive and non-graviresponsive roots. Amyloplasts, mitochondria, and dictyosomes are found in greatest numbers (and relative volumes) in the lower (i.e., "bottom") third of columella cells in both types of roots. The nucleus and vacuole tend to be located in the middle third of columella cells in both types of roots. Only the hyaloplasm is concentrated in the upper (i.e., "top") third of columella cells in roots of *Phaseolus vulgaris*. These trends of organelle distribution are consistent whether the data are calculated on a protoplasmic or cytoplasmic basis. Therefore, the presence of sedimented amyloplasts alone is not responsible for the differential distribution of other cellular organelles in columella cells of *Phaseolus vulgaris*. Since the columella cells of both lateral and primary roots have essentially the same intracellular distribution of organelles, it is unlikely that differences in graviresponsiveness between the two types of roots are due to ultrastructural factors within the individual cells.

REMPHREY, WILLIAM R.\*<sup>1</sup>, TAYLOR A. STEEVES<sup>2</sup>, and BRIAN R. NEAL<sup>2</sup>. <sup>1</sup>Department of Forest Resources, University of New Brunswick, Fredericton, NB, Canada E3B6C2, and <sup>2</sup>Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada S7N0W0.

- Simulation of the colonizing architecture of *Arctostaphylos uva-ursi* (L.) Spreng. (bearberry).

The architecture and development of the prostrate shrub, *Arctostaphylos uva-ursi* (L.) Spreng. (bearberry) was investigated on certain sand dune sites in Saskatchewan, Canada. A predominantly horizontal woody frame was laid down mainly by the activity of colonizing complexes located at the periphery of the bearberry patches. The development of these complexes, defined as consisting of not more than the four youngest annual growth increments or shoots, was simulated in plan view using quantitative field data. The model was based on the lengths of dominant horizontal shoots, the frequencies and relative positions of dominant daughter shoots on parental shoots and the divergence angles between daughter and parental shoots. A sequence of procedures, based on a set of ten rules, was devised. To accommodate observed variability, several stochastic elements were incorporated. The simulations showed growth patterns similar to colonizing complexes observed in nature.

## 30 Developmental and Structural Section

REYNOLDS, THOMAS L. Department of Biology, University of North Carolina, Charlotte, NC 28223. - An ultrastructural and stereological analysis of pollen grains of *Hyoscyamus niger* during induced embryogenic development.

Selected nuclear and cytoplasmic changes during embryogenic development, induced by the culture of anther segments of *H. niger*, were analyzed using stereological techniques for morphometry. When pollen grains were cultured at the uninucleate stage of development, potentially embryogenic grains could be identified within 6 h of culture by an increased area fraction of the nucleolus occupied by the granular zone. The ratio of dispersed to condensed chromatin in the nucleoplasm of these cells also increased. Nonembryogenic pollen in vitro and in vivo possessed prominent fibrillar zones in the nucleolus and a relatively constant ratio of dispersed to condensed chromatin. These differences may reflect changes in nuclear activity in potentially embryogenic pollen grains during early stages of culture. Following the first haploid mitosis, the nucleolus of the generative cell in potentially embryogenic pollen maintained an extensive granular zone through the first division to form a proembryoid. On the other hand, the nucleolus of the vegetative cell became primarily fibrillar and the cell did not divide. The area fraction of the cytoplasm occupied by RER, Golgi cisternae, mitochondria, and plastids differed in the generative cells of potentially embryogenic and nonembryogenic pollen. These results support the idea that embryogenic induction in *H. niger* takes place at the uninucleate stage of pollen development and that the first division of the potentially embryogenic generative cell to form a bicellular proembryoid completes the induction process.

Richards, J.H. and S.C.H. Barrett. Dept. of Biol., Fla. International U., Miami, FL 33199 and Botany Dept., U. of Toronto, Toronto, Ontario, M5S 1A1. Developmental basis of tristylly in *Eichhornia paniculata* Spreng. (Pontederiaceae).

*Eichhornia paniculata* is a short-lived perennial, emergent aquatic. The species is tristylous but self-compatible. Growth is sympodial. When flowering, paniculate inflorescences bear flowers alternately on first-order branches. Long, mid and short-styled morphs occur in the majority of Brazilian populations. A flower of a given morph has a style of one length and six stamens, three each of the other two lengths. Stamen insertion is dorsiventral. Within a flower, the relatively longer stamens are found on the lower side of the flower, while the relatively shorter stamens are on the upper side. Anther size is positively correlated with stamen height.

The general pattern of flower development does not differ between morphs. Flower primordia are triangular at initiation. Stamens arise in two whorls of three each in conjunction with tepal origin on the flat primordium apex. The three horseshoe-shaped carpel primordia arise simultaneously after the second set of stamens. Thus, initial organization of the flower is radial. Differences between the two stamen levels in size and number of microsporocytes are seen in anthers prior to meiosis. Meiosis occurs in buds app. 1 mm long. Thus the dorsiventral pattern of development first seen in the microsporocytes alters the initial radial pattern of growth.

RIDING, RICHARD T. Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 6E1.

-Structure of needles of *Pinus radiata* as influenced by light intensity or moisture stress.

Trees from four clones were grown in growth rooms at the New Zealand Forest Service, Forest Research Institute in Rotorua. Current year needles, collected from different heights in the crowns of these trees, yielded foliage samples from four light intensities per clone. Needle size increased with increasing light intensity. This was accompanied by an increase in the number of hypodermal layers, mesophyll layers, and resin ducts. The ratio of vascular tissue to needle cross-sectional area remained fairly constant; however, the discreteness of the two vascular bundles decreased as stelar size increased. Although the structure of epidermal cells and the stomatal complex did not vary with light intensity, the number of stomatal rows and stomatal frequency tended to increase with increasing light intensity. The influence of vapour pressure deficit (VPD) on needle structure was determined for plants from 3 clones grown under 3 different conditions of atmospheric moisture. The needles with the smallest cross-sectional area were from dry conditions while the thickness of the dermal system was greatest for plants grown under moist conditions. The number of resin ducts per needle increased with decreasing VPD. Again, the structure of the stomatal complex was constant for all conditions. In both studies there was clonal variation.

(Supported by grants from NSERC Canada. Thanks are due D.R. Smith and D.A. Rook of the Forest Research Institute.)

ROST, THOMAS L., PRIMAVERA IZAGUIRRE DE ARTUCIO\* AND EDWARD B. RISLEY. Department of Botany, University of California, Davis, CA 95616; \*Facultad de Agronomía, Universidad de la República Uruguay, Montevideo, Uruguay - Transfer cells in the placental pad and caryopsis coat of *Pappophorum subbulbosum* Arech. (Poaceae).

During caryopsis development the layers of the pericarp, integuments and nucellus all contribute to the formation of the caryopsis covering structures. The caryopsis coat is continuous around the entire caryopsis except at the style remnant and placental connection. The coat consists of a discontinuous outer pericarp epidermis transfer cell layer, crushed and senescent middle pericarp layers and a continuous inner pericarp epidermal transfer cell layer. This last layer, however, is not present across the placental pad. The integuments are present as a crushed dense layer, the nucellus is a discontinuous, thin and crushed layer. The placental pad occurs at the ventral surface of the caryopsis opposite the scutellum and coleorhiza. It consists of 15-20 crushed cell layers, including the remnant of the placental vascular bundle. From the inside several partially crushed nucellar layers occur that contain transfer cell walls. The middle dense layers, the pigment strand, consist of the middle pericarp remnant, plus the placental vascular bundle remains. The inner pericarp epidermis and aleurone layers do not extend across the pad. The outer pericarp epidermis extends across the entire pad as a connected layer of transfer cells. These cells contain membranous structures suggesting that they may be living cells, possibly functional in the mature caryopsis.

RUGENSTEIN, SEANNA R. Department of Botany,  
Louisiana State University, Baton Rouge,  
LA 70803.

- Seed testa patterns in Cercideae  
(Caesalpinioideae: Leguminosae).

The caesalpinoid legume tribe Cercideae contains six genera in two subtribes. Scanning electron microscopy was utilized to study the anatomy of seeds of 60 species representing 25% of the species in the largest subtribe and 83% of the species in the second. Several features of papilionoid legume seed anatomy have been shown to have taxonomic utility (Gunn, 1981; Kupicha, 1977; Lersten and Gunn, 1982). It was determined, during this study, that testa patterns in Cercideae differed in size rather than basic configuration, from those on papilionoid legume seeds. The basic testa patterns in Cercideae, as in papilionoid legumes, are papillose, reticulate, and foveolate. Other features of Cercideae seed anatomy, such as size and shape of hilar tongue, hilar groove, and micropyle, were also examined. The distribution of these anatomical features of the Cercideae seed seem to be indicative of subtribal and subgeneric taxonomic affiliations.

RUSSELL, SCOTT D. Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019 - Gametic fusion in Plumbago zeylanica: Ultrastructural evidence for gamete recognition and the preferential transmission of sperm plastids into the zygote.

The mature microgametophyte of Plumbago zeylanica contains two dimorphic sperm cells which may be identified by differences in both morphology and cytological content. One of the two male gametes is associated with the vegetative nucleus throughout its later development and is distinguished by the presence of a 30 micrometer long cellular projection which wraps around the vegetative nucleus. Cytological content of this sperm cell includes 0 to 2 plastids and an average of 256 mitochondria. The other sperm cell is connected to the first sperm by plasmodesmata, is not closely associated with the vegetative nucleus and lacks a prominent cellular projection. The second sperm cell contains 8 to 48 plastids and an average of 40 mitochondria. Upon discharge of the gametes from the pollen tube, both sperm cells are deposited in an intercellular region within the female gametophyte, located between the egg and central cell. The distinctive morphology of sperm plastids after fertilization can be used as a naturally occurring cytoplasmic marker to determine which of these two sperms fuses with the egg and central cell. Evidence to date has suggested a preferential pattern of fusions between the plastid-containing sperm and the egg cell, transmitting a number of plastids into the incipient embryo. The other, plastid-poor sperm fuses with the central cell, transmitting numerous mitochondria into the incipient endosperm. This preferential pattern of organelle inheritance strongly suggests that gametic fusion in the megagametophyte is not random in P. zeylanica. These results provide evidence for the presence of a final putative barrier to reproduction consisting of a gamete-level recognition system which may operate in the male and female gametes of this angiosperm.

SANGSTER, ALLAN, G. Division of Natural Sciences,  
Glendon College, York University, Toronto, Ontario,  
M4N 3M6

-Anatomy and silica distribution patterns in root  
and rhizome of the grass Miscanthus sacchariflorus.

Anatomy and deposited silica distributional patterns were investigated for the root and rhizome by means of scanning electron microscopy and energy dispersive X-ray microanalysis. In the root, silica deposits were confined to the single-layered endodermis in the form of large aggregates. In the rhizome, silica was present in two concentric regions consisting of the outer endodermis and the cells bordering the inner central cavity. Both these regions were several-layered, and the deposits were part of the cell wall layers rather than projecting aggregates. In both organs, a perivascular distribution pattern was evident, single-layered in the root but multi-layered in the rhizome. The root pattern is consistent with that investigated for other genera of the tribe Andropogoneae, as is the endodermal deposition site for the rhizome. However, rhizome deposits differ in form from other genera, and deposition around the central cavity has not been encountered previously.

SCRIBALLO, ROBIN W. and U. POSLUSZNY, Department  
of Botany and Genetics, University of Guelph,  
Guelph, Ontario, Canada N1G 2W1

- Morphology and establishment of seedlings of  
Hydrocharis morsus-ranae.

Hydrocharis morsus-ranae is an introduced aquatic plant species in North America. Little is known concerning the nature and morphology of seedling germination in this species. Consequently it has been assumed that Hydrocharis morsus-ranae must overwinter primarily through the production of large numbers of vegetative propagules. As part of a continuing study of this species an S.E.M. and field investigation of the seed and seedling morphology were initiated to contribute to the limited knowledge of germination patterns within this genus and the Hydrocharitaceae as a whole. The seeds of Hydrocharis morsus-ranae are highly unusual morphologically having their entire surface covered with hollow spiraliform tubercles. Germination occurs when the embryo of the exalbuminous seeds elongate splitting the tuberculate testa. The buoyant developing embryos then rise to the surface and the first foliage leaves emerge from a highly modified cotyledonary sheath. The young seedlings undergo several growth phases in which they first appear lemnid in habit before attaining their characteristic reniform leaf shape. In the field, substantial numbers of Hydrocharis morsus-ranae seedlings were found germinating among the turions of the same species. It is likely that reproduction from seed is more important in this species than previously thought.

SHULTZ, LEILA M. Department of Biology, Utah  
State University, Logan UT 84322. - Leaf vessel  
measurements in desert perennials.

The relationship of habitat and leaf vessel measurements is explored in comparative anatomical studies of sixteen closely related taxa (Artemisia spp.) from the cold deserts of western North America. Data are presented which document changes in vessel structure as well as relative volumes of tracheary tissue in habitats which are defined by a gradient of increasing aridity. As might be expected, vessel diameters decrease and width of cell walls increase with increasing aridity. Few studies, however, have addressed the possibility of volumetric changes in tracheary tissue. The relative volume of xylem to total tissue volume in the leaf appears to be a sensitive indicator of water stress. That ratio is presented and discussed here as a Xeromorphy Index.

## 32 Developmental and Structural Section

SLONE, J. HENRY\* and RICK G. KELSEY. Departments of Botany and Chemistry, University of Montana, Missoula, MT 59812.

### - Structural and histochemical studies of glandular trichomes of *Artemisia tridentata* ssp. *vaseyana*.

Fresh and plastic embedded buds and leaves were stained and observed by light microscopy. The gland has ten cells (2 rows of 5 cells), including a pair of epidermal basal and a pair of stalk cells below a six-celled head. Mature glands accumulate terpenoid secretion products that react with conc.  $H_2SO_4$  and also secrete small amounts of polysaccharide particles within a distended cuticle above the upper 2-3 tiers of head cells. In younger leaves, the glands occur as populations of mixed developmental stages. Older leaves support mainly senescent and collapsed glands. Chloroplasts are present in the lower and middle tiers but not in the upper tier of head cells, nor in the stalk and basal cells. The cytoplasm of early secretory glands stain lightly and uniformly for polysaccharides. In mid- to late secretory glands, the stalk cell constituents stain intensely for polysaccharides. Toluidine blue O, on the other hand, stains stalk cells intensely blue-green, but stains head and basal cells light blue in glands of early secretory stages. Glands at later secretory stages exhibit a preferential staining for protein at the periphery of the cytoplasm adjacent to the anticlinal and distal periclinal walls of the upper two tiers of head cells. The cellular contents (including small spherical bodies) of secretory glands stain with Sudan Black B, but presecretory glands do not. Sudan IV only stains cuticle. Sudan Black staining of the cytoplasm is probably due to phospholipids. As glands enter into the late secretion phase, cytoplasmic constituents become less distinct, the chloroplast stains less for protein, and the plasmalemma of the head cells detach from the cell wall.

SPERRY, JOHN S. Department of Biology, Harvard University, Harvard Forest, Petersham, MA 01366.

### - Hydraulic architecture of the palm *Rhapis excelsa*.

Resistance to flow (R), and pressure gradients ( $\Delta P/l$ ) along the stem-to-leaf xylary path under average flux rates (J) were investigated in aerial axes of *Rhapis excelsa* and related to xylem structure/development. R measurements were made on excised axes, and show a consistent pattern for the mature vascular path: R per unit length is lowest in the stem ( $\sim 7$  bars  $\cdot s(ml \cdot cm)^{-1}$ ), highest in the leaf base ( $\sim 34$  bars  $\cdot s(ml \cdot cm)^{-1}$ ), and intermediate in the petiole ( $\sim 18$  bars  $\cdot s(ml \cdot cm)^{-1}$ ). Results reflect vascular anatomy: the stem has wide (75-100  $\mu m$ ) metaxylem (mx) vessels, the leaf base has narrow (to 25  $\mu m$ ) protoxylem tracheids, and the petiole has intermediate mx vessels (35-60  $\mu m$ ). R has a consistent relationship to leaf age: the youngest expanded leaf (EL1; second-youngest = EL2, etc.) has relatively high R (e.g. 6600 bars  $\cdot s \cdot ml^{-1}$ ), R decreases with leaf development to minimal value in EL4,5 (e.g. 2500 bars  $\cdot s \cdot ml^{-1}$ ). Senescent leaves have R comparable to EL1. Decrease in R with leaf development correlates with the basipetal maturation of mx in the leaf axis which is not complete until EL4. Increased R in senescent leaves is due to xylem dysfunction in the leaf base. J was estimated from transpiration; variation with leaf age shows the inverse trend of R: EL1 has low J (e.g.  $9.1 \times 10^{-4} ml \cdot s^{-1}$ ), older leaves show progressively higher J to maximum in EL4 (e.g.  $63 \times 10^{-4} ml \cdot s^{-1}$ ). J in senescent leaves is similar to EL1.  $\Delta P/l$  calculated from J and R indicates recently mature leaves (EL4,5) are routinely subject to lower sap pressures than developing and senescing leaves. The bottleneck at the leaf base accounts for a large portion of the pressure drop

into the leaf: at maximum J it induces a drop of 7 bars. This bottleneck may act to confine sap cavitations to the leaf axis, thus preserving hydraulic integrity of stem xylem.

STEINGRAEBER, DAVID A.\* and JACK B. FISHER. Department of Botany & Plant Pathology, Colorado State University, Fort Collins, CO 80523 and Fairchild Tropical Garden, Miami, FL 33156. - Indeterminate growth of leaves in *Guarea* (Meliaceae): a twig analogue.

Leaves of seed plants are generally characterized as organs of determinate growth. In this regard, *Guarea* and related genera seem unusual in that their pinately compound leaves contain a bud at their tip from which new leaflets expand from time to time. Previous studies based upon superficial examinations of leaf-tip buds have produced contradictory conclusions regarding how long the leaf apex remains meristematic and produces leaflet primordia. In order to determine whether leaf development in *Guarea* is truly indeterminate, we microscopically examined leaf-tip buds of *Guarea guidonia* and *G. glabra*. In both species, the leaf apex remains meristematic and continues to produce new leaflet primordia as the leaf ages. Unexpanded leaves of *G. guidonia* contained an average of 23 leaflet primordia, while the oldest leaves we examined had initiated an average of 44 total leaflets. In *G. glabra*, unexpanded leaves contained 8 leaflets, whereas an average of 28 leaflets had been initiated on the oldest leaves. Periodic examination of individual intact leaves indicated that the leaves may continue their growth for 2 or more years. As new leaflets are initiated at the leaf apex (and subsequently expand in rhythmic flushes), older (basal) leaflets may abscise. In addition, the rachis of the leaf thickens and becomes woody due to the activity of a vascular cambium. *Guarea* leaves thus seem to be analogous to a typical twig (stem), in general habit as well as in their indeterminate apical growth and secondary thickening.

STEVENSON, DENNIS M. Barnard College of Columbia University, New York 10027 and New York Botanical Garden, Bronx, NY 10458. - Systematic implications of the floral morphology of the *Mavaceae*.

Vegetatively, this monogeneric aquatic family most closely resembles members of the Alismatidae, whereas the flowers clearly indicate that it is more properly placed in the Commelinidae. The flowers arise singly in the axils of large unvascularized bracts and the vegetative branches in the axils of vegetative leaves. Thus, the shoot system is clearly monopodial and not sympodial as previously believed. Salient floral features include parietal placentation, tenuicellular ovules, monosporic embryo-sac, anthers with an exothecium, and the radial expansion of the cells of the two layered integuments to form an embryostega. These are all characters shared with the Xyridaceae (more specifically with *Xyris*) and are not found in the Commelinaceae. In fact, there are no derived characters that are shared with the Commelinaceae and the *Mavaceae* is more properly placed near the Xyridaceae than near the Commelinaceae.

STREET, P.F.S.\* and E.J. ROBB. Department of Botany and Genetics, University of Guelph, Guelph, Ontario N1G 2W1. - Anatomy of terminating vessel members and their importance to vascular wilt disease.

Initial foliar symptoms in many leaves of plants

infected with vascular pathogens appear adjacent to vein endings. Terminating vessel members in leaves may be sites of accumulation of pathogen metabolites, degraded cell wall components or wound reactants. Anatomical studies of these terminal vessel members has provided scant evidence for their importance in vascular wilt disease and has centered on phylogenetic comparisons of terminating vessels. Our study therefore was aimed at a detailed anatomical appraisal of terminating vessels especially the structure of end walls. Leaves of tomato, chrysanthemum, alfalfa and hop were prepared for electron microscopy and serially sectioned from the tip. Tips of all terminal tracheids narrowed rapidly towards the ends and no perforation plates were observed. Tracheids ended either singly in chrysanthemum, tomato and hop or in pairs in alfalfa. Chrysanthemum and alfalfa endings were closely adpressed to parenchyma cells with little discernable distinction between the walls of both cells. This intimate association suggested a free transfer of xylem fluids through walls in the symplast. Tomato and hop endings were positioned in areas of less coherence being surrounded by many intercellular spaces. All the tracheid tips were triangular in cross-section and extensively thickened. The endings contained many pit surfaces and in chrysanthemum there was a characteristic tail which appeared to be composed of secondary thickened laminar fibres. Extensive accumulation of granular phenolics in the lumens of some tracheid tips suggested that this area was particularly susceptible to aggregations of plant and fungal metabolites which might contribute towards water flow restriction to leaf mesophyll cells and ensuing vascular wilt symptoms.

TUCKER, SHIRLEY C. Department of Botany,  
Louisiana State University, Baton Rouge, LA  
70803

- Character weighting in Leguminosae based on time of initiation.

Unifying ordinal or familial characteristics are by definition stable. These features should therefore be determined early in floral ontogeny, while those characteristics which separate related species should occur relatively late in ontogeny. Examples of early-determined features (to be illustrated with examples from Leguminosae) include floral symmetry, order of appendage initiation, number and kinds of whorls, number of parts per whorl, and order of initiation within a whorl. A second assemblage of characteristics is determined in mid-development stages; these include corolla aestivation, organ abortion to produce "loss", elongation of some parts, tube formation of calyx, corolla, and androecium, petal fusion, differential growth of petals, differential growth of the two stamen whorls, and formation of gynophore and staminodes. Some of these mid-development-determined characteristics are important in producing supra-generic distinctions, while others are more important at the generic level. Late-determined characteristics, which are likely to distinguish related species or sometimes genera, include differential changes in petal shape, petal color, filament elongation, nectaries, nectar and fragrance, epidermal elaborations (hairs, sculpturing, hooks, pits, cuticle), and changes in carpel shape. Although exceptions abound to these generalizations, the hypothesis offers a useful approach to re-examining and evaluating diagnostic characteristics in the light of their ontogenetic origin.

TUCKER, SHIRLEY C. Department of Botany,  
Louisiana State University, Baton Rouge, LA  
70803

- Developmental origins of petal aestivation in *Cadia purpurea* and other legumes.

Although petal aestivation is used to separate sub-families and some tribes of legumes, there is little developmental evidence on its control in these groups. Valvate aestivation typifies Mimosoideae, ascending cochlear aestivation typifies Caesalpinioideae, and descending cochlear typifies Papilionoideae. Petals are widely spaced and not imbricate at initiation, nor do the bases extend marginally to become imbricate. Overlapping occurs at the margins about halfway up the petals when they are about 300  $\mu$ m high. Features which determine which petal overlaps outside another include relative size, thickness, and degree of curvature of the petal in transsection. Petals which overlap have relatively attenuate margins, while those which appress and fuse have thick, blunt margins. *Cadia purpurea*, in the primitive papilionoid tribe Sophoreae, appears intermediate to the Caesalpinioideae because of its highly variable petal aestivation. Ascending cochlear and descending cochlear patterns are both common among flowers on the same plant. Also, two patterns occur which are rare in the legumes: 1) a pattern in which the standard petal is half inside, half outside the wings, and 2) completely quincuncial. Developmentally, *Cadia's* petal enlargement is delayed greatly, compared to other taxa. All the petals remain the same size and shape throughout development. When the petals finally approach one another, the pattern of overlap appears to be a matter of chance, unlike the pattern in most legumes.

VERBEKE, JUDITH\* and DAN B. WALKER. Department of Biology, UCLA, Los Angeles, CA 90024

- Characterization of the mechanism underlying induced epidermal dedifferentiation in the fusing carpels of *Catharanthus roseus*.

In the process of floral ontogeny in *Catharanthus roseus* approximately 400 epidermal cells are induced to dedifferentiate during the postgenital fusion of the two carpel primordia. Previously reported experiments involving the placement of gold foil barriers between pre-fusion carpels have shown that dedifferentiation occurred only at points of direct cell-to-cell contact. The morphogenetic stimulus in this system may, therefore, consist of either a diffusible messenger molecule or some kind of cell surface interaction. To characterize the mechanics of the induction of dedifferentiation we placed adaxial surfaces and monitored epidermal development as the carpel faces grew into contact. Plastic barriers (which permitted the diffusion of O<sub>2</sub> and CO<sub>2</sub> but which prohibited the diffusion of water) blocked dedifferentiation of the contacting epidermal cells, giving a response similar to that previously reported with the gold foil barriers. Polycarbonate membranes of known porosity which can allow for passage of water soluble agents did not block dedifferentiation of the contacting epidermal cells. Thus, it appears that a diffusible agent is involved in an intercellular communication that triggers the dedifferentiation response. Current efforts are aimed at better characterizing the agent(s).

## 34 Developmental and Structural Section

WALKER, DAN B. Department of Biology, UCLA,  
Los Angeles, CA 90024  
- Assessment of positional cell differentiation  
in plants and a proposed model.

Evidence from work in my laboratory and from published reports will be discussed, and a model proposed to explain aspects of cellular pattern formation. Both descriptive and experimental data indicate that epidermal and vascular tissues have fundamentally different mechanisms of ontogeny which probably evolved independently. A model to explain the patterning of plant tissues will be proposed that incorporates these different mechanisms as key positional indicators of cell differentiation. Major tenets of the model include the following. Positional information to control when and where patterned differentiation of cells occurs results from cell-to-cell communications between adjacent and nearby cells. Diffusible morphogens effect this communication, but these morphogens are not the major phytohormones, which play only an indirect role in the process. The epidermal and the vascular tissues are the sources of these differentiation-inducing morphogens with other tissue types keying their differentiation from one or a combination of these two tissues. The major phytohormones are coordinators of long distance communication, and while their presence is necessary for growth and differentiation to occur, they do not directly function in the role of short distance positional information.

WARMBRODT, ROBERT D. Department of Botany, The Ohio State University, Columbus, OH 43210. -  
Structure of the mature leaf of *Pyrossia longifolia*--an epiphytic, polypodiaceous fern exhibiting Crassulacean acid metabolism.

The leaf of *Pyrossia longifolia* was examined by light and electron microscopy to determine the cytological characteristics and various interrelationships of the ground and vascular tissue. The succulent leaf has a reticulate vascular system embedded in mesophyll tissue that is not differentiated into distinct palisade and spongy layers. The large, isodiametric mesophyll cells each contain a thin, parietal layer of cytoplasm surrounding a large, central vacuole. The chloroplast-microbody ratio in the mesophyll cells indicates *Pyrossia* may be a high photorespirer and, thus similar in that sense to C3 plants. Mesophyll tissue is separated from vascular tissue by a tightly-arranged layer of chlorenchyma cells and an endodermis with Casparian strips. The walls of both layers of cells lack suberin lamellae. The collateral veins contain vascular parenchyma cells, sieve elements and tracheids in addition to a layer of pericycle cells. The vascular parenchyma cells, each 2-3 times larger in diameter than the sieve elements, are characterized by dense cytoplasm and chloroplasts which contain a peripheral reticulum. Parenchymatic elements are connected by plasmodesmata which lack neck constrictions or sphincters or sphincter-like structures. Cytoplasmic connections between sieve elements and parenchymatic elements are pore-plasmodesmata with wall thickenings on the parenchymatic-element side of the wall. The relative frequencies of connections between various cell types of the leaf indicate photoassimilates may move from the mesophyll to the site of phloem loading solely in the symplast or by a combination of symplast and apoplast.

WEBB, DAVID T.\*, Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, SANDRA DE JESUS and MARIO NEVAREZ, Department of Biology, University of Puerto Rico, Rio Piedras, P.R.99031.

- Further in vitro studies of cycad root nodulation. Seedlings of *Zamia furfuraceae*, *Cycas revoluta* and *Encephalartos altensteinii* were aseptically cultured in modified White's minerals plus 2% sucrose on 1.5% agar slants in 35 x 300 mm test tubes at 27C. In all cases, root nodulation did not occur in darkness. However, exposure to fluorescent light of approximately 5 klux induced root nodulation in all three species. With *Z. furfuraceae* and *C. revoluta*, light exposure caused subapical callus formation by secondary roots previously formed in darkness. This was not observed with *E. altensteinii*. Massive calluses developed from *C. revoluta* primary roots in darkness and light, but callus formation was not as extensive in light-exposed cultures. Similar callus formation was not observed with the other two species tested. Apogeotropic secondary roots developed at the junction of the primary root and cotyledonary node with *E. altensteinii* grown in darkness, but apogeotropism was not induced by light and was not observed in other tested species.

WEBB, MARY ALICE\* and HOWARD J. ARNOTT. Department of Biology, The University of Texas at Arlington, Arlington, TX 76019-0498. - Druse development in the endosperm of *Vitis mustangensis*.

An understanding of crystal development as it relates to other developmental processes in a particular tissue is an essential prerequisite to comprehending any role crystal formation may have in cellular metabolism, in addition to clarifying the role of the cell in crystal formation. In the nutrient tissues of mature seeds crystals are often found within storage protein bodies, and in some such cases crystals are very abundant. Each cell in the mature endosperm of *Vitis mustangensis* contains either a calcium oxalate druse (crystal aggregate) or a large globoid composed of mineral salts of phytic acid; both forms of mineral deposits are found within large protein bodies, and the distribution of globoid cells and crystal cells within the endosperm appears to be random. The abundance of crystal cells in the tissue make it a good system for studying crystal development and relating crystal formation to the other processes involved in seed development. At the initiation of crystal formation the cell walls of the endosperm have begun to thicken, lipid bodies have accumulated within the cytoplasm, and the central vacuole has become subdivided into several smaller vacuoles. Large amounts of endoplasmic reticulum with swollen cisternae are present, and some accumulation of protein within vacuoles is evident. There is no evidence of phytin deposition at this stage of development. Crystal formation occurs within the vacuoles in association with a complex array of organic material, including at various stages paracrystalline arrays, membranes, and fibrillar structures. Some of this material persists and is present as a central organic core in the mature druse. The organic matrix associated with crystal formation in this system will be compared to that observed in other studies of crystal development in plant cells, as well as in certain animal systems.

WESTERLING, KARIN E.\*, INDIRA J. MEHTA, and PATRICK L. HEALEY. Department of Developmental and Cell Biology, University of California, Irvine, CA 92717. - The effect of 2-(3,4-dichlorophenoxy)-triethylamine on resin canal morphology in *Parthenium argentatum*, Gray.

Parthenium argentatum, Gray (guayule), a north American desert shrub, contains large quantities of high quality rubber. Unlike Hevea, P. argentatum stores rubber within parenchymatous cells. The first appearance of rubber occurs in the epithelial cells of the primary and secondary resin canals of six to eight month old plants. The morphology of these resin canals has been previously described. Bio-regulators, such as 2-(3,4-dichlorophenoxy)-triethylamine (DCPTA), are known to increase the total rubber content of P. argentatum. Experimental P. argentatum plants were treated by spraying with a solution of 50 ppm DCPTA and 250 ppm Ortho X-77 (a wetting agent) while control plants were sprayed with the Ortho X-77 only. An analysis was made of the effects of these treatments on resin canal morphology, including resin canal number and size and epithelial cell number and size.

WILDER, GEORGE J.\* and PHILIP B. TOMLINSON.  
Harvard Forest, Harvard University, Petersham, MA.  
- Functional and systematic-anatomical studies of laminae of the Cyclanthaceae. I. Epidermis.

Cyclanthaceous laminae are normally hypostomatic and their abaxial epidermis tends to exhibit longitudinal bands either with or without stomata. In the subfamily Carludovicoideae bands of the abaxial epidermis without stomata develop over fiber bundles, abaxial ridges, and sometimes veins; bands of epidermal expansion cells, also without stomata, occur in each epidermis above or below adaxial and abaxial ridges, and over expansion tissue of the mesophyll. Stomata are either functional or nonfunctional. The pore of a functional stomate extends between inner and outer ledges of the guard cells, and consists of a one or two-chambered front cavity, back cavity, and central pore. Both guard cells of a stomate may be connected by two obvious polar perforations. Nonfunctional stomata exhibit collapsed guard cells with or without lignified walls, and sometimes also have substomatal chambers occluded by the abnormal enlargement of adjacent cells, e.g. subsidiary cells. Subsidiary cells and undifferentiated epidermal cells may overlap one another in ways that appear mechanically advantageous. Each stomate is typically associated with four subsidiary cells which may differ from undifferentiated epidermal cells according to position, shape, non-nuclear contents, nuclear size, cuticular ornamentation, and cell walls. In each subfamily epidermal cells proper may exhibit lumen papillae and also cuticular ornamentation (papillae, ridges). An epidermis sometimes has substantial dorsiventral symmetry. In addition, one can sometimes determine (a) whether a noncostal fragment of epidermis belonged to the abaxial or adaxial leaf surface, (b) what types of cells or structures it occurred over, (c) which are its proximal or distal ends and, hence, (d) its right and left sides. Systematic conclusions will be given.

WILDER, GEORGE J.\* and PHILIP B. TOMLINSON.  
Harvard Forest, Harvard University, Petersham, MA 01366.

- Functional and systematic-anatomical studies of laminae of the Cyclanthaceae. II. Mesophyll and veins.

The mesophyll contains hypodermal cells, bundle sheath cells, epithelial cells of mucilage cavities (certain Carludovicoideae), and laticifer sheaths (Cyclanthus), which exhibit common features and, hence, are categorized together as "boundary layers". The remaining cells of the mesophyll between boundary

layers comprise adaxial, abaxial, and sometimes middle regions. Depending on the species, ordinary parenchyma cells between boundary layers are either monomorphic or dimorphic; where dimorphic, one of the two types - generally, with larger and more concentrated chloroplasts - is interpreted as more specialized for photosynthesis. Within ordinary parenchyma cells, tannin or tannin-like material may comprise very elaborate star figures which are refractile in preserved material. In certain species of Carludovicoideae the mesophyll contains thin-walled dead cells, and presence of these cells is of particular interest because of the occurrence of lysigenous intercellular spaces in Cyclanthus. Fibers of the mesophyll tend to differ from phloem fibers in ways which suggest that these two cell types are specialized to contribute tensile strength and rigidity, respectively. Raphide sacs and sometimes also styloid sacs occur, and what may superficially appear as one raphide is often compound, comprised of four or more subunits. Veins of an inter-ridge area (Carludovicoideae) or between principal veins (Cyclanthus) are of different orders of diameter, and vein number increases exponentially in increasingly higher orders. The smallest sieve elements in a vein tend to be grouped into one or two poles on the adaxial side of the phloem. Systematic conclusions will be presented.

WISNIEWSKI, MICHAEL\*, A. LINN BOGLE and C.L. WILSON  
Department of Botany and Plant Pathology, University of New Hampshire, Durham, 03824. Appalachian Fruit Research Station, USDA, Kearneysville, WV 25430 -  
The Developmental Anatomy of Wound Response in Current Year Shoots of Prunus persica L. Batsch.

The ability of peach trees to effectively compartmentalize wounds may play an important role in resistance to Cytospora canker. Little information exists in this area for peach. Therefore, an anatomical investigation of wound response was undertaken. Current year shoots of three cultivars were wounded by making a scratch with a fine forceps. Samples were collected periodically and examined using light microscopy and SEM. Initial wounding penetrated into the cortex and occasionally to the vascular cambium. Within two weeks, a well differentiated wound periderm was established from undifferentiated phloem and cortical cells. Normal xylem and phloem production was replaced in a wide area of the stem by parenchymatous tissue. These cells became hypertrophied and in some areas degenerated and formed gum cysts. Phellem cells produced by the wound periderm became quickly and heavily suberized in contrast to normal epidermal cells. A region exhibiting strong autofluorescence was observed at the radial edge of the wound periderm. Within four weeks, periderm formation was initiated in uninjured portions of the stem (i.e., the wound periderm acted as a center for and instigated premature periderm development in the rest of the stem). There was also an accumulation of druses in the cortical cells of the wound area. An EDXA of these crystals identified the presence of calcium. No major differences between cultivars were observed. Observations indicate that periderm formation occurs at a relatively fast rate compared to rates reported for other species and that the degree of gum cyst or gum duct formation is proportional to the severity of the wound.

WITTNER, GEORGE H.\* and JAMES D. MAUSETH. Department of Botany, University of Texas, Austin, TX 78712. - The ultrastructure of developing latex ducts in Mammillaria heyderi (Cactaceae)  
Electron microscopy was used to investigate early

development of latex ducts in *Mammillaria heyderi* (Cactaceae). Numerous vesicles (secondary vacuoles) form from invaginations of the plasmalemma near sites of wall thinning, from endoplasmic reticulum (ER) and from older plastids. Dictyosomes, though they occur in young duct cells, do not seem to be responsible for the formation of vesicles. Cytoplasmic vesicles may contain fibrillar, globular, or crystalline materials, or may be devoid of any type of particulate matter. They may be responsible for the production and storage of numerous laticiferous components. Lysosomal materials could be stored in some vesicles and contribute to the degradation of the protoplast. Some nuclei contain condensed chromatin and are subject to deformation and collapse. Mitochondria and spherosomes are common in young duct cells but ER is rare. When ducts form in young tissues, plastids in the lumen do not produce starch grains or extensive membranous networks. The plastids eventually degenerate to become a part of the latex. If ducts form in older, established tissues having mature plastids, the plastids undergo extreme modification.

YAKAR, NEBAHAT and OLGUN, GÖKSEL. Department of Biology, University of Istanbul, Turkey. Department of Biology, University of Trakya, Turkey.  
- Comparative studies on megasporogenesis and development of embryo sac in *Digitalis davisiana* Heyw and *Digitalis ambigua* Murr.

A new species of *Digitalis* which is very similar to *Digitalis ambigua* Murr., was collected by Davis in Antalya 1947. It was described as *Digitalis davisiana* by Heywood (1949). This new species has been studied morphologically and anatomically by Tözün (1961) and karyologically compared with *D. ambigua* by Yakar and

Tözün (1966). The present investigation was undertaken to elucidate the meiotic division in megaspor mother cells and development of embryo sac of *D. davisiana* and to compare it with *D. ambigua*.

YOU, RUILIN and WILLIAM A. JENSEN\*. Department of Botany, University of California, Berkeley, CA 94720. - Ultrastructural observations of the mature megagametophyte and fertilization in wheat. The mature embryo sac of wheat contains an egg apparatus composed of an egg cell and two synergids at the micropylar end, a central cell with two large polar nuclei in the middle, and a mass of 20 to 30 antipodals at the chalazal end. A comparison was made of the ultrastructural features of the various cells of the embryo sac. The cells of the egg apparatus have walls that extend half-way along the cells starting from the micropylar end. Both synergids appear to be degenerating before pollination. The pollen tube enters one synergid through the filiform apparatus from the micropyle. The penetration and discharge of the pollen tube causes the further degeneration of that synergid. The second synergid does not change further in appearance following the penetration of the first by the pollen tube. Thus, the two synergid cytoplasms look different after pollen tube discharge. Half an hour after pollination at 20-25°C, two male nuclei are seen in the cytoplasm of the egg and the central cell. At about one hour after pollination one sperm has made contact with the egg nucleus, while the other sperm is fusing with one of the polar nuclei. The phenomena of both synergids starting degeneration before pollination and the occurrence of the large mitochondria with complicated internal organization in the antipodals will be discussed.

## ECOLOGICAL SECTION

### Symposium: New Approaches to the Population Biology and Physiological Ecology of Plants

#### INTRODUCTION

Greater understanding of plant populations in the field is being achieved through the use of both new techniques and old techniques used in new ways. For example, the movement of photosynthates between old and new ramets, and between vegetative and reproductive tissue can be examined in the field using Carbon-14 labeling techniques, and in the lab using a non-destructive procedure with gamma-emitting Carbon-11. Greater ability to determine the genetic structure of populations can be achieved using detailed analysis of electrophoretic variation to determine the paternal parent of each seed and using distinct radionuclide markers to determine the paternal parent of seedlings. Such approaches can be combined with a greater ability to quantify within population variation in such characters as plant secondary compounds and even actual DNA sequences. In this way the genetic basis of resource allocation to specific adaptations can be investigated at the population level in the field.  
Organized by Richard B. Primack, Boston University, Boston, MA.

ELLSTRAND, NORMAN C. Department of Botany and Plant Sciences, University of California, Riverside, CA 92521. - Paternal fitness and gene flow measurements using electrophoretic analysis. Although gene flow can be an important evolutionary force, realized gene flow studies of natural plant populations remain few. Electrophoretic analysis of enough polymorphic loci scored from parents and progeny permits unambiguous identification of paternal parents and thus allows precise measurement of gene flow patterns. In particular, the following correlates of paternity can be examined: (1) whether nearest-neighbor pollen flow is extensive; (2) what role genetic relatedness plays in determining paternal success; (3) whether there are within-season changes in the successful paternal gene pool; (4) whether hermaphroditic plants actually have equal fitness as male and female parents; and (5) how many fathers sire the seed set within fruits and over the total seed set of a given individual. Preliminary data from such "plant parenthood" studies will be presented.

Lincoln, David E. Department of Biology, University of South Carolina, Columbia SC 29208.  
- Individual variation of plant secondary compounds

in relation to insect herbivory and carbon allocation.

Carbon allocation and energy budgets are useful concepts for predicting and examining the responses of organisms to environmental resources and stresses. Ecological processes are potentially amenable to this approach assuming many organisms have limited carbon or energy incomes and are therefore subject to at least some constraints in the allocation of these incomes. The allocation of plant resources to defense against herbivores can be approached by focussing on variation of secondary chemical production. Recent instrumentation improvements, particularly in gas and high pressure liquid chromatography, have facilitated a shift from preference/absence information toward quantitative measurement of leaf secondary chemicals. Variation in production of such chemicals within and among plants is examined in regard to ecological constraints which may influence patterns of carbon allocation. These include conditions which may: (a) directly influence chemical production, e.g. differing levels of herbivory, (b) influence plant carbon income, e.g. physical or chemical limitations on photosynthesis, or (c) affect both budgetary components, such as leaf nitrogen content. The implications of these variations will be examined within a plant-centered consideration of current models of the "cost" of plant antiherbivore chemicals.

PITELKA, LOUIS F.\* and JEFFREY W. ASHMUN, Bates College, Lewiston, Maine 04240. -The use of carbon-14 and other radioisotopes to study resource allocation in field populations.

C-14 and other radioisotopes have long been employed to follow the movement of photosynthate or other metabolites. Experiments using such tracers can be conducted quite easily in the field on natural populations. These techniques represent a useful tool for addressing problems of interest to population biologists. For instance, C-14 may be used to reveal spatial or temporal patterns of resource allocation that are difficult to detect with biomass or calorific analyses. By labelling plants at different times in a season or by harvesting plants at increasing intervals after labelling, seasonal patterns of resource allocation and reallocation can be analyzed. Especially in perennials, the role of stored reserves vs. current assimilation in supporting new growth or reproduction may be compared. A more specific use of tracers is seen in studies of connections between plants. In clonal plants, C-14 can be used to assess the degree to which persistent connections remain active and connected ramets function as single physiological units. Functional connections may affect how individual ramets respond to competition and herbivory and how they accommodate the demands and risks of reproduction. The use of isotopes other than C-14 may show that the movement of other resources differs from that of photosynthate. Connections can also exist among unrelated plants (same or different species) as a result of root grafts or fungal associations. Radioisotopes reveal how these function. This in turn should increase our understanding of the ecologically important costs and benefits of such connections.

PRIMACK, RICHARD B.\* and CHARLES K. LEVY, Biology Department, Boston University, Boston, MA 02215. Radionuclide labeling of seeds to assess fitness in plants.

One of the primary problems in estimating individual fitness in plant populations has been the difficulty of following seeds from one generation to the next. Individual adult plants can be characterized for traits which may be related to fitness, but we have little ability to identify individuals which actually leave more surviving offspring into the next generation. In this project, we are exploring techniques for tagging seeds with selected combinations of gamma-emitting radionuclides ( $^{60}\text{Co}$ ,  $^{137}\text{Cs}$ ,  $^{54}\text{Mn}$ , etc.). These labels are not harmful to either the plants or the investigators due to the extreme sensitivity of the crystal scintillation equipment. Our preliminary studies with radishes, beans, Impatiens, Bidens, and Polygonum have shown that these labels can be injected into the stem of the adult plant and are rapidly taken up by the developing seeds. In the lab, the labels are present in the cotyledons of the young seedlings. Following dispersal and germination, the maternal parent of the seedling can potentially be identified in the field without killing the seedling by sampling a small piece of the cotyledon. This technique will potentially allow us to determine the heritability of life history characters under field conditions, changes in genotype frequency with time, the dispersal and distribution of seedling families within the population, and the longevity of seeds in the soil. The fate of introduced or novel genotypes in a population can be studied experimentally by adding labeled seeds to a population. We are determining whether this technique can be used to label pollen of different plants to determine the male parent of a seed.

SCHAAL, BARBARA A. Department of Biology, Washington University, St. Louis MO 63130.

Variation of DNA sequences in plant populations. Genetic variation among individuals is essential for the evolutionary process, yet absolute levels of variation are known for very few species. The development of nucleic acid technologies, such as restriction fragment analyses and hybridization to cloned probes, has allowed the analysis of variation in specific DNA sequences. Analysis of the DNA sequences which code for ribosomal RNA (rDNA) show variation among individuals for DNA nucleotide sequence, variation in the length of the rDNA sequence, and variation for total gene copy number. Variability among individuals within species is predominantly in the non-transcribed spacer region of rDNA. Variation among taxa occurs in the evolutionarily conservative 17 S and 26 S coding regions. These molecular data are providing precise measures of variation within and among plant species.

STRAIN, B.R.\*<sup>1</sup>, J.D. GOESCHL<sup>2</sup>, Y. FARES<sup>2</sup>, C.E. MAGNUSON<sup>2</sup>, C.E. NELSON<sup>3</sup>, C.H. JAEGER<sup>1</sup>, and E.G. BILLPUCH<sup>3</sup>. <sup>1</sup>Department of Botany, Duke University, Durham, NC 27706, <sup>2</sup>Biosystems Research Division, Texas A&M University, College Station, TX 77843, and <sup>3</sup>Department of Physics, Duke University, Durham, NC 27706. - Use of carbon-11 for continuous non-destructive monitoring of photosynthate movement.

A system has been developed at the Duke University Phytotron which allows the study of carbon flow dynamics in plants without destructive sampling of tissues. The system utilizes the short half life (20.3 min) carbon-11 isotope continuously supplied to the plants as  $^{11}\text{CO}_2$ . The isotope is produced continuously with a dedicated 4 MeV Van de Graaff accelerator in the nearby (< 100 m) physics department. As a tracer,  $^{11}\text{C}$  has several advantages. It

decays by positron ( $\beta^+$ ) emission followed by positron-electron annihilation with the emission of two oppositely directed gamma rays. These  $\gamma$ -rays have sufficient energy to be detected through several cm of tissue and/or soil. This makes it possible to perform several sequential experiments on the same plant because no destructive tissue sampling is required. The system also includes infrared analyzers and dew point analyzers so the simultaneous measurement of  $^{12}\text{CO}_2$  and water vapor exchange may be made for comparison with  $^{11}\text{C}$  net photosynthesis measurements. Comparative studies of drought stress and  $\text{CO}_2$  enrichment on Abutilon theophrasti and Gossypium hirsutum suggest basically different phloem transport systems in these two genera of the Malvaceae. Effects of environmental factors on carbon allocation and flux rates are currently being examined in  $\text{C}_3$  and  $\text{C}_4$  plants by several other scientists. The facility is part of the analytical equipment of the Duke Phytotron and thus is available to all scientists using the Phytotron.

## Symposium: Size Hierarchies in Plant Populations

### INTRODUCTION

Size frequency distributions, which are usually size hierarchies, are a fundamental but little understood aspect of plant population ecology and genetics. It has become apparent in the last few years that mean plant performance is a very crude measure of population behavior. By contrast, a Darwinian view of the population puts more emphasis on the individual, and plant-to-plant variation, which may be very great, is of much interest. There is much evidence that, within a population, plant size is related to fitness, and in natural population the few largest individuals may be responsible for virtually all the population's reproduction. When allelic frequencies among the large individuals are different from those of the population as a whole, evolutionary change will occur. Size differences may be caused directly or through variation in growth rates by factors such as age differences, genetic variation, heterogeneity of resources, interference, or the effects of herbivores, parasites or pathogens. Which of these possible factors are important in determining size differences is unknown.

This symposium will explore the causes and consequences of size hierarchies through field, experimental and theoretical studies. Organized by Jacob Weiner, Swarthmore College, Swarthmore, PA.

DOLAN, REBECCA WILCOX. Department of Botany, University of Georgia, Athens, GA 30602 and Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, SC 29801 - Size hierarchies in *Ludwigia leptocarpa* (Onagraceae).

Ludwigia leptocarpa, an annual herb of stream banks in South Carolina, developed a nearly log-normal distribution of individual plant biomass during the 1981 growing season. Fecundity was highly correlated with plant size ( $r^2=0.89$ ) so that a few large plants produced most of the seeds (5% of plants yielded 39% of the seeds). Field observations documented the development of a dominance hierarchy through time and the relative contributions of large and small plants to population maintenance. Field and greenhouse studies showed that size hierarchies are not a direct result of hierarchies in seed size and that

early germination does not assure large adult size. Common garden studies showed no difference in growth rate of offspring from large and small plants. These data suggest that size hierarchies in Ludwigia leptocarpa are largely the result of responses to microhabitat differences and do not represent a process of evolutionary importance.

HUSTON, MICHAEL A. Division of Biological Sciences, University of Michigan, Ann Arbor, MI 48109

### - The effect of fertilization on size distributions of annual plants in a plowed oldfield.

Manipulation of productivity by fertilization has a predictable effect on the community structure of herbaceous communities, but less is known about the effect of such manipulation on the population structure of the component species. Size distributions were determined for populations of 4 species of annual weeds growing in fertilized and unfertilized plots at the University of Michigan Botanical Garden. The study plots were roto-tilled to a depth of 6 inches in April 1981 and April 1982, and 2 of 4 10 x 10 m areas were fertilized with 164 kg/ha NPK 26:3:3 at the beginning of each growing season. In September 1982 a total of 128 regularly spaced 0.25 m<sup>2</sup> quadrats were clipped, and dry weight determined by species. Height and biomass were recorded for each individual of Acalypha rhomboidea, Ambrosia artemisiifolia, Amaranthus powellii, and Chenopodium album. Low productivity sites have more even size distributions of individual populations, as well as more even distributions of biomass per species.

RABINOWITZ, DEBORAH. Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853-0239.

### - Size variation in crop monocultures.

Plant form and growth patterns influence how plants interact in monocultures. For a diversity of crop architectures (grains and vegetable crops), we investigated whether leaf arrays and growth rates were important in determining dominance and suppression and the distribution of individual sizes. How size of individuals determines plant-to-plant variance in crop yield was investigated as well.

WEINER, JACOB. Department of Biology Swarthmore College, Swarthmore, PA 19081

### - Size hierarchies in experimental plant populations.

Greenhouse experiments were conducted to address some of the causes of size hierarchies (size inequalities) in plant populations. There is controversy over whether or not competition increases the degree of hierarchy within a population, i.e. whether dominance and suppression result from interference between individual plants. I performed a series of greenhouse experiments on populations of Trifolium incarnatum and Lolium multiflorum to study the effects of several variables on size frequency distributions. The following hypotheses were observed to be consistent with the data:

- 1) Size inequality increases with increasing density.
- 2) Size inequality increases with increasing productivity.
- 3) Size inequality is lower when plants are sown in a uniform pattern than when sown in a random pattern.

4) In mixtures, the competitively superior species shows a relatively low degree of inequality, while the competitively inferior species shows high inequality.

The results support the dominance/suppression model of plant competition.

## Symposium: The Mire – Wetland Ecosystem

### INTRODUCTION

Wetland and mire ecosystems possess a unique set of characteristics that differentiate these systems from both terrestrial and aquatic habitats. The abundant research that has been done in Europe in these ecosystems is in marked contrast to the state of our knowledge in North America. However, in the past decade or so, significant work has been completed in the United States and Canada. This symposium hopes to examine some of this recent research and present the status of our knowledge of these ecosystems. Organized by Dale H. Vitt, University of Alberta, Edmonton, Alberta and Bruce Roberts, Canadian Forestry Service, St. John's Newfoundland.

ANDRUS, RICHARD E. Department of Biological Sciences, State University of New York at Binghamton, N.Y. 13901.  
- The ecology of Sphagnum.

Sphagnum species are ecologically unusual and prominent wetland plants with xerophytic adaptations and succession-directing acidification capabilities. Species are differentiated along environment gradients of pH, cation concentrations, hummock and hollow, wet vs. dry, shade vs. sun, coastal vs. inland and cold vs. warm. The known factors responsible for gradient differentiation include cation exchange capacity, desiccation tolerance, desiccation resistance, water-holding capacity, drying rates and photosynthetic response at differing water contents. Small-scale distribution of Sphagnum species on ombrotrophic sites can be partially explained but for minerotrophic sites, where acid precipitation influence is greatest, less is known.

BAYLEY, SUZANNE. Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba. R3T 2N6

- Comparisons of nutrient relationships in freshwater wetlands from Canada to Florida.

Nitrogen and phosphorus dynamics in southern swamp forests and fresh water marshes are compared to northern bogs, fens, and marshes. Latitudinal differences in nitrogen and phosphorus content of vegetation, nutrient concentrations of surface and pore water, and annual nutrient uptake are not apparent in the data reviewed. Substrate and hydrologic regimes appear to be more important. Vegetation on organic substrates contains less nitrogen and phosphorus in the above ground biomass (Wigham and Bayley 1978). Cypress wetlands in higher water flow contain higher concentrations of phosphorus in above ground biomass (Brown 1981). Other wetlands appear to follow the same trend. The ability of a wetland to retain added nutrients depends upon the hydrologic regime and organic substrate.

CARTER, VIRGINIA U.S. Geological Survey, 431 National Center, Reston, VA 22092 - Wetlands of the United States - ecology, hydrology, and research needs.

The wetlands of United States can be subdivided into classes, subclasses, and dominance types on the basis of vegetation, hydrology and soils using the "Classification of Wetlands and Deep Water Habitats" by Cowardin et al. (1979). There is a tremendous diversity in wetland types and wetland vegetation in the United States, caused primarily by regional topographic and climatic differences. Wetland hydrology, a primary driving force influencing wetland ecology and wetland development and persistence, is as yet poorly understood. The interaction between ground water and surface water, and the discharge-recharge relationships in wetlands influence water quality and nutrient budgets as well as vegetative composition. Anthropogenic influences, such as construction of drainage canals, diversions, storage areas and industrial facilities, or mining of peat may have unforeseen hydrologic consequences because of our lack of knowledge of water movement and water budgets. Expanded research and basic data collection are needed to manage and protect wetlands effectively.

DAMMAN, ANTONI W.H. Ecology Section, Biological Sciences Group, University of Connecticut, Storrs, CT 06268.  
- Ecological processes in ombrogenic peat bogs

Ombrogenic peat bogs differ from soligenic and topogenic peatlands in their hydrology and associated differences in water chemistry, organic matter accumulation and vegetation. The hydraulic potential is positive in most of the raised peat mass, and water flow is primarily through the relatively undecomposed surface peat. The extreme nutrient-deficiency of ombrotrophic peat and the growth of the Sphagnum carpet create conditions for release and accumulation of elements which are fundamentally different from those on minerotrophic sites. In ombrotrophic parts of these peatlands, productivity affects peat accumulation, but on minerotrophic sites decomposition overrides differences in productivity and peat does not accumulate to any significant degree above the water level. Potassium, and to a lesser degree Ca, concentrations show seasonal fluctuations in the drainage water with high concentrations in spring and autumn, and concentrations far below that of the precipitation during the summer. Na and Mg concentrations remain 5-10 times that of the precipitation. The chemistry of bog pool water depends on the topographical position within the bog; it differs least from rain water in the pools of the center or highest part of bogs in oceanic regions.

GORHAM, EVILLE. Department of Ecology & Behavioral Biology, University of Minnesota, Minneapolis, MN 55455-0302.  
- The biogeochemistry of Sphagnum bogs.

The following topics are discussed briefly from a historical perspective and with modern examples; factors controlling peat accumulation and paludification (waterlogging, nutrient limitation, roles of climate and topography), hydrological and chemical differentiation of bog from fen plant communities (surface waters and peats, peat profiles, plants), the acidity of bog waters (sources, ion-balances, sensitivity to

## 40 Ecological Section

acid rain), atmospheric deposition (sea salt, soil dust, pollutants--radioactive fallout, heavy metals, synthetic organics), element mobility (solubility, plant uptake, gaseous cycles), retention of elements (biophile, lithophile, pollutant), chemical budgets (inputs, storages, outputs), and organic geochemistry (labile and refractory molecules, the ion-exchange complex.

The focus is upon ombrotrophic *Sphagnum* bogs with surfaces receiving only atmospheric precipitation, but comparisons will be made with minerotrophic fens receiving water that has percolated through mineral soil.

HORTON, DIANA G. Department of Botany, University of Alberta, Edmonton, Alberta T6G 2E9  
- Applicability of the Scandinavian Concept to Fen Vegetation in North America.

According to the classical Scandinavian concept, fen vegetation can be subdivided into three types: poor, intermediate and rich, with each type defined by the occurrence of a number of indicator species. The environmental factor that appears to correlate most closely with this variation in the vegetation between the different types of fens is water chemistry. A survey of the fen vegetation that has been studied in North America reveals that many of the species considered to be indicators of particular conditions, with respect to water chemistry, in Fennoscandia reflect similar habitat conditions in North America. This is particularly true of the bryophytic component of the vegetation. Therefore, the Scandinavian concept appears to be an appropriate approach to the characterization of fen vegetation in North America, at least with respect to rich and poor fens.

JEGLUM, JOHN K. Canadian Forestry Service, Great Lakes Forest Research Centre, Box 490, Sault Ste. Marie, Ontario, P6A 5M7, Canada.  
- The swamp/treed bog sequence in Ontario's Clay Belt: Classification, ecology, and management for forestry.

A program of forest ecosystem classification was developed for Ontario's Clay Belt to provide operational working groups for forest management purposes. A high proportion of the merchantable black spruce forests in the Clay Belt are on organic soils. A sample of 120 forested stands on organic soils was described for vegetation soils and other site features and analyzed using classification, ordination and discriminant programs. Four operational groups were recognized -- 'herb-rich alder', 'herb-poor alder', 'Labrador-tea', and 'leather'leaf'. The latter encompasses minerotrophic and ombrotrophic conditions. The above sequence related to decreasing pits and channels, decreasing pH and calcium of ground water and peat, decreasing peat humification, and decreasing tree growth. The types are characterized in terms of vegetation and site features. Some aspects of peatland development, including paludification, are discussed for the groups. Current forest management practices, prescriptions, and research needs are presented.

MALMER, NILS, Department of Plant Ecology, Lund University, Östra Vallgatan 14, S-223 61 Lund Sweden - Vegetational gradients in relation to environmental conditions in NW European mires.

Floristically characterized gradients related to (1) wetness of micro-sites, (2) marginal compared to central areas, (3) ombrotrophic compared to different kinds of minerotrophic areas ("poor and rich mires"), and (4) distance from sea can be recognized in all mire vegetation in NW Europe. Along all gradients variation is found in (1) course of water level, (2) origin and flow of water and (3) supply of minerals, conditions influencing the decay processes and therefore also the peat accumulation rate, the pH, the mineral nutrient supply, and the productivity. The differences between marginal and open areas might result from differences in nutrient supply (N,P,K) while the differences between "poor and rich mires" more result from differences in pH. In *Sphagnum*-dominated vegetation most floristic variation might result from effects of differences in peat accumulation rate. Other climatic conditions than supply of minerals are most important in establishing floristic differences related to distance from sea.

ROBERTS, B.A. and A.W. ROBERTSON. Nfld. Forest Res. Centre, Canadian Forestry Service, P.O. Box 6028, St. John's, Nfld., ALC 5X8.

### - Atlantic salt marshes

This paper reviews current research on the Atlantic salt marshes of Eastern Canada. Specifically, this paper discusses salt marshes in the transition zone between the Subarctic and the Boreal phytogeographic regions. These salt marshes are also the northern limit of many temperate species partly due to anthropogenic influences. The floristics, the habitats and biophysical aspects of the Atlantic marshes are described. Aspects relating to anthropogenic influences on the Atlantic marshes are discussed in the context of archeology, contemporary rural settlement and vulnerability to offshore oil development. Guidelines for environment management, protection and rehabilitation research are proposed. Such guidelines are deemed important since more than half the 33 000 ha of salt marshes in Nova Scotia have been dyked for agriculture. Most of the salt marsh habitats in Newfoundland have a high degree of domestic grazing even though the marshes are small in size and rare in occurrence. The least disturbed in terms of domestic use are the Labrador salt marshes which although grazed by migratory ducks and geese have not yet been influenced by man's activities. In addition, the Labrador salt marshes are discussed and compared to the northern marshes of Arctic Canada in terms of their ecology and development.

SHAY, JENNIFER M. Department of Botany, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2  
- Prairie marshes in Western Canada.

Freshwater marshes are dynamic ecosystems that respond to environmental changes such as periodic water level fluctuations. Delta Marsh at the south end of Lake Manitoba covers 15,000 ha with open water, channels and emergent vegetation. Dominant macrophytes include the submerged aquatics *Potamogeton pectinatus*, *P. vaginatus* and *Myriophyllum exalbescens*; the emergents *Phragmites australis*, *Typha* spp. and *Scirpus acutus*; and the wet meadow species *Scolochloa festucacea* and *Carex atherodes*. The last natural high water cycle peaked in 1955 inundating and killing thousands of ha of vegetation. Recolonisation was monitored for four years as water levels fell, by which time most areas had returned to emerg-

ent dominants. Monitoring during the ensuing 20 years recorded the spread of *Typha*, changes in density and productivity of other dominants, and minor shifts in understory species. Analysis of alterations in species composition can be used to predict vegetation responses after flooding in similar marshes. *Phragmites*, *Typha*, *Scirpus* and *Scolochloa* life cycle characteristics and biomass have been monitored in a number of sites. Variations between sites and years will be compared with data from a transect from lat 51°N to lat 56°N.

VAN DER VALK, ARNOLD G. Department of Botany, Iowa State University, Ames, IA 50011.

- Vegetation dynamics in freshwater wetlands.

Vegetation change in freshwater wetlands will be reviewed as well as theories put forth to explain it. This review will focus on two basic questions: (1) What are the mechanisms that enable the establishment and persistence of wetland vegetation? (2) What are the mechanisms that cause the composition and structure of wetland vegetation to change? A new model is presented in which all vegetation change is due to one of three phenomena or a combination of them: Gleasonian succession, maturation, and fluctuation. These three phenomena are defined and then illustrated using data from prairie glacial marshes.

## Poster Session

AARSEN† LONNIE W. & ROY TURKINGTON. Botany Dept., University of British Columbia, Vancouver, B.C. V6T 2B1.

- Temporal vegetation patterns in three different aged pastures.

Three adjacent pastures (planted in 1977, 1958 and 1939) on a farm in the lower Fraser Valley of British Columbia were surveyed periodically over a 3 year period. In each survey, species cover was recorded in quadrats and contact sampling was used to investigate temporal patterns of fine-scale association between species. Ordination of time-series percentage cover surveys showed a trend of increasing community constancy in older pastures and suggested that the three communities have a developmental relationship. Soil analyses showed little correlation with species cover and the fewest correlations in the oldest pasture. Interspecific associations in younger communities were predominantly temporary in nature while older communities had more associations which persisted essentially unchanged. This data formed the basis of a qualitative model of pasture community evolution which attributes within-community temporal changes to the selective forces accruing from biotic interactions.

ATKINS, TREVOR A.\*\* Dept. of Botany, U. of Manitoba, Winnipeg, Manitoba, R3T 2N2; PETER F. LEE, Dept. of Biology, Lakehead U., Thunder Bay, Ontario, P7B 5E1; JOHN M. STEWART, Dept. of Botany, U. of Manitoba, Winnipeg, Manitoba, R3T 2N2.

- Environmental interactions influencing the growth and development of *Zizania aquatica*.

Two sites on Lake of the Woods, Ontario were monitored

bi-weekly in the summer of 1982. Wild rice growth (density, biomass, phenophase) and tissue nutrition (9 elements) were measured through sampling in randomized complete block experiments. Water depth was used as a blocking factor in both sites: One site also included blocking on the presence of lily pad (*Nuphar*) competition. The physical environments of the two sites were monitored for water depth, water column temperature and dissolved oxygen concentration profiles; and soils for pH, conductivity, bulk density and nutrient regime. Biomass, density, and nutrient contents of competing macrophytes were also measured. The growth and development of the wild rice population was then related to its physical environment through multi-variate analysis. Growth was found to be influenced by environmental factors common to other studies. The previously unexplored interactions amongst variables yielded insight into the growth and development of wild rice. Interactions with oxygen are of significant interest.

BARNES, FAIRLEY J.\*, and GARY L CUNNINGHAM. Dept. Biology, New Mexico State University, Las Cruces, NM 88003. - Water status of dominant species in pinyon-juniper habitat types.

*Pinus edulis* and *Juniperus monosperma* have overlapping distributions in the pinyon-juniper woodland of northern New Mexico. Forty sites representing the range of pinyon-juniper habitats in the Jemez Mountains were analyzed using vegetative and physical site characteristics. Three habitat types (HT) were distinguishable primarily on the densities of mature and seedling *P. edulis* and *J. monosperma*, and secondarily on the presence of specific perennial grasses. Sites within each HT were ranked using the same criteria and six sites selected to form a presumptive moisture gradient characteristic of the woodland. Predawn leaf water potentials of *P. edulis* and *J. monosperma* did not vary significantly among the sites. This may indicate that these dominant trees are occupying microsites of favorable moisture and that their densities within the various HT's are a reflection of the availability of such microsites.

BIGLEY, RICHARD E. and PAUL G. HARRISON\*. Department of Botany, University of British Columbia, Vancouver, B.C., Canada V6T 2B1. - The population biology of two intertidal seagrasses, *Zostera japonica* and *Ruppia maritima*, at Roberts Bank, British Columbia.

Vegetative and flowering components of co-occurring intertidal populations of *Zostera japonica* Ascherson and Graebner (a recent introduction) and *Ruppia maritima* L. s.l. (more commonly found in inland brackish water) were studied in southwestern British Columbia. Results from one year of repeated mapping and examination of shoots in permanent plots on a tidal gradient showed that shoot flux, age structure, survivorship, growth of leaves and rhizomes, and seed production all were affected by the amount of exposure to the air. Plots having the greatest exposure had fewer shoots (of both species), a greater percent of shoots flowering early in the season, and lower seed production than plots with less exposure. The length of the life cycle of *R. maritima* was the same regardless of differences in exposure, while plants of *Z. japonica* subject to the longest exposure to the air initiated and ended flowering and entered a quiescent overwintering state earlier than plants lower in the intertidal zone.

## 42 Ecological Section

DOUGHERTY, KEVIN W.\* and JOHN L. VANKAT. Department of Botany, Miami University, Oxford, Ohio 45056. - Soil properties and community distributions on serpentine areas of Pennsylvania and Maryland.

Serpentine outcrops occur as a discontinuous series of ridges in southeastern Pennsylvania and northern Maryland. Soils derived from this ultra-basic metamorphic material support unusual floras and distinctive plant communities. Several hypotheses based on the physical and chemical properties of these soils have been offered to account for the distribution and diversity of plant communities on these areas. To test these hypotheses, soil samples and vegetation data were collected from eight localities representing the three major serpentine ridges in the eastern United States. Soil cores were subdivided into five depth increments and analyzed for selected physical and chemical properties. Classification and ordination of vegetation data from 67 releves were performed using the TWINSpan, DECORANA and ORDIFLEX computer programs. Classification procedures have tentatively identified four grassland and three forest community types. Preliminary results indicate correlations between ordination axes and subsoil pH, soil depth and organic phosphorous concentrations.

ELLIS, BARBARA A. Department of Botany, San Diego State University, San Diego, CA 92182 - Seedling mortality and reestablishment in an early post-fire chaparral community

Seedling mortality of two major chaparral shrub species was assessed in the first year following fire. Survival of 3-10% was observed after the first growing season. Excavation of seedlings revealed a range of root to shoot ratios of 1.0-1.2 in six month-old seedlings and 0.3-0.5 in one year-old seedlings. In the first 6 months, *Ceanothus greggii* produced sparsely branched seedling roots about 80 mm long, while *Adenostoma fasciculatum* seedling roots were somewhat shorter with profuse branching in the upper 50 mm of their extension. By the end of the first growing season the seedling root of both species ranged from 220-260 mm in length. Competition between *A. fasciculatum* stump sprouts and *C. greggii* seedlings was observed. Removal of stump sprouts significantly increased *C. greggii* seedling survival.

SMRECIU, E. ANN\* and RANDOLPH CURRAH. Devonian Botanic Garden, University of Alberta, Edmonton Alberta. T6G 2E1.

- Germination procedures for some prairie wildflowers native to Alberta.

Revegetating disturbed areas in the prairies with native plant communities requires baseline data on propagation of component species. During a 3 year study to collect these data, 46 wildflower species, representing 13 families, were examined with respect to their germination characteristics before and after pretreatments. For 19 species (largely Compositae), germination increased significantly following stratification with *Thermopsis rhombifolia* and *Allium textile* requiring mechanical scarification prior to stratification. Mechanical scarification alone increased germination of 8 species of Leguminosae. The remaining 20 species either germinated well without pretreatment or showed no appreciable effect. Of this latter group *Lithospermum ruderales*, *Musineon divaricatum* var. *hookeri*, *Opuntia polyacantha* and *Zizia aptera* germinated less than 10% regardless of technique used.

UNO, GORDON E. Botany-Microbiology Department, University of Oklahoma, Norman, OK 73019. - Buffalo wallows: habitats for weeds and wetland species in grasslands.

Oklahoma buffalo wallows are inhabited by two distinctly different assemblages of plant species every year. In the fall, a collection of winter annual weeds dominates, reproducing quickly in the spring. After spring rains fill the wallows, a collection of wetland species dominates whose flowering-fruiting season lasts through the summer. The weedy species are mostly small self-pollinating plants, with inconspicuous flowers, low pollen/ovule ratios, and small seeds. The wetland species are predominately outcrossing plants with showy flowers or inflorescences, and have relatively high pollen/ovule ratios and large seeds. Soil cores taken in the fall and early summer, 1982, differ tremendously in seed bank composition, and the seeds have different germination requirements. It is hypothesized that buffalo wallows have served as sites for the introduction of weeds and weedy species into the plains and have served as safe sites for plant species that are restricted to wet habitats.

## Contributed Papers

AARSEN, LONNIE W. Biology Dept., Queen's University, Kingston, Ontario, Canada. K7L 3N6.

- Two types of combining ability in plants:

Alternative evolutionary mechanisms of coexistence.

Recent studies suggest that selection in response to competition and other neighbour interactions (e.g. beneficence) may result in two alternative types of combining ability in plants: 1) ecological combining ability (niche differentiation) and 2) competitive combining ability (balanced competitive abilities). Selection for ecological combining ability implies an increase in total yield of a species mixture. Selection for competitive combining ability also implies an increased yield but only for the inferior component of the mixture; the superior component declines in yield so that total yield is unaffected. Competitive combining ability is a special type of combining ability which takes account of the variability which may occur in the relative contribution of the two components and is a reflection of their potential to contribute equally to the total yield. Both types of selection for combining ability are likely to operate in concert in nature. Competitive combining ability however has a special relevance to plants where frequently coexistence is incompletely explained by ecological combining ability.

AARSEN, LONNIE, W. & ROY TURKINGTON\* Botany Dept., University of British Columbia, Vancouver, B.C. V6T 2B1.

- Intraspecific diversity in natural populations of *Trifolium repens*, *Lolium perenne* and *Holcus lanatus* from four different ages of pastures.

An investigation of the range of diversity in single populations of *Trifolium repens*, *Lolium perenne* and *Holcus lanatus* from adjacent 4, 23, 42, and 60 yr-old pastures in the lower Fraser Valley of British Columbia was carried out. One hundred ramets of each species were collected from each pasture and planted in common garden conditions. The 1200 clones were assessed for a wide range of vegetative (e.g. stolon length, leaf length, plant height) and floral (e.g. flower number, peduncle length) characters. The

degree of variability within each population was large and for most characters the mean values, and the variance, decreased with increasing pasture age. It is argued that the overall high diversity has resulted from the heterogeneity of the biotic environment, and the general decrease in diversity is attributable to continuous elimination of the less fit genotypes by competition and grazing.

ACKERMAN, JAMES D.\* and ARLEE M. MONTALVO. Department of Biology, University of Puerto Rico, Río Piedras, PR 00931. -- Limitations to natural fruit production in *Epidendrum ciliare*, a tropical orchid.

Natural fruit set of *Epidendrum ciliare* (Orchidaceae) at one large population in Puerto Rico was 6 % during the first of two flowering seasons studied. The flowers are allogamous and self-compatible. They lack pollen and nectar rewards. In the second season, hand-pollinated plants produced substantially more fruits (74 % fruit set) than control groups (13 %), which suggests that the paucity of pollinations is one factor limiting natural fruit production at this population. However, other constraints are likely operating as well. Correlation analysis shows that large inflorescences have a higher percent fruit set than small inflorescences, yet most inflorescences are small. Thus, factors affecting the vigor of a plant may also contribute to the low fruit production of this species.

ADAMS, JILL D.\* Department of Botany, University of Washington, and MILTON SMITH. College of Forest Resources, University of Washington, Seattle, WA 98195.  
- Using LANDSAT images to study plant succession: A case in Hawaii.

LANDSAT images have been used for rapidly defining and classifying successional sequences on the lava flows of Mauna Loa, Hawaii. Mauna Loa, a shield-type volcano (elevation 13,680 feet), has flows of various recorded ages that extend from high elevations to sea level on both the wet and dry sides of the Island of Hawaii. Successional patterns on the flows depend primarily on the roughness of the substrate, the rainfall, and the elevation. The rougher aa flows have slower vegetation development than the smoother pahoehoe flows in all except the wettest regions. In addition, succession on aa often leads to an *Ohia*/fern sparse forest, whereas pahoehoe flows of the same age and aspect will give rise to savannah and mixed *Koa* forest. On a given flow succession proceeds more slowly at higher elevations, thus it is often possible to observe a range of successional stages by examining the changes occurring in the LANDSAT spectral signature from the top to the base of the flow.

ANTLFINGER, ANN E. Biology Department, University of Nebraska at Omaha, Omaha, NE 68182.  
- The genetic and ecological consequences of outcrossing in *Impatiens capensis*.

Because genetic transmission occurs through the process of mating, a plant's mating system has significant effects on the genotypic structure and the dynamics of evolutionary change of plant populations. The mixed mating system of *Impatiens capensis* takes the form of floral dimorphism where chasmogamous and cleistogamous flowers are produced on the same individual. To estimate the fitness of cleistogamous

(CL) and chasmogamous (CH) individuals, germination, growth and survival of seedlings in field and greenhouse populations were compared. Mean percent field germination for spring, 1982, was 63.4 for CL seeds and 39.8 for CH seeds. CH seedlings were larger in size than CL seedlings. However, under uniform greenhouse conditions, growth rates were similar in both mating types. These experiments were repeated with seeds germinated in spring, 1983. Genetic variation was assessed using starch gel electrophoresis and family-structured common garden experiments.

ARMBRUSTER, W. SCOTT. Department of Biology, University of Alaska, Fairbanks, AK 99701.  
- Phenological Organization and Pollination Ecology of the Plant Communities on South-facing bluffs in the Subarctic.

Flowering phenology and plant-pollinator relationships were observed on a series of south-facing bluffs in interior Alaska. The communities comprise a distinctive assemblage of plant and insect species; many of the species are endemics, disjuncts, or vicariants of taxa of temperate North America or Asia. The major pollinators of the zoophilous flora include solitary bees (Andrenidae, Halictidae, Megachilidae, Anthophoridae), *Bombus* (Apidae), and bee flies (Bombyliidae). Three functional flower classes were distinguished: open flowers, short-tube flowers, and long-tube flowers. Each class has a characteristic assemblage of pollinators. Overlap of flowering period among members of the same flower class was measured and compared with the overlap among members of different flower classes. Members of the open and short-tube flower classes had significantly less overlap than the null expectation, whereas long-tube flowers had more overlap. This difference may be a consequence of the fact that members of the open and short-tube classes share locations of pollen placement on pollinators with members of their own class, whereas long-tube species place pollen in 2-3 distinct locations on the pollinators' bodies.

BASKIN, CAROL C.\* and JERRY M. BASKIN. School of Biological Sciences, University of Kentucky, Lexington, KY 40506. - Germination ecophysiology of eastern deciduous forest herbs: *Stylophorum diphyllum*.

*Stylophorum diphyllum* is an herbaceous perennial of mesic deciduous forests in the eastern USA. Seeds are dormant at dispersal in spring, and dormancy is due to a rudimentary embryo which requires incubation at low moist temperatures for growth. In nature embryo elongation occurs during the cold season, and seeds germinate in early spring. A warm pretreatment is not required for subsequent embryo growth and germination. Embryos in freshly-matured seeds averaged 0.41 mm long, but after 10 w of chilling at 5 C they averaged 1.41 mm. Germination of seeds incubated continuously at 5 C began after 11 w; after 19 w 80% had germinated. Seeds chilled for 6 w germinated to 75 and 65% at daily thermoperiods of 15/6 and 20/10 C, respectively, while 12 w of chilling were required for comparable germination at 25/15 C. Seeds of *S. diphyllum* fit Nikolaeva's (1977) definition of morpho-physiological complex dormancy.

BASKIN, JERRY M.\* and CAROL C. BASKIN. School of Biological Sciences, University of Kentucky, Lexington, KY 40506. - Effect of temperature regimes during burial on dormant and non-dormant seeds of *Lamium amplexicaule* and ecological implications.

Dormant spring-produced seeds of *Lamium amplexicaule* afterripened when buried and stored over a range of temperatures, becoming conditionally dormant at low (5, 15/6 and 20/10 C) and non-dormant at high (25/15, 30/15 and 35/20 C) temperatures. Conditionally dormant seeds germinated to high percentages at 5 and 15/6 C, and nondormant seeds germinated to high percentages at 5, 15/6, 20/10, 25/15 and 30/15 C. Buried seeds that became nondormant in a greenhouse during summer were still nondormant after 12 w of storage at 30/15 C, while those stored at 5 C for 12 w were conditionally dormant. Thus, low temperatures reverse the afterripening that occurs at high temperatures, but not that which occurs both at low and at high temperatures. Low winter temperatures cause dormant autumn-produced seeds and nondormant seeds in the soil seed pool to become conditionally dormant.

BELL\*, TIMOTHY J., AND JAMES A. QUINN. Department of Biological Sciences, Rutgers University, New Brunswick, New Jersey, 08903.-Effects of soil moisture on reproductive effort and its components in the perennial grass *Dichanthelium clandestinum* (L.) Gould.

Individuals from six New Jersey populations of *Dichanthelium clandestinum* were grown in the greenhouse on a soil moisture gradient. Initial data show that total plant biomass was greatest at intermediate soil moistures suggesting that high and low soil moisture ranges were stressful to the plants. Reproductive effort, ranging from 0.5% to 9.5%, was greatest at intermediate soil moistures. Percent allocation to chasmogamy was consistently lower ( $\bar{X}=0.9\pm 0.41SE$ ) than allocation to cleistogamy ( $3.5\pm 0.51$ ) and showed a significant positive correlation with total biomass. There was a small, but significant, negative correlation between cleistogamous allocation and total biomass. Under conditions of increasing soil moisture stress in *D. clandestinum*, total reproductive effort decreases, and the allocation to cleistogamy increases at the expense of chasmogamy. This response appears to be related to the lower costs of cleistogamous seeds.

\*BERGERON, Y. and A. BOUCHARD. Centre de recherches écologiques de Montréal et Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succ. A, Montréal, Québec, H3C 3J7. - Use of ecological groups in analysis and classification of plant communities in a section of western Quebec.

Plant communities analysis and classification were done for an integrated ecological study, in the lake Abitibi region, Quebec. Two levels of vegetation analysis were used: the ecological group level and the community level. Species were first grouped according to their sociological affinities. The ecological significance of those groupings was studied by principal component analysis, with the inclusion of abiotic variables, and by the study of ecological profiles. Secondly, the concurrent use of

ecological groups permitted the definition and characterisation of *noda*. The relationships between the *noda*, in the space defined by the ecological groups, were analysed by principal coordinate analysis on which is superimposed the shortest spanning tree. Those combined analyses permitted the determination of 35 community types which vary mainly according to the surficial deposits (organic or mineral), the drainage, the relative richness of soils in bases, the submersion, the presence of bedrock outcrops, the fire perturbations and the microclimate.

BERN, CHRISTINE M. Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132.

- Factors influencing the distribution of *Calamagrostis ophiditis*, a serpentine endemic.

*Calamagrostis ophiditis* is a serpentine endemic bunchgrass restricted distributionally to northern California. It is found generally in chaparral or in open grassy areas in shallow soils, and occurs rarely in deeper serpentine derived soils. This study is concerned with relative roles of biotic and physical factors influencing this pattern of distribution. Possible interspecific interference was examined using replacement series design experiments. *Calamagrostis ophiditis* was paired against two dominants from adjacent, deeper-soil serpentine areas, *Stipa pulchra* and *Festuca idahoensis*. Pairs were grown under greenhouse conditions reciprocally in three field-collected soils with six nutrient treatments. These results are compared to a preliminary field experiment of reciprocal transplants in a similar replacement series design. Initial data show *C. ophiditis* distribution is not correlated to the soil's calcium/magnesium ratio, but to areas of moderate to moderately-high levels of magnesium.

BERRY, PAUL E. Dpto. de Biología de Organismos, Univ. Simón Bolívar, Apartado 80659, Caracas 1080, Venezuela.

- Reproductive biology of five high elevation species of *Espeletia* (Compositae) from the Venezuelan Andes.

The breeding systems, phenology and pollination systems of five high altitude species of *Espeletia* (sensu lato) were investigated in a Venezuelan páramo. All species are monoecious and are adapted for obligate outcrossing through the possession of genetic self-incompatibility. Natural seed set varies from 35% in high elevation populations of *E. mortiziana* to 90% in the widespread *E. schultzii*. Each species has a distinct flowering peak but flowers over a 2-3 month period with sufficient overlap to allow simultaneous flowering of 4 species. Time from anthesis to seed dispersal is correlated with average plant size and altitude, lasting from 2 to 5 months in different species. No pollinators were observed on *E. moritziana* or *E. timotensis*, and the possibility of wind pollination is being investigated. *Espeletia schultzii*, *E. batata* and *E. floccosa* are widely pollinated by hummingbirds (*Oxyptogon*), bumblebees and other bees or Diptera, depending on weather conditions and density of flowering individuals.

BILDERBACK, DAVID E., CLINTON E. CARLSON, J. HENRY SLOANE and STEPHEN C. MARVEL. Department of Botany, University of Montana and Forestry Sciences Laboratory, U.S. Forest Service, Missoula, MT 59812.

- The effects of ash from Mount St. Helens on chlorophyll content, photosynthesis and radial stem growth of Douglas fir (*Pseudotsuga menziesii*).

During the eruption of Mount St. Helens on May 18, 1980, a forest site south of Coeur d'Alene, Idaho received 1.0 cm or more of ash. Needles of Douglas fir at this site retained 422 mg of ash/gm needle dry weight during the summer and fall of 1980. Trees northeast of Coeur d'Alene received a light dusting of ash. Chlorophyll content and radial growth of trees were compared at the two sites. Chlorophyll content of 1979 and 1980 needles heavily coated with ash was significantly less than the chlorophyll from needles lightly dusted with ash. There was no significant difference in the chlorophyll content of 1981 needles or the radial stem growth. Seedlings of Douglas fir were artificially dusted with ash. Eight weeks later, needles had significantly less nonstructural carbohydrates than did needles of undusted plants. Ash-coated and control seedlings had similar dark respiration rates, compensation points and light saturation levels; however, ash-coated seedlings exhibited an enhanced photosynthetic rate.

BRADFELD, GARY E. and DANIEL GAGNON. Department of Botany, U.B.C., Vancouver, BC V6T1W5; Departement des Sciences biologiques, Universite du Quebec a Montreal, Montreal, PQ H3C3P8.

- Correlations among strata and environmental gradients in forests of Vancouver Island, B.C.

West central Vancouver Island vegetation data were used to investigate if forest strata patterns (trees, saplings, seedlings, shrubs, herbs and bryophytes) are correlated and if these strata respond similarly to environmental gradients. These hypotheses were evaluated with three data sets: (1) a moist coastal sector of the study area, (2) a dryer inland sector, and (3) a combined data set to provide greater environmental diversity. Product moment correlations and cononical correlation analyses were used to assess the degree of correlation among strata, and with environmental gradients. Patterns of correlation were different in each sector, with different strata showing the strongest correlation among them, as well as with environmental gradients.

BRUEDERLE, LEO P.\* and FOREST STEARNS. Biological Sciences (Botany), Rutgers University, New Brunswick, NJ 08854 and Department of Botany, University of Wisconsin, Milwaukee, WI 53211. - Ice storm damage to a southern Wisconsin mesic forest.

In January 1976, an ice storm followed by strong winds struck southern Wisconsin. This storm deposited up to 12 cm of glaze causing substantial damage to wooded areas. At the UWM Cedar-Sauk Field Station a forest fuel sampling technique was modified to measure macro-litter volume by species resulting from the storm. Changes in the canopy were photoassayed using wide-angle and fish-eye lenses. The storm resulted in 19.1 m<sup>3</sup>/ha macro-litter with approximately 43 percent of the canopy removed. Damage was uneven, influenced by geographic and climatic factors. Wind and aspect of slope were found to be of particular

importance with macro-litter volume varying from 22.6 m<sup>3</sup>/ha on the windward slope to 10.4 m<sup>3</sup>/ha on the leeward. *Ulmus rubra* and *Fraxinus americana* suffered the heaviest damage and *Ostrya virginiana* and *Tilia americana* the least. Biotic factors responsible for species susceptibility include growth form, wood mechanical properties, age, decay, and phytosociological position.

CARTER, M. ELOISE BROWN\* AND WILLIAM H. MURDY. Biology Department, Agnes Scott College, Decatur, GA 30030 and Biology Department, Emory University, Atlanta, GA 30322.

- Character Displacement in *Talinum mengesii* (Portulacaceae).

Character displacement was investigated in populations of *Talinum mengesii* and *T. teretifolium*, which were sampled from granite outcrops along a 100 mile transect, including both sympatric and allopatric populations. The results from analysis of floral traits, diurnal flowering times, heritability estimates, and experiments in the field, greenhouse and laboratory supported the hypothesis of unilateral reproductive character displacement in *T. mengesii*. The sympatric populations exhibited large flowers with long, exerted styles and early flower opening; characteristics which were shown to be important in reducing interspecific hybridization. Heritability estimates for the displaced traits were greater than 75%. Exerted styles in the sympatric populations resulted in a primarily outcrossing breeding system requiring insect-assisted pollination. Reproductive losses in these plants during periods of low pollinator activity may be compensated by a large number of ovules and extensive vegetative reproduction.

CAZA,\* CAROLINE L. and PAMELA M. STOKES. Department of Botany, University of Toronto, Toronto, Ontario, M5S 1A1.

- Variation in the distribution of *Populus tremuloïdes* on an unamended uranium tailings site, Ontario, Canada.

Spatial variation in the biotic and abiotic environment was studied in the biotic and abiotic environment was studied in an aspen population on an unamended uranium tailings site near Bancroft, Ontario. The site was divided into four zones based on type of ground cover. Vegetation and substrate characteristics were measured within each zone. Principal components analysis was used to summarize physical, chemical and biological differences between zones. The distribution of aspens on the site was correlated with substrate characteristics such as elevation, temperature, moisture and nutrient content. Other parameters displayed large variation within the site but were not related to aspen distribution. Additional data were collected from aspen populations on non-tailings (reference) sites. There was no indication of differences in factors influencing distribution between uranium tailings and these substrates. All physical and chemical factors measured on the tailings were within ranges reported for natural substrates. It is suggested that large variation in these factors, occurring over small distances on the tailings, is the most important determinant of aspen distribution on these wastes.

CID-BENEVENTO, CARMEN R.\*, and PATRICIA A. WERNER. Kellogg Biological Station, Michigan State Univ., Hickory Corners, MI 49060. - Experiment on the relative effects of light and soil moisture on germination, survivorship and reproduction of old-field and woodland annuals.

Seeds of two old-field (Chenopodium album, Polygonum pensylvanicum) and three woodland annuals (Acalypha rhomboidea, Pilea pumila, Impatiens capensis) were sown in a greenhouse in all combinations of six light levels (from 2%-100% of incoming sunlight) and three soil moisture levels (different sand:soil ratios). Germination, survivorship, plant size and total reproduction were monitored. Woodland annuals had higher germination and survivorship than old-field annuals for all treatment combinations, except those with 100% light. Light had no effect on germination of old-field annuals but high light significantly decreased germination of woodland annuals. Soil type had no effect on germination. Survivorship, seed production and size were greatest at intermediate light levels for both groups but the breadth of the peak varied between groups. Differences among light treatments in the seed production:emergent seedling ratio for both groups, and differences between groups in seed dormancy seem most important in explaining their distribution.

Clay, Keith. Department of Botany, University of Texas, Austin, TX 78712.

- Symbiotic mutualism between grasses and fungi.

Survival, growth, and reproduction of ramets of the grass Danthonia spicata (L.) Beauv. infected by the systemic ascomycete fungus Atkinsonella hypoxylon Diehl were compared with noninfected ramets in one natural population. D. spicata bears dimorphic chasmogamous and cleistogamous flowers normally but infected individuals bear only cleistogamous flowers. Grasses not bearing similar cleistogamous flowers are rendered sterile by infection by related fungi. The survival and growth rates and long-term reproductive rates of infected ramets were higher compared to noninfected ramets. The relationship between D. spicata and A. hypoxylon is therefore mutualistic rather than parasitic as has been reported in the literature. Other grasses (Cenchrus and Agrostis) are sterilized by infection but show increased vegetative vigor suggesting beneficial interactions between grasses and fungi are more widespread than previously realized.

CODY, MARTIN L. Department of Biology, University of California, Los Angeles, CA 90024

- Multiple influences on cactus branching patterns.

The branching patterns of columnar cacti were investigated in the Sonoran Desert (Baja California, Sonora and Arizona) and in adjacent thorn scrub and Mediterranean-climate coastal scrub. Within communities at a site species segregate by branching pattern, with species of larger stem radius taller and less branched. Photosynthetic area per unit volume scales as the inverse of stem radius, but capacity for rapid water uptake is proportional to stem radius and rib number. At higher latitudes both low temperature and

low light may affect branching, and stem radius, but at lower latitudes water availability is a predominant influence. Root systems apparently overlap between species within sites, but species with large stem radius appear to be shallow rooted and those of small stem radius deeper rooted. Climatic factors, local environmental factors, and biotic factors all influence branching pattern, with a major role played by the presence of other species.

Colosi, Joe C., and P. B. Cavers, Biology Dept. Allentown College of St. Francis de Sales, Center Valley, PA 18034 and Dept. of Plant Sciences, University of Western Ontario, London, Canada N6A 5B7

- Biotype by environment effects on winter seed survival.

At least six biotypes of proso millet (Panicum miliaceum) are weeds of corn in southern Ontario. A black grained biotype is spreading faster than the others. We tested the idea that this difference is due to greater dormancy and winter survival of the black grains. In November 1981, grains of the six biotypes were sown at three soil depths: surface, 5cm and 20cm. They were retrieved in April and June 1982. Ungerminated grains were germinated in an incubator or tested for viability with tetrazolium. Over 50% of the black grains were viable but dormant in June while most grains of the other biotypes were germinated or dead. Grains at the 5cm depth had the lowest dormancy and also the lowest survival of the three depths. We conclude that the higher grain dormancy and winter survivability of the black grained biotype contribute to its faster expansion.

FLINN, MARGUERITE A.\*, SHARON E. FISHER, EARL V. MARTIN. Mount Saint Vincent University, Halifax, N.S. B3M 2J6.

- Seasonal nonstructural carbohydrate composition of rhizomes of forest understory species.

Rhizomes of eight forest understory species were analyzed seasonally (spring, summer and autumn) for percent total nonstructural carbohydrate (% TNC) by determining the individual components: starch, fructosans, free reducing sugars and sucrose. Species studied were: Maianthemum canadense, Pteridium aquilinum, Cornus canadensis, Rhododendron canadense, Kalmia angustifolia, Vaccinium angustifolium, Gaultheria procumbens and Chamaedaphne calyculata. The technique used was a modification of the Soxhlet alcohol extraction (Heinze and Murneek 1940) and enzyme hydrolysis with takadiastase (Smith 1969). Results generally showed more % TNC in autumn than in spring and summer. Data indicated that the highest single nonstructural carbohydrate was the percent starch found in all species except for that found in M. canadense. In this species the percent fructosans was highest (51%). The amount of free reducing sugars was less than 4% in all species and sucrose was found in the least percent (1.5%). Ecological implication and recovery after fire will be discussed.

GAGNON, DANIEL and GARY E. BRADFIELD. Département des Sciences biologiques, Université du Québec à Montréal, Montréal, PQ H3C 3P8; Department of Botany, U.B.C., Vancouver, BC V6T 1W5.

- The vegetation of west central Vancouver Island, B.C.: a gradient analysis.

Forests of the study area are dominated by Thuja plicata near the coast, and increasingly by Pseudotsuga menziesii progressing inland. The vegetation and soils were sampled in 172 plots to determine which environmental gradients could explain the observed patterns. Following successive reciprocal averaging ordinations, six distinct vegetation groups and 24 community types were defined. An ordination (RA) of only the modal communities suggests that the predominant vegetation pattern is under control of a "complex" precipitation - continentality climatic gradient. Variables strongly correlated with the ordination's major axis were: positively, distance from the coast and fire disturbance, and negatively, wind disturbance and thickness of organic horizons/rooting depth ratio. Vascular species richness also increased with distance from the coast.

GALEN, CANDACE. Department of Botany, University of Texas, Austin, TX 78712

- Ants, bumblebees, and seed production in floral scent morphs of *Polemonium viscosum*.

Plants of *Polemonium viscosum* have flowers which are either sweet or skunky-scented. The effects of bumblebee pollinators and ant nectar thieves on seed-set in these morphs were examined at 3528 m and 3640 m in alpine Colorado. The following patterns were found.

Bumblebees accounted for 90% of the total pollination at 3640 m, but only 50% of that at 3528 m. No differences in average seed-set of sweet and skunky morphs resulted from bumblebee visitation at either altitude.

Ants reduced seed-set of sweet flowers at both locations by negating the pollination effectiveness of bumblebees. Damage to floral tissues by ants prevented subsequent fertilization or survival of ovules. Ants did not alter seed-set of skunky flowers.

Activities of bumblebees and ants are therefore likely to influence success of *P. viscosum*. While ants may have significant effects on frequencies of floral morphs at both altitudes studied, similar conclusions cannot be drawn about bumblebees from this experiment.

GOVIL, SUDHA R. AND HARENDRA N. PANDEY.\*  
Department of Botany, Banaras Hindu University, Varanasi - 221005, India.

- Studies on the crop-weed interaction.  
The interaction of *Cyperus rotundus* (weed) with wheat and maize crops was studied at three densities and five ages under field conditions. There was 37-40% reduction in the weed density as the number of crop plants (27 to 81 plants m<sup>-2</sup> in wheat and 4.5 to 13.5 plants m<sup>-2</sup> in maize) increased in the experimental plots. In wheat - *Cyperus* interaction, peak values of dry weight, leaf area, chlorophyll and N, P, K contents of the crop and weed plants showed 45-74% and 6-17% reduction respectively. Similarly in the maize-*Cyperus* interaction, the crop suffered more (17-75%) than the weed (8-43%). During the

cropping cycle, in both maize and wheat fields, weed parameter values were higher relative to corresponding measures for crops in the earlier phases for dry matter production, leaf area index and standing crop of chlorophyll. The trend, however, was reversed at the later ages due to suppression of weeds by the crop, and the onset of weed's senile stage. It is concluded that this serious perennial weed is equally harmful to both rainy and winter season crops and increasing density of crop plants proves to be more harmful for themselves than to the weed.

\*Department of Botany, U.P. College, Varanasi-221002, India.

GROVE, KATHRYN F. Department of Botany, University of Iowa, Iowa City, IA 52242.

- A cryptic stylar outcrossing mechanism in an autogamous tropical herb.

The stigma of *Spigelia humboltiana* Cham. & Schlechter (Loganiaceae) has a proximal region which is self-pollinated before anthesis and a distal region which may receive cross pollen. Thus, cross pollen appears to have a twofold disadvantage: it arrives on the stigma after self pollen and further from the ovary. Fluorescence microscopy was used to discover whether these apparent disadvantages to cross pollen are compensated for by differences in the timing of germination or pollen tube growth of cross vs self pollen. Studies of open- and hand-pollinated flowers reveal that: 1) pollen does not germinate on the selfing region of the stigma until about 5 hours after anthesis; 2) pollen on the stigmatic tip, however, germinates promptly; 3) the earlier cross pollen arrives on the stigma, the greater are its chances of growth beyond the selfing region before self pollen germination; 4) some natural cross-pollinations are ineffective because pollen arrives too late; 5) there are no differences in self and cross pollen tube growth rates. Cryptic stylar outcrossing mechanisms may occur in other autogamous species.

HANYCH, DAVID A. Dept. Ecology & Behavioral Biology, University of Minnesota, Mpls., MN 55455.

- The relation of seed size and seed weight to seed set in the white campion, *Lychnis alba* (Caryophyllaceae).

Mature *Lychnis alba* capsules were randomly and selectively collected from an old field population during two sampling years (1981 & 1982). The mature seeds from each capsule were dried to constant weight and then sized by measuring the axis parallel to the hilum using a dissecting microscope equipped with an ocular micrometer. A significant positive correlation was documented between mean seed size and mean seed weight on a per capsule basis during both sampling years. However, both mean seed size and mean seed weight were inversely related to the number of seeds per capsule during both years. Similar statistically significant trends were observed among capsules collected from individually marked plants during 1982. Since seed weight may be considered a measure of the energetic investment in a seed by the plant, the variance in relative investment per seed as a function of capsule seed number may reflect a reproductive effort characterized by variable resource allocation to seeds within individual fruits.

## 48 Ecological Section

HAYNES, JARED\* and MICHAEL R. MESLER. Department of Biological Sciences, Humboldt State University, Arcata, CA 95521.

- Pollen foraging by bumblebees: foraging patterns and efficiency on *Lupinus polyphyllus*.

Bumblebees foraging on vertical inflorescences start near the bottom and work up, behavior commonly interpreted as a response to greater amounts of nectar available in lower flowers. *Lupinus polyphyllus*, which produces no nectar, has more pollen available in upper flowers. Although bees are probably unable to detect any gradient, since pollen is hidden in each flower's keel, they still start low and forage up. Therefore we concluded that the bees' tendency to forage upward on vertical inflorescences is not tied to a reward gradient. In addition, bees use only about 15% of the flowers per inflorescence, although they could be much more efficient by visiting and revisiting every flower systematically. In general, revisits would not be penalized because only a small portion of the pollen in a keel is dispensed at each visit. Such gross inefficiency may be explained as a transferal of efficient nectar-gathering behavior patterns to pollen inflorescences.

HERNANDEZ, HELIOS. 16 Valleyview Drive, Winnipeg, Manitoba, Canada, R2Y 0R6.

- Effects of winter roads on terrain and vegetation: Initial response and subsequent recovery.

Three winter road test sites were examined in 1981: summer 1, ice-aggregate work pad, Quill Creek, Yukon; summer 9, ice-capped snow road and ice road, Norman Wells, N.W.T.; summer 8, snow road, Inuvik N.W.T. Initial responses at Quill Creek were similar to those at Norman Wells in 1973 (Arctic 30(1): 13-27 (1977)) and at Inuvik in 1974 (Proceedings Third International Permafrost Conference (1978), Edmonton: 481-486). Total live plant cover was greatly reduced and peat bulk density increased. Thaw depth response differences between sites are attributable to canopy density differences and subsequent site history. Recent winter use of the Norman Wells site retarded recovery. Recovery at Inuvik, however, continued. The shrub layer was well developed and ground cover extensive. When compared to adjacent, unprotected, similarly-disturbed areas, properly built and maintained winter roads can protect underlying terrain and vegetation.

HOGG, E.H. & J.K. MORTON, Department of Biology, University of Waterloo, Ontario, Canada, N2L 3G1.

The Effects of nesting gulls on the flora, vegetation and soils of islands in the Great Lakes.

Nesting Ring-billed and Herring Gulls were observed to have a profound effect on the flora, vegetation and soil of Barrier Is. (a limestone island in Georgian Bay) during a 4-year study period. Annual aliens dominated the nesting site and native species were almost eliminated. Nutrient levels in the soil increased dramatically. The gulls commute from the island to the mainland to forage on garbage dumps and arable land. They are effective agents of dispersal for weed seeds which grow successfully in the disturbed nutrient-rich soil of nesting sites. Succession in the vegetation of abandoned nesting areas was characterized by a rapid decline in annual aliens as perennial native grasses become established. Nutrient levels in the soil rapidly

returned to near normal except for phosphorus which persisted at high levels. After 4 years, species composition in the regenerating vegetation was still very different from that in undisturbed areas.

HOPKINS, DALE R. AND V. THOMAS PARKER\*.

Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132.

- Seedling emergence and the seed bank of a salt marsh in northern San Francisco Bay.

Abundance, species composition and distribution of buried seeds in a San Francisco Bay salt marsh were studied by collecting soil samples in October and February and observing seedling emergence in the greenhouse. Results were compared with existing vegetation patterns and field germination. Average numbers of buried viable seed down to a 5 cm depth were 380/m<sup>2</sup> in October and 700/m<sup>2</sup> in February, with field germination averaging 118/m<sup>2</sup>. *Salicornia virginica* dominated the seed bank in the greenhouse and in the field germination. Most other marsh species were present in the seed bank but numbers of seeds were low. A significant correlation was found between highest species diversity and proximity to intramarsh channels. The nature of the seed bank reflects the dominance of perennial species, seed dispersal patterns, tidal influence and selective environmental pressures.

HURT, VALINA KAY. Department of Botany-Microbiology, University of Oklahoma, Norman, OK 73019. - Allelochemic effects on the growth of *Thiobacillus ferrooxidans* Temple and Colmer, a bacterium involved in acid mine drainage.

Acidic water drainage with a pH as low as 2.2 is common for strip mine areas. This acid mine water is partially due to the bacterium, *Thiobacillus ferrooxidans* Temple and Colmer which oxidizes iron pyrite. This bacterium is an obligate chemolitho-autotroph. Any chemical inhibition of this species might prove to be an important management tool in reclamation. This study showed inhibition of *T. ferrooxidans* growing in *T. ferrooxidans* media by sterile dilute extracts from leaf and litter leachates and root exudates of 100%, 80%, 60%, 40%, and 20% concentrations. Distilled water was used as the control. A total of 47 orphan coal strip mines were surveyed. Sixty-three tree species of 43 different genera were examined. Extracts from the following species inhibited *T. ferrooxidans* growth: *Acer saccharinum*, *A. negundo*, *Celtis laevigata*, *Juglens nigra*, *Platanus occidentalis*, *Quercus marilandica*, *Q. falcata*, and *Q. stellata*. Abandoned coal strip mines having a combination of these species have lower populations of the bacterium.

KEDDY, CATHY J. 644 Chapel St., Ottawa, Ontario, K1N 7Z9.

- 60 years after Fernald- *Sabatia kennedyana* and *Coreopsis rosea* in southwestern Nova Scotia.

About 60 years ago, M.L. Fernald discovered a disjunct occurrence of Atlantic Coastal Plain species in

southwestern Nova Scotia. Two of the rarest of these species are Sabatia kennedyana and Coreopsis rosea found only in the Tusket area of Yarmouth Co. In the summer of 1982, this area was explored to obtain information on abundance, distribution and threats to these species. Both were found on gently sloping, sheltered, gravel and peat lakeshores which are alternately flooded and exposed with fluctuating river levels. During low water years, these species flower (July to Sept.). As well, they reproduce by stolons or rhizomes. S. kennedyana occasionally forms dense colonies (two bays had more than 1000 plants in flower). C. rosea was restricted to two lakes through which the Tusket R. flows plus one that drains directly into it. S. kennedyana occurred in six lakes forming part of a 30km stretch of the river and two lakes draining into it. When Fernald collected in 1920 and 1921, both species were also present in the lowest lakes in the Tusket and Carleton river systems, but have since been eliminated from the lower Tusket (and probably Carleton) lakes because they have been turned into reservoirs for the Tusket Falls generating station. In the remaining lakes, the major threat to both species now is cottage development accompanied by vehicle traffic along the shoreline during low water periods. Some of the largest populations of S. kennedyana and the largest population of C. rosea occur on shorelines which are already heavily cotted.

KEELER, KATHLEEN H. School of Life Sciences  
University of Nebraska, Lincoln, NE 68588-0118  
- Plants with Extrafloral Nectaries in Ecosystems Without Ants

Extrafloral nectaries are plant glands which secrete water, sugars, and amino acids present anywhere except in the flower. These secretions attract numerous nectar-feeding insects other than pollinators. They have been repeatedly shown to be the site of ant-plant mutualism: plants are protected from herbivores by ants while the ants receive food. Since there are no ants native to Hawaii, it was hypothesized that none of the endemic plants would have extrafloral nectaries.

Thirty-one of 614 species growing in Hawaii Volcanoes National Park have extrafloral nectaries. Ten of these are of pantropic distribution or were introduced by the Polynesians, 19 are recently introduced exotics and 2 are endemics. Acacia koa, (Fabaceae) and Pteridium aquilinum var. decompositum (Polypodiaceae) are the endemics with functional extrafloral nectaries. Two species which produce extrafloral nectar elsewhere, Passiflora foetida and Ipomoea indica do not secrete nectar in H.V.N.P. The abundance of EFN-plants in H.V.N.P. communities is low: except for koa-dominated sites, cover by plants with extrafloral nectaries was less than 3%. It is impossible to evaluate the complete flora of the Hawaiian islands but plants with EFNs occur occasionally in additional endemic species, e.g. Ipomoea tuboides (convolvulaceae), and Hibiscus (Malvaceae), and an endemic genus, Kokia (Malvaceae). Despite this, frequency of plants with extrafloral nectaries is very low in Hawaii compared to other floras. It is hypothesized that plant species evolving in Hawaii tended to lose nectaries, but that a few species established mutualism with some, presently unknown Hawaiian invertebrate.

LABOVITZ, MARK L., ROBIN BELL\*, AND EDWARD J. MASUOKA. NASA/GSFC, Code 922, Greenbelt, MD 20771. -Delay of winter dormancy recovery in Quercus spp. associated with anomalous soil mineralization.

Vegetation growing in mineralized versus non-mineralized soil was examined in early Spring for the potential of using remote sensing techniques to discriminate the two environments. Two test sites, located in the Mineral Sulphide District, Louisa County, VA, differed only in that one was situated on a mineralized contact. At both sites, 16 trees (Quercus spp., predominantly Q. alba L.) arranged in a 4x4 matrix, were observed repeatedly during recovery from winter dormancy. As buds broke, the percentage of burst versus closed was tallied. During leaf flush, nominally 50 measurements per tree of the maximum blade lengths both parallel to and normal to the midvein were collected. Results show 1) the percentage of buds burst remained higher at the non-mineralized site for more than two weeks after observable recovery from dormancy had begun; and 2) non-mineralized leaves possessed a greater surface area for a period of at least two weeks.

LACEY, ELIZABETH P.\* AND CINDY CAPPS Department of Biology, University of North Carolina, Greensboro, NC 27412 - Latitudinal variation in seed viability in Daucus carota.

Daucus carota grows in old fields and along roadsides from Georgia into southern Canada. Seed tests both indoors under controlled conditions and outdoors in experimental plots show that southern populations set fewer viable seeds than do northern populations. Tests of seeds produced in reciprocal transplant plots in North Carolina and Michigan indicate that these differences are environmentally rather than genetically based. Developing seeds in southern populations appear to suffer more insect damage, suggesting that biotic factors may help regulate population size more in the southern part of the species' range.

LECHOWICZ, MARTIN J. Department of Biology, McGill University, Montreal, Quebec, Canada H3A 1B1 - The defenses of deciduous trees against defoliation by the gypsy moth, Lymantria dispar  
From 1979 through 1981 I studied the leaf characteristics of 14 deciduous tree species in a southern Quebec forest in relation to their utilization by gypsy moth. Traits that might influence host selection by gypsy moth were monitored: leaf phenology, toughness, water content, nitrogen concentration, tannin and phenolic concentrations, and leaf acidity and buffer capacity. Defoliation was higher on tree species that have more tender, nitrogen- and water-rich foliage during the period of larval dispersal in early spring. Since these qualities favorable for gypsy moth larvae diminish rapidly with leaf age, trees that leaf out relatively early escape serious defoliation. Defoliation levels among trees leafing out later are mediated at least in part by leaf chemistry. Defoliation is less on trees with young leaves that have relatively high concentrations of condensed tannins and greater on trees with acidic young leaves rich in phenolics and hydrolyzable tannins but poor in condensed tannins.

## 50 Ecological Section

LEE, PETER F. Department of Biology, Lakehead U., Thunder Bay, Ontario, P7B 5E1. STEWART\*\* JOHN M. Department of Botany, U. of Manitoba, Winnipeg, Manitoba, R3T 2N2.

- Selected environmental characteristics of commercial wild rice stands in NW Ontario and NE Minnesota.

Before optimizing the commercial management of natural wild rice stands, the ecological relationships of wild rice should be understood in terms of their biological, chemical and physical requirements. 71 commercial stands were sampled between late July and mid August during peak biomass. Observations and determinations were made on plant density, seeds per panicle, seed length, dry weights of plant organs and plant tissue, water and sediment analyses of Fe, Mn, Zn, Ca, Mg, K and P concentrations. Chemical characteristics indicate that wild rice grows in either soft or moderately hard waters and within aerobic to anaerobic moderately acid sediments. The elemental concentrations of wild rice leaves are similar to those found in other macrophytes, except for P, which was below normal. Plant tissue concentrations were poorly correlated with the corresponding elemental concentrations in sediments. Changes in water depth (0.42-1.20m) from year to year are thought to be responsible for the fluctuations in the size of commercial harvests.

LIEFFERS VICTOR J.\* AND JOHN S. CAMPBELL.  
Department of Biological Sciences, University of Lethbridge, Lethbridge, Alberta Canada T1K 3M4  
-Productivity of *Populus tremuloides* in even-aged stands in northeastern Alberta.

The circumference at breast height was measured on all trees, in 20 X 20 m plots, in 39 even-aged *Populus tremuloides* stands. Increment cores or cross-sectional discs were collected from 10-15 randomly selected trees. For each of these trees, the radial increment for five years preceding the current year was determined. In each stand, the increment in radius of each tree was proportional to the circumference of that tree. Using this relationship and the mean circumference of all the trees in the plot, the mean change in basal area and biomass for the entire stand was determined by double sampling by regression. Stands ranged from 21 to 55 years old. The mean change in biomass per tree was greatest in the older stands and stands with low stem density. Aboveground net production varied from 1.1 to 4.7 t/ha/yr, which is lower than values reported for the Great Lakes area.

LINK, STEVEN O.\* and THOMAS H. NASH III.  
Department of Botany and Microbiology,  
Arizona State University, Tempe, AZ. 85287.  
- A mathematical model of lichen gas exchange based on laboratory data for the prediction of field data.

Laboratory data consisted of net CO<sub>2</sub> gas exchange at several levels of light and temperature while thalli dried from full saturation. Estimates of internal CO<sub>2</sub> were derived from drying curves by considering resistance to be proportional to water content. Parameter estimates include a light use efficiency of 0.022 mmole CO<sub>2</sub> mE<sup>-1</sup>, an energy of activation for carboxylation of 59000 J mole<sup>-1</sup>, an energy of denaturation of 108000

J mole<sup>-1</sup>, an entropy of denaturation of 364 J mole<sup>-1</sup> C<sup>-1</sup>, an energy of activation for dark respiration of 36000 J mole<sup>-1</sup>, and the water content yielding a half-maximal dark respiration rate of 77%. The model had an R<sup>2</sup> of 0.85. When the model was applied to field data 76% of the variation was explained. Field rates were underestimated in some cases possibly due to handling, short term adaptation to laboratory conditions, or population variation.

MARSH, LELAND C. and PAUL E. BORK\*. Biology Department, State University of New York Oswego, NY 13126

-Bioaccumulation of cadmium, lead, and zinc in *Typha latifolia* under experimental conditions.

Dormant rhizomes from a single clone of *T. latifolia* were grown for 90 days in the greenhouse and treated with increasing doses of three heavy metals. There were no observable external differences in the aerial portions of the treated vs. the control plants, even though the final doses were 10,000 ppm. The data include biomass yield, aboveground/belowground ratios, growth rates of aerial plants, and concentrations of heavy metals in all plant parts and at three soil levels. *Typha latifolia* accumulates significant quantities of heavy metals. Data are presented for the accumulation rates of cadmium, lead, and zinc in kg/hectare.

MAUN, M. A. Department of Plant Sciences, University of Western Ontario, London, Ontario N6A 5B7. - Colonizing ability of *Ammophila breviligulata* through vegetative reproduction.

The plant populations of *A. breviligulata* expanded towards the lake by forming an advancing front consisting entirely of plagiotropic rhizomes. Ice thrust up against the high beach, violent storm waves and water currents destroyed the lakeward end of the population, thus fragmenting rhizomes into varying lengths and creating bare areas below the farthest inland reach of waves. Fragmented rhizomes were dispersed by wave action and consequently served as important sources of new plants in alien habitats. The rhizome fragments occurring in greatest frequency contained 2 to 5 nodes. Only a few of the rhizome buds developed into new shoots. Severing of the rhizome into single node units caused a significant increase in bud initiation. However, a large proportion (76%) of the initiated buds aborted and the shoots failed to emerge from the soil.

MCBRIEN, HEATHER, RUDOLF HARMSSEN and ADELE CROWDER,  
Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6

- Plant-herbivore interaction in *Solidago canadensis* L. and *Trirhabda* spp.

*Solidago canadensis* is often the dominant plant in abandoned hayfields. Plant cover and arthropod numbers have been monitored since 1975 in sample plots in Leeds Co., Ontario. During a population build-up of *Trirhabda*, whose larvae eat goldenrod leaves, the cover of goldenrod declined. Cover of grasses increased. Adult beetles emigrated, and the local

population of larvae crashed as food diminished. Goldenrod cover did not return to pre-outbreak values but, when insecticide was used, goldenrod recovery was greater. Manual defoliation was used to mimic the damage by larvae and three defoliations during the summer reduced cover in the subsequent year.

MCKERNAN\*, J. MICHAEL & JENNIFER M. SHAY.  
MacLaren Plansearch Inc., Winnipeg MB R3G 0T6  
Department of Botany, U. Manitoba, Winnipeg MB  
R3T 2N2.

- Effects of military training on mixedgrass prairie and utility of recovery procedures.

Stressed and control areas were studied within the C.F.B. Shilo Military Reserve, 40 000 ha of Bouteloua-Stipa-Carex mixedgrass prairie on light sandy soils 25 km east of Brandon, Manitoba. Since 1974, military manoeuvres using tanks and armoured personnel carriers have been conducted annually. Impacts arising include increased frequency of Bouteloua gracilis (6-64%) and Carex spp (19-56%), reduced species diversity (26-30%), and increased litter (8%) and bare ground (24%). Penetrometer soil strengths were 50% greater in stressed areas. Most soil chemistry variables show increased concentration (Cu 88-934%, Zn 16-111%, Na 3-101%) in response to a military stress gradient.

Recovery procedures tested indicated that greater renovation was achieved by light harrowing of damaged areas and 2 years' protection than by seeding with combinations of Agropyron intermedium, A. cristatum, A. trachycaulum, Bromus inermis, Elymus junceus, Festuca rubra, Medicago sativa, and Melilotus officinalis and similar protection.

MCLEOD, KENNETH W., THOMAS G. CIRAVOLO, K. C. SHERROD, JR. Savannah River Ecology Laboratory, Aiken, SC 29801 - Fertilization of pine forests: canopy response.

Loblolly pine forests on the Savannah River Plant have been fertilized at rates of 400 and 800 kg N/ha by the addition of sewage sludge. Two types of sludge representing aerobic and anaerobic digestion processes were used. The plots treated with anaerobically digested sewage sludge had increased elemental concentrations of nitrogen and phosphorus in the throughfall and greater amounts of needlefall. The response increases with an increase in the fertilization rate. High rates of needlefall during the late summer were also observed in this treatment. Aerobically digested sewage sludge, which contains a much higher percent of solids and which appears to not have decomposed substantially, has had no effect to date on either throughfall or needlefall. Whether the increased amounts of N and P moving from the canopy to the forest floor will continue to cycle and furnish trees with increased nutrients or be bound and immobilized by the forest floor is as yet unknown, but could strongly effect future productivity.

MCMILLEN, JACK D.\* and THEODORE J. CROVELLO.  
Department of Biology, University of Notre Dame,  
Notre Dame, IN 46556.

- Quantitative determination of macroclimatic niches of Pinus species in the eastern U.S.

We captured data on 30 climatic variables and the distribution of 14 Pinus species in 211 state cli-

matic divisions of the eastern U.S. Discriminant analysis indicated how much of the distribution could be described by climatic variables and which of these variables are the best descriptors. Tree distributions can also be represented in terms of statistical distributions of each climatic factor (i.e. means and standard deviations). Discriminant analysis using all variables estimates the distribution of each species at greater than 93% accuracy. In most cases, a few factors give 90% accuracy. Additional variables contribute little information due to correlation with other variables. Different climatic factors are important for different species.

Meidinger, Del V. Research Branch, British Columbia Ministry of Forests, 1450 Government Street, Victoria, British Columbia, Canada, V8W 3E7

Ecosystem classification in British Columbia and its application to forest management

Since the early 1970's, the British Columbia Ministry of Forests has been developing and implementing a system of ecological classification designed to provide a rational framework for both forest and range management. The classification system follows, with some modification, the Biogeoclimatic Ecosystem Classification system developed by Dr. V.J. Krajina and his students. The units result from a synthesis of vegetation, soil, and climate data. The province is presently divided into thirteen biogeoclimatic zones and 122 biogeoclimatic subzones. The classification for one subzone of the Interior Cedar - Hemlock zone will be presented and compared with adjacent subzones. Ten biogeocoenotic associations, which occur primarily along a moisture gradient, have been differentiated in the Wet Interior Cedar - Hemlock subzone. Utilizing the classification framework, silvicultural interpretations for tree species selection and site preparation have been developed.

MURDY, WILLIAM H.\* and DONALD L. PHILLIPS.  
Department of Biology, Emory University, Atlanta,  
GA 30322.

- Effects of Rhododendron maximum L. on regeneration of southern Appalachian hardwoods

Long-term forest inventory data at the Coweeta Hydrologic Laboratory, North Carolina, were used to assess the changes in tree regeneration patterns since 1934-35 and to evaluate the impact of Rhododendron maximum L. Density diameter distributions of dominant tree species were determined from 1934-1935 and 1969-1972 inventories of high density rhododendron (HR) and low density rhododendron (LR) plots. Oak and maple regeneration, which was abundant in 1934-35 due to past disturbance, decreased by 1969-72 as the canopy closed. Total tree regeneration was lower in HR plots than in LR plots and the magnitude of the difference increased with time. In 1969-1972, regeneration of chestnut oak and white oak was reduced in HR plots, whereas that of red maple was not. Scarlet oak and black oak regeneration was reduced at all sites regardless of rhododendron. Hemlock sapling density increased with time and abundance of rhododendron.

## 52 Ecological Section

Nash III, Thomas H. and W. Bradley Kincaid.  
Department of Botany and Microbiology, Arizona  
State University, Tempe, AZ 85287  
- Relationship of SO<sub>2</sub> and climate to dendro-  
chronological variation in western larch.

The effect of sulfur dioxide on growth of western larch (Larix occidentalis) near Trail, British Columbia, was examined using tree-ring analysis in a montane forest ecosystem of the Pacific Northwest. A previous investigation demonstrated association of long-term growth variation at several sites within the Columbia River valley with estimates of sulfur emissions. Herein, we report results of a regression study using a portion of the tree-ring chronologies for which 30 years of SO<sub>2</sub> monitoring data were available. To assess tree-ring variation in relation to climate, data from two control locations were used to build a regression model in which the principal variables were 1) last year's tree-ring index, 2) spring temperature, 3) autumn precipitation, and 4) last year's summer temperature. For the Columbia valley sites, this model explained less than 30% of the variation. Inclusion of seasonalized SO<sub>2</sub> data significantly increased the variation explained for these regressions and enable us to make dose-response predictions.

Nicholson, A.C. and E.H. Hamilton. Research  
Branch Ministry of Forests, 1450 Government  
Street, Victoria, British Columbia, Canada, V8W 3E7.  
Grasslands of southern interior British Columbia

Climax grasslands dominated by bunchgrass and semi-desert shrubs occur on Chernozemic soils in the major valleys of southern interior British Columbia. A Braun-Blanquet table sort and ordination techniques were used to delineate five major ecosystems. The Agropyron spicatum - Artemisia tridentata association occupies the hot dry valley bottoms (below approximately 600 m) on Brown Chernozemic soils. The Agropyron spicatum - Poa sandbergii - (Chrysothamnus nauseosus) association occupies a less arid band at approximately 600 to 900 m elevation on Dark Brown Chernozemic soils. Bordering the forest at elevations ranging from approximately 800 to 1200 m are: the Agropyron spicatum - Festuca spp. association (south of 51° N lat.); the Agropyron spicatum - Koeleria macrantha - (Artemisia frigida) association (predominately north of 51° N lat.); and the Stipa richardsonii association (extensive on moist sites north of 51° N lat.). These latter associations are characterized by Dark Gray and Black Chernozemic soils, a cooler moister climate and a more diverse and productive vegetation.

PAEZ, ALEJANDRA\*, HENRY HELLMERS AND BOYD R. STRAIN  
Botany Department, Duke University, Durham, NC.  
27706. - CO<sub>2</sub> enrichment and drought stress inter-  
action in determinate and indeterminate cultivars.

The interaction of increased atmospheric carbon dioxide and drought stress was investigated in determinate and indeterminate cultivars of pea (Pisum sativum) and tomato (Lycopersicum esculentum). Plants were grown in controlled environments using low and high CO<sub>2</sub>; well-watered and drought-stressed regimes. When water was withheld total leaf water potential and osmotic potential decreased less rapidly under the high CO<sub>2</sub> regime. Thus, high CO<sub>2</sub> plants maintained positive turgor and did not wilt

when drought-stressed. The differences were due to the reduced stomatal conductance and reduced transpiration. Additional CO<sub>2</sub> had no effect on branch number. Drought stress inhibited branch development in pea and significantly reduced it in tomato. Elevated CO<sub>2</sub> partly overcomes the inhibiting effect of drought stress on plant growth and results in a more rapid recovery of drought-stressed plants. These results have important ecological significance because the relative competitiveness of plant species in ecosystems may be altered.

PARRISH, JAY B.\* Department of Geophysics, Penn  
State University, University Park, PA 16802  
ROCK, Barrett Jet Propulsion Laboratory,  
Padadena, CA 91109.

-The effect of soil methane on in vitro growth  
and vigor of Quercus prinus seedlings.

A suspected site of hydrocarbon microseepage in Lost River, West Virginia, is marked by high soil Mn content and an anomolous growth of Acer rubrum to the exclusion of the dominant species in the region, Quercus prinus. An in vitro experiment tested the hypothesis that hydrocarbon microseepage adversely affects the ability of Q. prinus to absorb necessary nutrients by interfering with its ectomycorrhizal fungal association. Plants grown in soil collected from the gas field had a very high Mn content. Plants exposed to methane had lower amounts of essential elements than those exposed to air; this is consistent with the hypothesis that ectomycorrhizae are adversely affected by methane.

PHILBRICK, C. THOMAS. Dept. of Botany and Plant  
Pathology, University of New Hampshire, Durham, NH.  
03824. - Aspects of pollination and floral biology  
in three Potamogeton species.

Field experiments were conducted on P. spirillus, P. epihydrus and P. pusillus; all three are protogynous. Stigma receptivity lasts beyond anther dehiscence in P. epihydrus and the aerial flowers of P. spirillus, and the pollen is self-compatible. Self-pollination occurs after anther dehiscence if outcrossing has not taken place; facultative autogamy. Potamogeton spirillus produces dimorphic flowers, facultatively autogamous aerial flowers, borne on many-flowered inflorescences which are larger than the obligately autogamous submersed flowers, borne on few-flowered inflorescences. Autogamy is illustrated by consistent 100% fruit production on bagged inflorescences. In P. pusillus, anthesis occurs on both aerial and submersed flowers, but the flowers are not dimorphic as in P. spirillus. Submersed anther dehiscence is characterized by production of gas bubbles expelled from the anther sac. Pollen is released from the anther sac on the bubble surface. Apparent self-incompatibility of the pollen suggests that bubble production aids in outcrossing. The obligate outcrossing nature is illustrated by no fruit production on bagged inflorescences.

PITELKA, LOUIS F. and JEFFREY W. ASHMUN\*, Biology  
Department, Bates College, Lewiston, Maine 04240 -  
Survival, growth and reproduction of Aster  
acuminatus in reciprocal transplant gardens.

A reciprocal transplant experiment was undertaken to determine the extent to which variation in growth and reproduction among patches of Aster acuminatus is genetic versus environmentally-induced. In April,

1980, 200 ramets of *A. acuminatus* were collected from each of two different source populations and divided equally among eight transplant gardens. Transplanted ramets were censused at regular intervals through the summer of 1982 and then harvested. Data were collected on survival, growth, reproduction and resource allocation. Significant variation among the gardens in several important demographic variables was correlated with microenvironmental differences. By 1982, the number of ramets in the gardens ranged from 48 to 148 and the percent of ramets that flowered ranged from 0% to 22%. There were few source population effects suggesting that environment is more important than genotype in determining growth and reproduction in this understory herb.

PITELKA, LOUIS F.\*, SANDRA B. HANSEN and JEFFREY W. ASHMUN, Biology Department, Bates College, Lewiston, Maine 04240 - Growth rates and longevities of patches of *Clintonia borealis*.

Patches of *Clintonia borealis* can be found in a wide range of understory microenvironments and can vary dramatically in total ramet number, density and mean ramet size. Pooled demographic data from 16 patches show that overall rates of ramet mortality and branching (vegetative reproduction) are low. Recruitment from seeds is extremely rare. Although individual patches show some variation in net rates of clonal growth, the pattern of slow to moderate growth over a period of years is remarkably consistent among patches. Additional data on patch growth rates comes from excavating small patches and counting internodes and branch points. These data confirm the patterns revealed by the demographic data and show that patches are often composed of only one or a few long-lived genets. New genets establish only rarely but once established can apparently persist for decades. There is probably little if any genet turnover or selection in established patches.

POLLARD, A. JOSEPH. Department of Botany and Microbiology, Oklahoma State University, Stillwater, OK 74078.  
- Ecological genetics of the interaction between stinging nettles (*Urtica dioica*) and mammalian herbivores.

Stinging trichomes of *Urtica dioica* are often described as defenses against grazing; however, no prior studies have tested this proposition or attempted to identify particular herbivores which might be deterred. *U. dioica* is highly variable in many respects, including the density of the stinging hair investiture. An extreme population of virtually stingless plants has been studied intensively. Variation in hair density was shown to be continuous, genetic, and heritable. Grazing preferences of two species of mammalian herbivores (rabbits and sheep) were studied under laboratory and field conditions. Grazing intensity on a range of genotypes of known stinging hair density was compared. Both species of herbivores preferentially grazed less well armed variants, although there was some indication that the two species responded differently. Results suggest that the evolutionary consequences of mammalian herbivory may be quite different from those brought about by invertebrate grazing, which is more often studied.

PRITTS, MARVIN P. and JIM F. HANCOCK. Department of Horticulture, Michigan State University, East Lansing, MI 48824  
- A comparison of reproductive strategies within and between wild species of blueberry (*Vaccinium*) in Michigan.

Biomass allocation patterns were determined for 12 highbush blueberry plants (*V. corymbosum*) from bogs in southern Michigan, and for 10 lowbush plants (*V. angustifolium*) in each of 17 diverse environments varying in temperature, light, moisture, and nutrient availability. With the exception of one site which experienced a late frost, and another in heavy shade, lowbush blueberries did not differ in annual allocation to leaves (23.0%), stems (9.9%), underground tissues (25.5%) or fruits (41.6%). Differences in new ramet production were observed however, and were correlated with light availability ( $r = .756$ ,  $p < .05$ ). Growth of highbush plants was very predictable. In fact, cane numbers and sizes accounted for >99% of the variability in leaf, cane, and root biomass over a 500-fold range of plant sizes. On the average, highbush reproductive allocation (46.2%) was similar to lowbush plants (41.6%), but was quite variable and appeared to be associated with pollination. Analysis of yield components suggest that different life history strategies have occurred under divergent selection pressures, both within and between species of *Vaccinium*.

RITCHIE, J.C. Scarborough College, University of Toronto, 1265 Military Trail, Toronto M1C 1A4, Canada. - Late Holocene pollen evidence for deforestation in the High Plains of Algeria.

A core of marsh sediment from a site in the Télijdjène valley, 40 km west of Tebessa, yielded a radiocarbon-dated sequence of pollen. The area has over 200 mm annual precipitation. A treeless steppe, dominated by *Artemisia-Stipa* occupies upland sites. The pollen record supports the hypothesis of Le Houerou that the steppe is of anthropogenic origin. From 6000 to 2000 yr the spectra are dominated by *Pinus* with *Ephedra*, *Juniperus* and *Quercus*. The modern pollen assemblage, dominated by *Artemisia* and grass, was established abruptly at 2000 yr BP. A short phase of *Olea* pollen near this pollen zone boundary marks the widespread olive cultivation of the Roman occupation. Independent palaeoclimatic data indicate only minor climate change during the past 3000 yr, inadequate to explain the major shift in vegetation.

ROBERTS, B.A. and A.W. ROBERTSON. Nfld. Forest Res. Centre, Canadian Forestry Service, P.O. Box 6028, St. John's, Nfld., A1C 5X8.

- Atlantic salt marshes

This paper reviews current research on the Atlantic salt marshes of Eastern Canada. Specifically, this paper discusses salt marshes in the transition zone between the Subarctic and the Boreal phytogeographic regions. These salt marshes are also the northern limit of many temperate species partly due to

anthropogenic influences. The floristics, the habitats and biophysical aspects of the Atlantic marshes are described. Aspects relating to anthropogenic influences on the Atlantic marshes are discussed in the context of archeology, contemporary rural settlement and vulnerability to offshore oil development. Guidelines for environment management, protection and rehabilitation research are proposed. Such guidelines are deemed important since more than half the 33 000 ha of salt marshes in Nova Scotia have been dyked for agriculture. Most of the salt marsh habitats in Newfoundland have a high degree of domestic grazing even though the marshes are small in size and rare in occurrence. The least disturbed in terms of domestic use are the Labrador salt marshes which although grazed by migratory ducks and geese have not yet been influenced by man's activities. In addition, the Labrador salt marshes are discussed and compared to the northern marshes of Arctic Canada in terms of their ecology and development.

ROCK, BARRETT N. Geobotany and Renewable Resources, Jet Propulsion Laboratory, Pasadena, CA 91109. - Mapping of deciduous forest cover using airborne thematic mapper simulator (TMS) data.

Highly accurate vegetation maps have been produced using an airborne version of the advanced multi-spectral scanner (Thematic Mapper) on board Landsat 4. The area mapped is in the eastern panhandle of West Virginia. Data were acquired on October 21, 1980, at the peak of fall foliage display. The vegetation maps were prepared using the VICAR FASTCLAS supervised classification program developed by JPL. A total of 35 training areas, identified on the basis of false color IR photography (aerial and ground) and ground observation (0.1 acre circular plot analyses) were used to produce the supervised classification images. Raw bands (TMS) used to produce the images were: band 3 (.63-.69  $\mu\text{m}$ ), band 4 (.76-.90  $\mu\text{m}$ ), band 5 (1.00-1.30  $\mu\text{m}$ ), and band 6 (1.55-1.75  $\mu\text{m}$ ). A total of 10 vegetation classes are recognized. In terms of correct classification of tree species and species associations, the images are approximately 90% accurate (based on ground checks).

Ruess, Roger W. Biology research labs, Syracuse University, Syracuse, NY 13210, and M.A.K. Lodhi, Dept. of Biology, Forest Park College, St. Louis, Mo. 63110. Variation in soil nitrification, nitrifiers and leaf nitrate reductase activity in selected tree species in a forest community.

Five different tree species and associated soil were studied in a forest community to determine the ecological function(s) as related to nitrification, nitrifiers, leaf NRA and total leaf nitrogen. Soil  $\text{NH}_4\text{-N}$  was always higher than the  $\text{NO}_3\text{-N}$  under all tree species, with the exception of Basswood where  $\text{NO}_3\text{-N}$  was almost three times higher than the  $\text{NH}_4\text{-N}$ . Further, Nitrosomonas and Nitrobacter counts were higher under Basswood than any other tree stand. Leaf nitrate reductase activity was significantly correlated ( $P < .001$ ) with the soil  $\text{NO}_3\text{-N}$  under all five tree stands. Leaf NRA was 20-50 times higher in Basswood than in hemlock, Beech, Maple and Oak species. Similarly, dry leaf nitrogen was highest in Basswood than all other species studied. Our data supports that low nitrification, nitrifiers and leaf

NRA are variably influenced by the indivisulistic pressure exerted by different tree species to conserve energy by inhibiting soil nitrification, thus avoiding the reduction of leaf  $\text{NO}_3\text{-N}$  into  $\text{NH}_4\text{-N}$ . Consequently, species will absorb readily available  $\text{NH}_4\text{-N}$ , which can incorporate directly in the synthesis of amino acids. However, Basswood is an exception to the case which accumulated a large amount of leaf nitrogen (5.0%) in very early growing period. We suspect that such a rapid nitrogen accumulation could not be only due to relatively high nitrification but due to a parallel absorption of  $\text{NH}_4$ ,  $\text{NO}_3$  and possibly a function of mycorrhizael infection.

SCHWARZ, A.G.\* AND R.E. REDMANN. Department of Crop Science and Plant Ecology, University of Saskatchewan, Saskatoon, Sask. S7N 0W0. - Phenology of northern halophytic  $C_3$  and  $C_4$  grasses.

In Saskatchewan,  $C_3$  and  $C_4$  species coexist in saline habitats. The phenology of Agropyron trachycaulum ( $C_3$ ), Spartina gracilis ( $C_4$ ), Puccinellia nuttalliana ( $C_3$ ), and Distichlis stricta ( $C_4$ ) was studied from May to September. Observations of growth stage, height, number of leaves, and number of tillers were made on twenty individuals of each population. Environmental measurements included air and soil temperatures, rainfall, soil water content, and salinity. Spring regrowth began earlier in  $C_3$  plants than in  $C_4$  plants. Species from the strongly saline vegetation zone (P. nuttalliana and D. stricta) began flowering earlier than species from the moderately saline vegetation zone (A. trachycaulum and S. gracilis). Within both zones, flowering of  $C_3$  and  $C_4$  species was essentially simultaneous. New growth occurred in autumn among the  $C_3$  plants. Distinct temporal separation of the  $C_3$  and  $C_4$  grasses probably is impossible, because of the relatively short growing season.

SELTNER, CAROL M.\* and WANNA D. PITTS. Department of Biology, San Jose State University, San Jose, CA 95112.

- Site microenvironment characteristics and seedling survival of Shasta Red Fir (Abies magnifica var. shastensis).

Distribution of newly established red fir seedlings is generally patchy. Areas of regeneration lie side-by-side with apparently similar areas where establishment has not occurred. To differentiate establishment from non-establishment conditions, adjoining paired plots (with and without the youngest established seedlings) were sited at six locations in the northern California Coast Ranges. Plots were examined for differences in duration and character of insolation, soil temperatures and moisture content, litter depth and composition, and physical characteristics. Plots without established seedlings were distinguished by long midday periods of full sunlight along with high surface temperatures. By contrast, establishment plots generally received more insolation in the form of dappled sunlight and experienced lower surface temperatures. Other attributes were more variable. Patterns of one season's seedling mortality were consistent with these differences, and suggest that patchiness may be the result of death in midsummer of seedlings in sunny microsites.

SEMPLE, KATHLEEN S. Department of E.P.O. Biology, University of Colorado, Boulder, CO 80309.

-Relationships among age, size, and reproductive patterns in Engelmann spruce.

Age and size structure and reproductive patterns were measured in Picea engelmannii (Engelmann spruce) as part of a study on the reproductive biology of subalpine forest trees in Colorado. A nondestructive method was developed for aging seedlings, using height, diameter, and number of branch whorls in a predictive equation. Ages of adult trees were measured by coring. Age analyses indicated that the two populations studied are self-maintaining. Seedlings were common and there was an approximately uniform distribution of individuals in age classes of mature trees (75-325 years old). Height and diameter were highly correlated with age in seedlings, but not in mature trees. Trees reproducing by seed had significantly larger heights and diameters than trees that reproduced vegetatively or not at all. Numbers of seed produced and seed size were also correlated with tree size and age. Size, rather than age appears to be the better predictor of reproductive status in Engelmann spruce.

SOHLBERG E.H.\* & L.C.BLISS. Dept. of Botany KB-15 University of Washington, Seattle WA 98195

- Interactions between moss and a vascular plant species (*Ranunculus sabinei*) in a High Arctic meadow.

Small vascular plants grow nearly embedded in moss mats in moist polar semi-desert plant communities. Interactions between a species of vascular plant, (*R. sabinei*) and the moss were examined at King Christian Island N.W.T., Canada (77°45'N, 101°10'W)

Effect of moss presence on *R. sabinei* was tested by clipping and removing moss in plots containing *R. sabinei*. Phenology and aboveground production of experimental and control *R. sabinei* plants were recorded through two growing seasons.

Significantly ( $p < .05$ ) higher mean maximum aboveground biomass of *R. sabinei* was found for no-moss plants vs controls in the second year after treatment. Increased rooting zone temperature (0.5-1.0°C) in no-moss plots accounts for some of the *R. sabinei* response. Increased soil nutrients due to factors including competition effects from mosses may have accounted for most of the increase in *R. sabinei* productivity.

SPIRA, TIMOTHY P. Department of Botany, University of California, Berkeley, California 94720

-What limits seed production in the alpine perennial, *Gentiana newberryi* (Gentianaceae)?

Fruit and seed production in the alpine perennial *Gentiana newberryi* (Gentianaceae) were extremely low during three consecutive years in the White Mountains of California. The removal of flowers by herbivores and the availability of pollinators reduce the reproductive potential of this species. An additional factor is an unusually late flowering period. While inflorescences of *G. newberryi* are present early in the growing season, anthesis does not occur until late in the season, and flowers often fail to mature fruits and seeds prior to the onset of winter conditions. An explanation which may account for the late flowering period in this species is that available resources are utilized to fill vegetative sinks prior to reproductive functions.

SQUIERS, EDWIN R. Departments of Biology and Environmental Science, Taylor University, Upland, IN - An Analysis of the Community Gradient Between an Aspen - Maple Upland Forest and an Alder - Cedar Swamp Forest in Northern Lower Michigan.

The structure of the plant community in the ecotone between an aspen - maple upland forest and an alder - cedar swamp forest was studied at the Grass River Natural Area, Antrim County, Michigan. Basal area, density, and frequency data were collected by taxonomic species from circular quadrats of 100 square meters each, spaced at 30 meter intervals along six parallel transects between the two community types. Elevation and depth to ground water was also recorded at each quadrat. The ecological distance between quadrats was assessed using a variety of indices of diversity and community similarity, Bray-Curtis ordination, and principle component analysis. Microcomputer generated 3-dimensional graphics were used to aid in data display and interpretation. The results indicate that the changes along the ecocline are complex and species specific with dominant species such as large-toothed aspen, northern white cedar, and bracken fern displaying relatively sharp distributional boundaries while the abundance of many of subdominants changes very gradually.

STAIRS, FELICITE and M. A. MAUN. Department of Plant Sciences, University of Western Ontario, London, Ontario N6A 5B7. - Population characteristics of *Artemisia campestris* in 4 sand dune habitats along Lake Huron.

Populations of *Artemisia campestris* a facultative polycarpy were studied in 4 habitats in the sand dune system at Pinery Provincial Park. The presence of facultative polycarpy present in a wild population was habitat related and correlated with the age specific mortality rate and duration of the vegetative phase. Flowering phenology differed in both duration and timing of anthesis. Rosette size as a predictor of flowering readiness was analysed at different periods and was found to be habitat specific. Root crown diameter as an alternate predictor was also examined. Germination patterns differed between habitats and years. A high variance within the pattern was correlated with the absence of polycarpy and a high mortality rate for all age groups.

STEWART, COLIN C\* and BILL FREEDMAN, Biology Dept. and Institute for Resource and Environmental Studies, Dalhousie University, Halifax, Nova Scotia, B3H 4J1

- Comparison of aquatic macrophyte communities in two small oligotrophic lakes in Kejimikujik National Park, Nova Scotia.

The aquatic macrophytes of two small oligotrophic lakes are compared. Beaverskin Lake (50 ha, pH 5.4, 1.25 Hazen units) and Pebblelogitch Lake (33 ha, pH 4.5, 80 Hazen units) are remote headwater lakes within 2 km of each other. The major macrophyte communities for each lake have been mapped and standing crops determined. Beaverskin Lake has several spec-

ies, including Potamogeton confervoides, Ranunculus reptans and Myriophyllum tenellum, that are not found in Pebblelogitch. Both lakes have Eriocaulon septangulare dominated communities as well as Scirpus subterminalis - Utricularia spp dominated areas. A Sphagnum community occupies shallow bays in Pebblelogitch, whereas Sphagnum forms a deepwater (ca 6 m) community in Beaverskin. The floating-leaved communities in Beaverskin are dominated by Nymphoides cordata, whereas Pebblelogitch has large area of Nuphar variegatum. As both lakes are receiving acidic deposition (the weighted annual meanprecipitation pH is 4.6), this study provides a baseline for assessing future changes.

STEWART, JIM D. and BILL FREEDMAN Biology Dept., Dalhousie University, Halifax, Nova Scotia, B3H4J1  
- Patterns of biomass allocation among a group of sympatric species of Saxifraga in the high Arctic.  
The within-plant allocation of biomass was investigated for four species of Saxifraga, growing on Ellesmere Island, N.W.T., Canada. Populations of Saxifraga cernua, S. nivalis, S. rivularis, and S. tricuspidata were observed and subsamples harvested seasonally, in 1981 and 1982. At mid-season, the dry-site evergreen S. tricuspidata had ca. 75% of its aboveground biomass as attached dead material, ca. 10% as foliage, and ca. 3% as reproductive organs. The mesophytic evergreen S. nivalis allocated ca. 30%, 15%, and 20% to dead material, foliage, and reproductive organs, respectively. The mesophytic summergreen S. rivularis allocated ca. 25%, 30%, and 35%, respectively; while the hygrophytic summergreen S. cernua allocated ca. 35%, 30%, and 25%, respectively. Their respective allocations to roots were ca. 75%, 30%, 25%, and 35% (percent total aboveground biomass). These allocation patterns follow trends observed in temperate plants, but with modifications due to Arctic conditions where the principal cause of mortality is the severe environment, and competition effects are minimal.

SUFFLING, ROGER. Faculty of Environmental Studies, University of Waterloo, Waterloo, Ontario N2L 3G1.

- Incidence of fire during succession in Ontario Boreal and Great Lakes forests.

For many landscapes, log ecosystem area of a given age since last disturbance may be plotted against age to give a polygon analogous to the survivorship curve of population biology. Its shape indicates whether disturbance is more likely in early than in late succession. Log area versus age polygons were plotted for 21 fire-prone Ontario landscapes, using forest resource inventory data. In most cases there is an equal chance of disturbance relative to age in stands older than 50 years, but recent fire control obscures the trends in younger stands. A more detailed reconstruction of a pre-fire control northwest Ontario landscape indicates a fire-resistant period in early succession, and then an equal chance of fire in older stands. The fire resistant period is longer in swamp forests than in upland sites.

TAYLOR\*, GREGORY J., and ADELE A. CROWDER. Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6.

- Uptake and accumulation of copper, nickel and iron by Typha latifolia L. grown in solution culture.

Concentrations of Cu, Ni and Fe in leaf and root tissue of Typha latifolia grown in a series of solution cultures containing 5 - 100  $\mu\text{g g}^{-1}$  Cu, 10 - 150  $\mu\text{g g}^{-1}$  Ni, or 10 - 100  $\mu\text{g g}^{-1}$  Fe were correlated with concentrations of the same metals in the growth medium. In contrast to plants growing in contaminated wetlands near Sudbury, Ontario, plants grown in solution culture were unable to minimize entry of Cu and Ni into leaf tissue. Leaves of T. latifolia accumulated 467 + 50  $\mu\text{g g}^{-1}$  Ni and did not show toxicity symptoms. Leaf Cu concentrations reached 127 + 28  $\mu\text{g g}^{-1}$  and toxicity symptoms (reduced leaf elongation and biomass production) appeared at leaf Cu concentrations of approximately 80  $\mu\text{g g}^{-1}$ . Thus exclusion of Cu and Ni from above ground tissues would appear to be a phenomena related to growth in the field, and T. latifolia would appear to have internal Cu and Ni tolerance mechanisms.

THOMAS, A. GORDON\* and GARRY BOWES. Agriculture Canada, Research Station, Box 440, Regina, Sask. S4P 3A2 - Germination patterns in Euphorbia esula L. using a 100-cell seed germinator.

The germination of E. esula seeds in response to constant and alternating temperatures was studied using a 100-cell germinator. This equipment is a new design with 100 independently controlled germination cells, each of which holds one standard 100 mm petri dish. Temperatures were set to include all combinations between 0° and 45°C in 5°C increments. The equipment proved valuable for describing the total germination pattern of E. esula. Germination failed when daily maximum temperatures were below 15°C and daily minimum temperatures were above 35°C. Seeds from cells with a maximum temperature below 15°C germinated when transferred to a germination cabinet set at 30/10°C. Daily minimum temperatures above 40°C were lethal. Maximum germination occurred when (1) the temperature for part of the diurnal cycle was between 15 and 35°C, (2) the average daily temperature ranged from 22 to 27°C and (3) the daily temperature difference was 15 to 20°C.

UNGAR, IRWIN A. Department of Botany, Ohio University, Athens, Ohio 45701. - Factors influencing growth and survival in populations of Atriplex triangularis.

Studies were conducted to determine the effects of biotic interference and salinity stress on the survival of Atriplex triangularis in an Ohio inland salt marsh. Transplants of soil cores containing ten A. triangularis plants that were put into hypersaline environments had very high plant mortality. Plants transferred into cleared plots in less saline zones showed optimal growth. Thinning experiments indicated that high plant densities, 50 to 100 plants per 100  $\text{cm}^2$ , caused a reduction in dry weight production equal to about 80% of single plant controls. Mortality was not directly related to plant density levels, but was strongly affected by increasing salinity stress. Laboratory studies indicated that salinity concentrations above 1% NaCl were inhibitory to both seed germination and growth of A. triangularis plants. The quantity of seeds produced per plant showed a positive linear relationship ( $P < 0.01$ ) to total plant biomass production.

VINCENT, G. and Y. BERGERON. Jardin botanique de la Ville de Montréal, 4101 est, rue Sherbrooke, Montréal, Qué. HLX 2B2 and Centre de Recherches Ecologiques de Montréal, 5858 Chemin de la Côte des Neiges, C.P. 6128, Succ. "A" Montréal, Qué. H3C 3J7. - Plant community pattern analysis in Lake of Two Mountains area (Quebec).

Following quantitative sampling of riparian and forest plant communities bordering on Lake of Two Mountains, a classification and a plant community pattern analysis have been made. In a first step, a community classification was established by using ordination and hierarchic agglomeration cluster analysis techniques. Phytosociological types were distinguished among forest communities dominated by Sugar Maple, White Pine, Red Ash, Red Oak, etc. and among typical shrubby and herbaceous shore communities. The so-defined communities have been mapped at a 1:10,000 scale. As a second step, by superposing on this map, soil and topographic maps of the same region, a systematic sampling was made. The sampling analysis, by means of information theory, makes possible the evaluation of the abiotic variables which most control the plant community pattern distribution in this area.

WHIGHAM, DENNIS F. Chesapeake Bay Center for Environmental Studies, Smithsonian Institution, Edgewater, MD 21037 - Biomass and nutrient allocation of *Tipularia discolor* (Orchidaceae).

Biomass and nutrient allocation patterns in *Tipularia discolor* (Orchidaceae) were studied in a deciduous forest in Maryland. Plants were sampled to determine how biomass and nutrients were allocated to different plant structures during an annual cycle. Corms older than 1 year lose weight gradually during the year and most new vegetative growth goes into current year corms and leaves. Sexual reproductive structures, and similarly leaves, account for a maximum of approximately 20% of the total plant biomass. The largest percentages of macronutrients (N, P, Mg, Ca, K) and micronutrients (Fe, Al, B, Sr, Pb) were found in corms 2 years and older, and nutrient concentrations were also high in newly formed leaves, and inflorescences. Analyses of the biomass and nutrient data suggest that translocation is important, but that it does not account for all of the uptake in new growth. Plants must, therefore, assimilate nutrients

from the soil during all periods of growth. The importance of large underground storage structures is discussed.

WINN, ALICE A. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060. - Differences in seed size and the role of seed size in seedling establishment in two populations of *Prunella vulgaris*.

Differences in seed size within plants, among plants, and between populations in *Prunella vulgaris* have been investigated at two sites in Southwest Michigan. Plants in a second-growth forest produce larger seeds than plants in an old-field population. Within each population, seeds produced in terminal inflorescences are significantly heavier than those produced in axial inflorescences. Under standard conditions in the greenhouse, plants from the old-field are smaller, produce significantly smaller seeds, and have proportionately fewer terminal inflorescences than plants from the forest. The role of seed size in determining seedling emergence and survival in the field has been investigated in each population. Differences between populations in the number and sizes of seeds produced will be related to between-site differences in the pattern of seedling success.

WINTERHALDER, KEITH. Department of Biology, Laurentian University, Sudbury, Ontario P3E 2C6.

- Metal-calcium-pH interactions affecting germination and early growth of *Agrostis gigantea* Roth, and their significance on acid, metal-contaminated soils of the Sudbury region, Ontario.

Ions of aluminum, copper and nickel applied singly and in combination to germinating grains of *Agrostis gigantea* have a differential inhibitory effect on germination, root growth and leaf growth. Metals in combination work synergistically with respect to inhibition, except in the case of the aluminum-nickel interaction, in which case aluminum ions reduce the inhibitory effects of nickel ions. Calcium in the form of sulphate has a small ameliorative effect on metal toxicity, while calcium carbonate is a highly effective ameliorant. Results are discussed in the context of factors limiting natural and assisted recolonization of Sudbury area soils, in which all three metals occur at toxic levels.

## ECONOMIC BOTANY SECTION

### Poster Session

DHARMAWARDHAN, SURANGANIE\*, MICHAEL S. STRAUSS and DANIEL C. SCHEIRER. Department of Biology, Northeastern University, Boston, MA 02115. Anatomical and Histochemical changes accompanying germination in taro, *Colocasia esculenta* (L.) Schott.

The changes accompanying germinating taro, *Colocasia esculenta* (L.) Schott cv PD II were examined from imbibition to cotyledon emergence. Seeds were germinated on sterile vermiculite, harvested every two days and fixed by previously described procedures with 3% glutaraldehyde in 0.02 M HEPES buffer, pH 6.8 and 2% osmium tetroxide. Thick sections were

stained with toluidine blue, periodic acid-Schiff's, sudan III or aniline blue for histochemical study. Previous work has shown the presence of an aleurone layer, prior to imbibition, which reacts positively for protein and lipid. As the cotyledon expands aleurone cells become flattened and stain weakly for protein or lipid. A few cells near the root-hypocotyl interface appear larger and react positively to sudan III stain. Such cells in other species have been termed aleurone transfer cells. The endosperm remains rich in carbohydrate with the exception of a 2-4 cell deep area surrounding the embryo. These show considerable decrease in PAS reactivity. At approximately 4-7 days the radicle emerges and is soon followed by the expanding, bilobed, cotyledon.

STERN, BARRY D. and MICHAEL S. STRAUSS.\*  
Department of Biology, Northeastern University,  
Boston, MA 02115. - Density, distribution and  
structure of stomata of taro, *Colocasia esculenta*  
(L.) Schott, Araceae.

Taro, *Colocasia esculenta* (L.) Schott, Araceae, is cultivated for its corm in the tropics and subtropics. Before the present study few articles dealt with its anatomy. An early work was concerned with the density of stomata. Our study is focused on the anatomy of taro, with emphasis on stomatal distribution and structure. Stomatal density was determined for *C. esculenta* cvs. Akado, Bun long, Ex. Florida, Lehua. Mo'i, and Taro hoia by examining replicas of the adaxial and abaxial surfaces of the leaf. Distribution for *C. esculenta* cv. Bun long was also determined. Leaves of *C. esculenta* cv. Bun long were fixed in 3% glutaraldehyde in 0.02 M, pH 6.8, Hepes buffer; postfixated in osmium tetroxide, and embedded in Spurr's embedding medium. Sections were examined by light and electron microscopy. The density of stomata was greater than that previously reported for the blade. A large variation was found between cultivars as well as between individual plants of *C. esculenta* cv. Bun long. The petiole of *C. esculenta* cv. Bun long had one hundredth as many stomata as the blade. Little difference was seen for the older leaves. The structure of stomata differs from monocot stomata previously examined and is similar to that of dicots.

## Contributed Papers

BRETTING, B. K. Natural History Division,  
Institute of Jamaica, 12 East St., Kingston,  
Jamaica. - Generic relationships in the Martyniaceae  
and their implications for economic botany.

Generic relationships in the Martyniaceae have been problematic. My research reveals that Proboscidea and Ibicella share a nearly identical pollen topography, a very similar floral morphology (melittophilous), and dehiscent fruits containing many seeds with corky testae and 'firm' embryos. The pollen topography and floral morphology of Martynia are somewhat similar to the former genera, but Martynia bears two rather than four fertile stamens. Indehiscent fruits containing fewer than 10 seeds with papery testae and 'crumbly' embryos distinguish Martynia from the former genera, but ally it with Cranioalaria, whose pollen topography and sphingid-pollinated flowers are unique in the family. These findings are potentially valuable for economic botanists. Species of Proboscidea show promise as oilseed crops for aridlands; species of Ibicella with similar seeds should also be investigated in this regard. Evidently, species of Cranioalaria have roots with medicinal value; hence Martynia should also be examined pharmacologically.

FRYXELL, PAUL A. U.S.D.A., Texas A&M University,  
COLLEGE STATION, TX 77843. Floral symmetry and  
zygomorphy in this Malvaceae.

Flowers of the Malvaceae are typically actinomorphic, with radial symmetry. The petals are individually more or less asymmetrical, giving the corolla a "pinwheel" appearance. The five imbricate petals may overlap in a left-handed or right-handed manner (i.e. clockwise or counterclockwise). Studies have shown that in most species, flowers of an individual plant are about 50% of each type, that is the direct-

ion of aestivation is random. In a few species, however, the direction of aestivation is evidently non-random, although the significance of this phenomenon is not clear. In typically actinomorphic malvaceous flowers, other flower parts (calyx, androecium, gynoecium) are symmetrical -- with the exception of the genus Abelmoschus in which the calyx splits laterally to an asymmetrical form; the flowers of Abelmoschus are otherwise radially symmetrical. A small number of species of Malvaceae, however, have developed a more or less zygomorphic (i.e. bilaterally symmetrical) form. This development of zygomorphy is correlated with floral presentation and is presumably also correlated with pollinating animals, although observations on pollinators are scarce. In these cases, all flower parts (sometimes with the exception of the calyx) show bilateral symmetry, i.e. the flowers as a whole are zygomorphic. Three distinct patterns of zygomorphy have been observed. Two of these have evidently occurred only once each (in Hibiscadelphus spp. and in Periptera sp. nov.), whereas the third has evidently occurred repeatedly in several different genera (e.g. Pavonia, Hibiscus, Kosteletzkya). As might be expected, zygomorphy tends to occur in species with relatively showy flowers.

JAROSZ, ANDREW M.\* and MORRIS LEVY. Department of  
Biological Sciences, Purdue University, West  
Lafayette, Indiana 47907. - The Phlox-Erysiphe  
cichoracearum interaction: influences of phylogeny  
and ecogeography on patterns of host resistance.

Host resistance patterns in natural plant-pathogen systems are little studied. They are postulated to be much different than the homogeneous and species-specific patterns that are hallmarks in agriculture. Patterns of resistance to an Indiana isolate of E. cichoracearum, an obligate fungal pathogen causing a powdery mildew disease, were determined for ten feral Phlox taxa. A total of 866 plants from 113 populations were inoculated and scored for the severity of infection after 2 weeks. Host responses were examined for correlates with phylogenetic and ecogeographic factors. The Indiana pathogen isolate can infect some plants in all host taxa; this contrasts with the extreme specialization in agricultural systems. Resistance polymorphisms occur in all taxa but the pattern of resistance does not parallel host phylogenetic relationships nor is it correlated with ploidy level. The level of resistance within populations is best correlated with habitat. Populations from forest sites tend to be more resistant than exposed site populations. Apparently, forest microclimates are more conducive for E. cichoracearum growth which increases selection favoring resistant individuals. One hundred host plants were subsequently reinfected with an E. cichoracearum isolate of Louisiana origin. Although ca. 25% of the plants exhibit differential responses to the two pathogen isolates, the overall resistance patterns are not significantly different. Thus, despite pathogen variability, habitat features remain the strongest proximate determinant of host resistance patterns.

KENNEALLY, KEVIN F.\* and EDWARD L. SCHNEIDER,  
Western Australian Herbarium, South Perth,  
Western Australia 6151, and Department of Biology,  
Southwest Texas State University, San Marcos, TX  
78666. - The genus *Ondinea* (Nymphaeaceae)  
including a new subspecies from the Kimberley  
region, Western Australia.

A new subspecies, *Ondinea purpurea* den Hartog subsp.  
petaloidea, has been recently discovered. The

occurrence of previously unreported petaloid flowers in the genus and the discovery of seedlings necessitates expanding the species description. The gradation from sepals to petals to petaloid stamens to conventional stamens provides additional morphological data to support the placement of Ondinea in the Nymphaeaceae sensu stricto.

KNAPP, SANDRA. L. H. Bailey Hortorium, Cornell University, Ithaca, New York 14853. - Biogeographic patterns in Solanum section Geminata.

The members of Solanum section Geminata are shrubs and small trees found in the understory of primary rainforest and secondary vegetation. The section is unusual in that many of its species grow in primary forest habitats. Species in section Geminata occur from southern Mexico to northern Argentina. No one species occupies the entire range, but several widespread and variable species do occur. Principal centers of species diversity are: 1) southern Mexico to Costa Rica, 2) the eastern Andean slope in northwestern South America (primarily Colombia), and 3) southeastern Brazil. This circum-Amazonian distribution is common in Solanum. Closely related species in section Geminata generally occur sympatrically within centers of diversity rather than allopatrically between centers. Several widespread species occur in northwestern South America and Central America, indicating a close connection between the two areas. No close species relationships appear to exist between northwestern South America and southeastern Brazil. Many of the species of section Geminata with more restricted ranges occur in some of the postulated Pleistocene rainforest refugia. This biogeographic pattern will be considered with respect to the distribution of primary forest species of section Geminata.

KRESS, W. JOHN. Department of Botany, Duke University, Durham, NC 27706.

- Adaptive differences in the floral biology of Old and New World species of Heliconia.

Heliconia is an example of a banana relative that has undergone evolutionary modification of reproductive characteristics in response to different pollinators. The great majority of the species are found in the American tropics and they all have brightly colored inflorescences. The short-lived flowers are open during the day and are pollinated exclusively by hummingbirds. A small disjunct group of heliconias are native to the South Pacific Islands of Melanesia. The inflorescences of the Old World species are dull green and the flowers are nocturnal. These features are similar to sympatric species of the wild banana that are known to be pollinated by macroglossine bats. This paper presents the results of field research in Central America and the South Pacific and develops a hypothesis on the derivation and spread of the Old World introductions.

LEE, PETER F. Department of Biology, Lakehead University, Thunder Bay, Ontario P7B 5E1.  
- Production of wild rice on a seeded lake near Ignace, Ontario.

The objective of this study was to determine the factors affecting wild rice production on Oval Lake which was uniformly seeded with 2270 kg of wild rice seed in the winter of 1979. In the spring the depth of the lake was lowered to a mean value of 31 cm. In August of 1979, sampling of the lake was done along transects for intraspecific competition, interspecific competition, sediment pH, nitrogen, phosphorus, potassium, calcium, magnesium, iron, manganese, zinc, copper and loss on ignition. Utilizing cluster and discriminant analyses, the lake was divided into production regions. Factors affecting these production regions were primarily intraspecific competition and organic, phosphorus, and micro-nutrient concentrations of the sediment. Trials under greenhouse conditions revealed that production could be greatly increased with the addition of nutrients. Since 1979 other production problems including interspecific plant competition, seed survival and nutrient depletion have developed. Management implications to increase the commercial harvest of approximately 10000 kg per year are discussed.

MISHLER, BRENT D. Farlow Herbarium, Harvard University, Cambridge, MA 02138 - Phylogenetic relationships and generic limits of Tortula (Musci: Pottiaceae): evidence from SEM studies of the peristome.

The genus Tortula (Hedw.) has historically been considered a "basal" group in the phylogeny of the subfamily Pottiaceae. Work in progress on the cladistic relationships of the subfamily, based on a number of characters, shows that the genus Tortula (as currently delimited) is indeed an artificial, paraphyletic group. SEM studies of peristomes have yielded a wealth of characters useful in determining monophyletic groups at various levels of analysis. The presence of a basal membrane is a widespread feature, not useful for defining Tortula, or even the whole subfamily. However, details of the sculpturing, position, and arrangement of the cell walls making up the basal membrane, particularly the pro-tean variation of the fine ornamentation, have proved to be useful indicators of relationship. A monophyletic group can be distinguished that roughly corresponds to the segregate genus Syntrichia Brid. (which, however, must be called Tortula because the type species of the latter is included), by a suite of characters including the high basal membrane with its unique fine-scale ornamentation. Other species now placed in Tortula seem to be more closely related to other genera.

OKOLI, 'BOSA EBENEZER. Department of Botany, University of Port Harcourt, P.M.B. 5323, Port Harcourt, Nigeria. - Wild and cultivated cucurbits in Nigeria: their uses and economic potentials.

The family Cucurbitaceae is well-represented in Nigeria by about 20 genera and 45 species. It is an extremely interesting and unusual family distributed largely in the tropics. Most of the species are wild but a good number are cultivated. The family has perhaps the greatest number of species in cultivation for diverse purposes in different parts

of the country. Certain genera such as Telfairia, Cucurbita, Citrullus, Cucumeropsis, Cucumis and Trichosanthes are cultivated in southern Nigeria since their fruits and/or leaves constitute important items in the diet. Other genera are important as oil plants, medicinal plants, sources of tanning materials, sponges and house-hold utensils. An outline biology and potential uses of the lesser known indigenous species are discussed.

PRYER, KATHLEEN M.,\* DONALD M. BRITTON and JOHN McNEILL. Department of Biology, University of Ottawa, Ottawa, Ontario, Canada, K1N 6N5 and Department of Botany and Genetics, University of Guelph, Guelph, Ontario, Canada N1H 2W1. - Systematic studies in the genus *Gymnocarpium* Newm. (Aspleniaceae) in North America.

Morphological, phytochemical and cytological studies have resulted in a systematic revision of the genus *Gymnocarpium* in North America. Multivariate analysis of the morphological data supports the recognition of six taxa. Additionally, cluster analysis and ordination of the phytochemical data established that each of these taxa can be recognized by its chromatographic profile alone. These data support the recognition of *G. robertianum* and *G. jessoense* subsp. *parvulum* as distinct taxa, and the hybrid origin of *G. x intermedium*. The chromatographic profile of *G. intermedium* is essentially a summation of the profiles of its presumed parents, *G. dryopteris* subsp.

*disjunctum* and *G. jessoense* subsp. *parvulum*. Scanning electron microscopy was used to examine variation in perispore characters both within and between taxa. In contrast to previous studies in the genus, spore morphology proved to be impractical in species discrimination, since all taxa exhibited similar patterns of variation. However, spore size was correlated with ploidy level, permitting delimitation between the diploid and tetraploid subspecies of *G. dryopteris*.

WELLS, ELIZABETH FORTSON. Department of Biological Sciences, The George Washington University, Washington, D.C. 20052. - Comparative floral development in four species of *Heuchera* (Saxifragaceae).

Flower development was studied in four species of *Heuchera*. Mature flowers of the four species differ as to size, exertion of stigmas and anthers, and hypanthium length. Flower development is very similar among the four species in the very early stages but later diverges in several significant ways. A size difference is first evident in the undifferentiated flower primordium. After sepals, petals, and stamens appear, intercalary growth at their base forms a free hypanthium, which varies in length and degree of asymmetry from species to species and serves as a key character in recognizing each species. The major differences between the flowers of the four species are shown to result from differences in the size of the undifferentiated flower primordium and in the onset, duration, and asymmetry of intercalary growth.

## GENETICS SECTION

### Symposium: Competence, Determination and Canalization in Plant Development

#### INTRODUCTION

The symposium will focus on the concepts of developmental genetics and consequent concern with cellular, intracellular and molecular events. Current interest in such an analytical approach to the study of plant development coupled with the experimental questions that can now be answered using molecular probes and in situ hybridization suggest that this subject area will be one of rapid progress and exciting discoveries in the next few years.

Organized by Michael L. Christianson, Zeecon Corporation, Palo Alto, CA.

CHRISTIANSON, MICHAEL L.\* and DEBRA A. WARNICK. Department of Molecular Biology, Zeecon Corporation, Palo Alto, CA 94304. - Competence and determination in shoot initiation *in vitro* by *Convolvulus arvensis*.

The process of shoot organogenesis from leaf explants *in vitro* includes two events of developmental biology. The explants acquire competence, and as a result of the induction which ensues, they become determined for shoot formation. This latter event precedes the appearance of shoot apices in paraffin section. Unlike the

developmentally plastic meristemoids in *Convolvulus arvensis* roots *in vitro* and *in vivo*, the meristemoids formed in callus have unique fates. Culture on shoot-inducing medium, SIM, produces cells or groups of cells determined specifically for shoot formation; transfers from SIM to root-inducing medium, RIM, near the time the tissue becomes determined do not lead to root formation. In contrast, the competence which explants acquire during the first days in culture is general. Exposure of explants to SIM, RIM, or simply callus-inducing medium, CIM, develops competence for shoot induction. Indeed, some genotypes of *C. arvensis* which do not make shoots on SIM, will make shoots when culture on SIM is preceded by brief preculture on CIM. Varying the amount of preculture on CIM shows that the duration and stability of the competent state is genotype specific. Extended culture on CIM shows that competence is not synonymous with callus initiation or growth.

DAVIDSON, D. Department of Biology, McMaster University, Hamilton, Ontario, L8S 4K1. - Patterns of cell proliferation and mitotic asymmetry in root meristems.

Meristems are ordered structures: their different tissue types form a well defined pattern and their overall growth results in increases in cell number and cell size along a single axis. This constancy of pattern is maintained in spite of the variation, in

different tissues, in the rates, axes and degree of asymmetry of cell division. Evidence for such variation will be presented and will be related to fluctuations: 1) in cell cycle duration within individual cell lineages; 2) in the orientation of asymmetrical divisions. These fluctuations will be shown to occur independently even in adjacent columns of cells. Division asymmetry produces two nuclei and two cells of different sizes; the sister nuclei also differ in RNA and protein content and in cell cycle duration. Evidence will also be presented for changes in nuclear:cytoplasmic ratios in roots of germinating seeds. It will be argued that cell cycle duration is a phenotypic trait that is plastic, that may vary independently of cell size and of the rate of cell elongation, and that is regulated, to a large degree, autonomously in individual lineages of cells.

MCDANIEL, CARL N. Department of Biology,  
Rensselaer Polytechnic Institute, Troy, NY 12181.  
Determination for floral development in day-neutral tobacco and sunflower.

Populations of day-neutral tobacco (*Nicotiana tabacum* L.) and sunflower (*Helianthus annuus* L.) plants form reproductive structures after a uniform amount of vegetative growth as measured by number of nodes (Dev. Biol 66: 250-255; Growth 36: 339-349). The total number of nodes produced by the terminal meristem of a sunflower plant cannot be increased by rooting or grafting. These observations indicate that early in development the sunflower meristem becomes determined for floral development. In contrast, the tobacco terminal meristem can be made to produce significantly more nodes by grafting and rooting. By continually rooting the terminal portion of the shoot, the meristem will remain vegetative indefinitely (Planta 148: 462-467). However, during the normal course of growth the tobacco meristem does become determined to form a flower. This determination is not only expressed by axillary buds but also by internodal cells. That is, axillary buds near the inflorescence exhibit determinant growth and internodal cells from the inflorescence can form *de novo* floral buds (Planta 115: 87-92). These two species exhibit stable determination for floral development but the timing of the determination event is markedly different. As a result, two distinct patterns of growth are observed. The sunflower has a determinant growth pattern which is established prior to or soon after germination. The determinant growth pattern of tobacco is not initiated until long after germination. Although only determination has been considered in the above, competence and induction are involved in the flowering process and will be considered. Support from NSF, PCM 82-04491.

MURRY, LYNN E. Zoecon Corporation, 975 California Avenue, Palo Alto, CA 94304. - Competence and determination in the developing root epidermis of barley. In tissue culture, the term competence describes the time after which cells in a callus are responsive to changes in the growth medium, i.e., inducible. Once physical or chemical induction takes place, certain cells organize to become either a root or shoot. The term determination defines the latter point beyond which induction is irreversible. While these terms work well at the organ level of plant organization, they may have slightly different meanings when applied to developing tissue systems. In the progression of cellular events which produces the mature root epidermis, competence is assumed to occur in the proximal

protoderm which gives rise to trichoblasts and atrichoblasts. Trichoblasts are distinguishable in many species as short, densely cytoplasmic cells which result from an asymmetric cell division, contain elevated amounts of nuclear DNA, and give rise to root hairs. They represent the cell in which determination would normally occur. My data indicates that determination is not a single, irreversible event in developing epidermal tissues. In *Hordeum vulgare* Larker, environmental influences greatly affect root hair development. Under control conditions, morphological differentiation of trichoblasts proceeds in a timely manner, and nuclear DNA amounts are double (2C) that found in the meristem (1C) of the same root. With 300 mM NaCl stress, root hair growth and differentiation are slow, and differential replication of the DNA is suppressed. In 200-300 mM  $KH_2PO_4$ , epidermal nuclei become increasingly vacuolate, nuclear DNA doubles, and root hair differentiation is completely suppressed. In barley, epidermal development and differentiation requires two commitments, one involving the nuclear state and the other, the morphological state.

SAWHNEY, VIPEN K. Department of Biology,  
University of Saskatchewan, Saskatoon, Sask. S7N  
OWO, Canada - Developmental regulation of a male-sterile, stamenless-2 mutant of tomato.

The single gene recessive mutant, stamenless-2 (sl-2/sl-2), of tomato (*Lycopersicon esculentum*) produces structurally abnormal stamens and non-viable pollen. The development of stamens can be regulated by plant hormones and temperature conditions. Gibberellic acid ( $GA_3$ ) induces the formation of normal stamens with viable pollen whereas indole-acetic acid (IAA) causes the formation of carpel-like structures in place of stamens with no evidence of microsporogenesis. Similarly, low temperatures (18°C day/15°C night) promote the formation of normal stamens, and high temperatures (28°C day/23°C night) induce the formation of carpel-like structures. Relative growth studies of stamens and timing experiments with  $GA_3$  have shown that at the time of initiation, the stamen primordia of mutant flowers, although morphologically similar to the normal, possess some differences from them and that their developmental path is not completely fixed at this time. Further it was shown that various features of stamens are canalised sequentially at later stages of development. A comparison of protein patterns, by using iso-electric focusing and second dimension SDS-PAGE, has shown some differences in the mutant and normal stamens.

WALKER, KEITH A. Plant Genetics, Inc.  
1930 5th Street, Davis, CA., 95616.

-Modeling morphogenesis. Experimental approaches with alfalfa somatic embryogenesis. Researchers of the last two decades have developed physiological models for the control of induction and expression of regeneration in cells cultured *in vitro*. Over this time work on asexual embryogenesis in somatic cell cultures has contributed greatly to our current understanding of hormonal, nutritional, and environmental factors which influence the process. Nevertheless, these studies have not led to a deeper understanding of the mechanism underlying those forces which shape the development of the embryo either *in vitro* or *in vivo*. The view is presented that to achieve a greater understanding

of the developmental regulation during adventive embryogenesis, systems which permit the spacial and temporal separation of induction, determination and differentiation processes as well as the availability of competent and noncompetent populations of cells will be required. In this context, the suitability of alfalfa somatic embryogenesis as a system for the study of basic developmental mechanisms shall be examined. The state of knowledge regarding the role of this process played by the hormonal factor 2,4-D, and other trophic factors shall be presented with the goal of suggesting opportunities for future research.

WARNICK, D. A. Department of Molecular Biology, Zeecon Corporation, Palo Alto CA 94304. - Convolvulus arvensis: Rhizogenesis in vitro.

Leaf explants of Convolvulus arvensis can produce either roots or shoots when cultured on a basal medium of Murashige and Skoog salts, vitamins and sucrose with the addition of 12 mg/l IBA for root-inducing medium, RIM, or 0.05 mg/l IAA and 7.0 mg/l 2-ip for shoot-inducing medium, SIM. A screen of 105 seed derived individuals from two localities shows that root- and shoot-organogenesis are independent phenomena. Successive transfers to basal medium show that culture on root-inducing medium, RIM, results in the explants becoming determined for root formation: development proceeds to completion on basal medium. The minimal, necessary exposure to RIM is reproducible, genotype-specific and varies from 3 to 10 days. Histological examination reveals meristemoids at the time of determination and that roots arise endogenously in the callus produced at the edges of the explant. Despite the apparent independence of the ability of explants to produce roots on RIM and shoots on SIM, transfer experiments find that preculture on SIM can improve root formation on RIM. Other experiments show that RIM can substitute for SIM during the first few days of shoot induction. Description of the similarities and differences in the early events of root- and shoot-organogenesis may be important to achieve whole plant regeneration in certain agronomically important species.

## Symposium: Developmental Genetics of Higher Plants

FREELING, MICHAEL. Department of Genetics, University of California, Berkeley, CA 94720. - Developmental consequences of insertions in the Adh1 gene of maize.

Almost every gene in higher organisms is regulated differentially per tissue or developmental stage; maize Adh1 is no exception (cf.1). We are trying to understand the regulatory properties of Adh1 by inducing mutants in a known progenitor allele, Adh1-S. We then compare mutants and progenitor at every level down to nucleotide sequence and sequence arrangement. The Adh1 variants and mutants that affect ADH expression in different organs coordinately are caused by small changes at the DNA level. Five independent insertions lower or obliterate ADH1 expression; all are within the about 4 kb transcriptional unit. Mutant alleles caused by the insertion of 1.4 kb Mu1 express various, lower mRNA levels (1). The three Mu1 insertion alleles have the element in the first intron, but at different sites; one has been located to the nucleotide (Bennetzen, Strommer, Taylor and Freeling, in preparation). Two other, different

insertions are transcribed, the message is appropriately larger than 1650 nt, and these are genetically linked to poor transmission through the pollen and, in one case, a dominant leaf growth morphology called "Knotted". I suspect that some insertions at Adh1, a dispensable gene, initiate chromosomal position effects on nearby, indispensable genes.

It may yet be possible to work backwards from regulatory mutants to developmental programs.

(1) Strommer, J. N., S. Hake, J. Bennetzen, W. C. Taylor and M. Freeling, 1982. *Nature* 300:542-544.

POETHIG, R. SCOTT. Department of Biology, University of Pennsylvania, Philadelphia, PA 19104. - The use of genetic mosaics for the analysis of plant development.

Traditional histological techniques provide limited information about the cellular dynamics of morphogenesis and the fate of initial cells. These morphogenetic parameters can be established easily and unequivocally, however, from x-ray induced somatic sectors (a technique called clonal analysis). Recent clonal analyses of leaf morphogenesis in tobacco, and of embryogenesis and shoot development in maize, have provided dramatically new pictures of these phenomena. Clonal patterns in tobacco, for example, demonstrate that the leaf is not derived from a small group of apical initials as is generally assumed, but from a relatively large group of cells, each of which contributes to a characteristic section of the leaf. Furthermore, there is no evidence for the existence of a marginal meristem; the expansion of the lamina depends entirely on intercalary growth. Somatic sectors induced during the development of the shoot apical meristem in maize demonstrate that, like the tobacco leaf, it arises from a large group of cells each of which has a characteristic (though not determined!) fate. Two general conclusions can be drawn from these studies: 1) within the constraints imposed by their position within a plant, the fate of individual cells is variable; and 2) apically situated cells in a determinate meristem make only a limited contribution to the growth of the meristem.

SHERIDAN, WILLIAM F. Department of Biology, University of North Dakota, Grand Forks, ND 58202. - Genetic Regulation of Plant Embryogenesis

Three promising systems for studying the genetic regulation of plant embryo development have been reported. These are the embryo-lethal mutants of Arabidopsis, the carrot temperature-sensitive variants blocked in somatic embryogenesis and the defective kernel (dek) mutants of maize. A model system for a genetic analysis of plant embryo development utilizing embryo-lethal mutants of Arabidopsis was proposed and six nonallelic recessive mutants that were characteristically arrested at early stages of embryo development were described by Meinke and Sussex (1979a, b). Recently, the isolation of a number of temperature-sensitive carrot cell variants was reported by Breton and Sung (1982). These variants are stable in culture and most are maintained through plant regeneration and exhibit the ts trait when put back into culture. The variants are blocked at different stages of development including some that cannot grow in embryogenic medium, others than can grow only as callus, and others blocked prior to the heart stage of embryogenesis. The variants are all spontaneous in origin and their stability and temperature sensitivity are consistent with their being mutants. The examination of a large group of de-

fective kernel mutants, representing many gene loci (Neuffer and Sheridan 1980), by morphological and embryo culture techniques (Sheridan and Neuffer 1980) led to the suggestion that many were potential candidates as developmental mutants (Sheridan and Neuffer 1981). A group of 20 such mutants were identified and examination of mature North Dakota grown ears of 17 of these 20 revealed that 14 of them were indeed blocked prior to leaf primordia formation (Sheridan and Neuffer 1982). Recent results with these maize mutants will be presented.

SMITH, J. D. Plant Sciences Department, Texas A&M University, College Station, Texas 77843.

#### Regulation of Seed Development in *Zea mays*.

The termination of seed development in a dormant seed is so prevalent that it is easy to think of dormancy as an obligatory final stage of seed development. However, the existence of viviparous seed in a variety of species establishes dormancy as an optional rather than obligatory developmental stage, and the viviparous mutants of *Zea mays* indicate that the induction of seed dormancy is genetically regulated. Abscisic acid (ABA) is unquestionably involved, but its mode of action, the cellular reorientations it affects, the ontogenetic stage when these events occur, and even its biosynthetic pathway have not been defined. Investigations of the viviparous mutants have established that the carotenoid-deficient mutants are also ABA deficient and the *vp* mutant, which has normal ABA content and is insensitive to exogenous ABA, appears to be an ABA-receptor mutant. The carotenogenesis inhibitor fluridone indirectly inhibits ABA synthesis and induces vivipary if applied at the appropriate time. Experiments with genetically and chemically induced viviparous seed have elucidated the ABA biosynthetic pathway, defined the ontogenetic stage when the induction of dormancy is initiated, and identified some of the biochemical events that are affected by ABA at this time. Supported by USDA CRGO Grant No. 79-59-2485-1-1-370-1.

## Contributed Papers

AMOAH, VICTOR and PAUL GRUN. Department of Horticulture, Pennsylvania State University, University Park, PA 16802.

#### - Maternal regulatory control of yield components in *Solanum*.

Analyses of yield components of back-cross two progenies of *S. tuberosum* ssp. *andigena* x ssp. *tuberosum* and (*S. phureja* x *chacoense*) x ssp. *tuberosum* showed the presence of significant differences between reciprocals. The inheritance of the reciprocal differences was not that of cytoplasmic factors. They cannot be ascribed to the "maternal effect" since the differences were maintained over a time period well beyond that when contents of the egg contributed by the maternal parent would have been diluted by gene products of the plant's somatic chromosomes. The phenomenon cannot be ascribed to dauermodifications since differences between the parents were not environmentally induced. An interpretation of this

phenomenon will be discussed based on a concept of maternal regulatory genes.

HART, GARY E. Department of Plant Sciences, Texas A&M University, College Station, TX 77843.

#### - Discovery and genetic control of a hexaploid wheat NAD-dependent alcohol dehydrogenase which acts on aromatic alcohols.

Genes which encode isozymes are valuable markers for the chromosomes and chromosome arms of *Triticum aestivum* (hexaploid wheat,  $2n = 6x = 42$ , genomes AABBDD) and its relatives in the Gramineae tribe Triticeae. Approximately 80 isozyme genes have previously been identified and located in chromosome arms in hexaploid wheat cv. Chinese Spring. I report here the discovery of a NAD-dependent aryl-alcohol dehydrogenase (ADH, E.C. 1.1.1.90) which utilizes cinnamyl alcohol as a substrate. Analysis of the available compensating nullisomic-tetrasomic derivatives and the homoeologous chromosome group 6 ditelosomic strains of Chinese Spring have provided strong evidence that this enzyme, which has been designated ADH-3, is active as a dimer and is encoded by a paralogous set of three genes, designated *Adh-A3*, *Adh-B3*, and *Adh-D3*, which are located in chromosome arms 6Aq, 6Bq, and 6Dq respectively. Orthologous *Adh-3* genes have been detected and located in chromosomes in *Elytrigia elongata* (chromosome 6E), *Secale cereale* cv. Imperial (6R) and *Hordeum vulgare* cv. Betzes (6H). The *Adh-3* genes should serve as additional useful markers for group 6 chromosomes in the Triticeae.

HENKE, R. R.\*, G. L. FOWLER, J. K. THOMPSON and B. C. MULLIN. Department of Botany, The University of Tennessee, Knoxville, TN 37996-1100. - The selection of p-fluorophenylalanine resistant mutants in barley.

Mutagenized  $M_2$  populations of barley, *Hordeum vulgare* cv. Atlas 57 were screened for resistance to the phenylalanine analog, p-fluorophenylalanine (Pfp). The initial selection was carried out by screening embryoless halved seeds for the capacity of their aleurone tissue to synthesize and release a functional  $\alpha$ -amylase when incubated in the presence of the analog. The  $\alpha$ -amylase activity was determined visually using a  $I_2/KI$ /soluble starch assay. Individual half-seeds when incubated in the presence of soluble potato starch and  $GA_3$  under appropriate conditions produced sufficient  $\alpha$ -amylase to completely hydrolyze the starch. This resulted in a clear, yellow-colored incubation medium when stained with  $I_2/KI$ . Pfp inhibited the synthesis of functional  $\alpha$ -amylase in wild type half-seeds resulting in visually distinct blue-black color reaction with  $I_2/KI$ /medium color reaction, indicating aleurone expression of a functional  $\alpha$ -amylase in the presence of the inhibitor. Approximately 14,000  $M_2$  half-seeds were screened. This resulted in the isolation of 186 putative Pfp-resistant mutant half-seeds. The embryo-containing portion of these half-seeds was grown to maturity and their progeny tested for Pfp-resistance. Segregation, in various ratios of the mutant trait was observed in the progeny of 12 of the parents tested. One of the  $M_2$  plants gave rise to progeny that were homozygous for Pfp-resistance and were also homozygous for darkly pigmented seeds. This phenotype has remained stable through a subsequent generation. Details of the screening protocol and some properties of the Pfp-resistant mutants will be presented.

KOKONTIS, JOHN M. AND E.D. GARBER  
Department of Biology, University of Chicago,  
Chicago, IL 60637

-Spontaneous and induced mitotic recombination in *Ustilago violacea* detected at the cellular level.

Spontaneous and induced mitotic recombination in the heterobasidiomycete *Ustilago violacea* was detected at the cellular level using the recessive morphological mutation "pseudohyphal" (*ph*). Mitotic recombination in a *ph+ph* diploid sporidium giving a *ph/ph* condition results in a drastically elongated cell which is microscopically distinguishable from *ph+ph* cells. The percentage of microcolonies (50-100 cells) containing at least one *ph/ph* cell is an accurate measure of recombination between the *ph* locus and its centromere. Recombination was induced by ultraviolet light (UV), nitrogen mustard (NM) and metabolically non-activated cyclophosphamide (CP). Spontaneous recombination giving a *ph/ph* cell occurred in  $4.1 \pm 0.5\%$  of microcolonies. While maximal UV and NM induction was 85-95%, maximal CP induction of recombination was only 6.7%. Low temperature (14°C) applied after inductive treatment uniformly reduced recombination to spontaneous levels, while high temperature (30°C) increased UV-induced recombination, had no effect on NM-induced recombination and reduced CP-induced recombination to spontaneous levels. Temperature alone had no effect on recombination. UV induction of recombination was dependent on the rate of cell division; rapidly dividing log-phase cells were most sensitive to UV induction of recombination. The cellular detection of mitotic recombination is a method of assaying post-replication repair of genetic damage and a possible screen for agents causing genetic damage in eukaryotic cells.

MULCAHY, DAVID L.\* AND GABRIELLA B. MULCAHY.  
Department of Botany, University of Massachusetts,  
Amherst, MA 01003.

- Gametophytic self incompatibility reexamined.

Gametophytic self incompatibility is generally understood to involve the active inhibition of self pollen tubes by a specific molecule. This is the classical, "oppositional model." The model, however, is unable to accommodate a number of well established observations: quantitative variation in the incompatibility reaction, the activation of new incompatibility alleles by inbreeding, the difficulty of mapping the S-gene, the inexplicably large numbers of S-alleles observed in natural populations, and the presence of self compatible individuals among dihaploid derivatives of self incompatible plants. Each of these anomalies can be explained if we assume that there are complementary interactions between pollen tubes and the styles. Interesting implications of this hypothesis include possible explanations for several types of pollen-style interactions presumably not related to self incompatibility. There is also the suggestion that, with some cases of gametophytic self incompatibility, there may be no S-gene, as classically envisioned.

PRICE, H. J., K. CHAMBERS, and K. BACHMANN, Texas A&M University, College Station, TX 77843, Oregon State University, Corvallis, OR 97331, and Heidelberg University, West Germany. -

Temporal changes in DNA content of *Microseris douglasii* populations.

Nuclear 2C DNA content of *M. douglasii* varies over 20% among plants and by 14% among populations. High DNA content populations are restricted to more mesic sites. A correlation between the amount of annual rainfall and DNA content was temporally observed within a single site near Jolon, CA, over a 15-year interim. Only high DNA content plants (ca. 23.50 FAU = Feulgen absorbancy units) were found in the 1973 collection prior to the last major drought. Only low values (ca. 21.50 FAU) were found in plants collected in 1977 which marked the end of the drought. There have been five successive growing seasons with ample rainfall beginning 1978. We have sampled several populations annually since 1980 to see if high DNA content plants increase in frequency over several high rainfall years, and decrease during successive drought years. High DNA content plants comprise about 5% and 40%, respectively, of the plants measured from the 1980 and 1981 Jolon collections. A sample in 1977 from a population near the Parkfield-Coalinga Road summit was highly variable in DNA content,  $X = 23.03 \pm 1.06$  FAU. The 1980 and 1981 populations were individually fairly uniform with respective mean DNA contents of  $22.57 \pm .21$  and  $23.19 \pm .23$  FAU. Subsequent sampling of these populations should allow us to determine whether DNA content evolves in response to environmental changes. Supported by NSF grant DEB 8009427 and the Texas Agricultural Experiment Station.

UHL, CHARLES H. Section of Plant Biology, Cornell University, Ithaca, NY 14853. - Preferential pairing of chromosomes in hybrids of the Mexican Crassulaceae.

Natural polyploids in the Mexican Crassulaceae appear to be autopolyploids, and no plants from the wild have yet been definitely identified as allopolyploids. Hybrids also appear to be very rare in nature. Nevertheless, hundreds of allopolyploid hybrids (AABB), many of them intergeneric, have been produced in cultivation. Parents of most of these hybrids had different chromosome numbers, but at meiosis most or all of their chromosomes regularly form bivalents only, regardless of the parental chromosome numbers, and most such hybrids yield abundant second-generation progeny. Evidently pairing here is strongly preferential between corresponding chromosomes of two sets received from the same polyploid parent (autosomesynesis). Appropriate crosses and backcrosses have produced second-generation hybrids having one, two, or three sets of chromosomes from an original wild tetraploid, with phenotypes to match. Second-generation hybrids with a third autotetraploid (CCCC) are autoallotetraploids (ABCC) and show similar preferential pairing between homologues of the two C-genomes. Most also show considerable pairing between chromosomes of the A and B sets, even where they differ in number and failed to pair with each other in the  $F_1$  (where full homologues were present). (Extensive chromosome pairing also characterizes most diploid hybrids here, regardless of differences in their chromosome numbers.) The basis for the high preference and selectivity in chromosome pairing here is not known, but the situation seems different from the regulated chromosome pairing that is well known, for example, in allopolyploids of wheat.

## HISTORICAL SECTION

Special Lecture: Darwin's *Beagle* Collection

PORTER, DUNCAN M. Department of Biology, VPI & SU, Blacksburg, VA 24061.

- Darwin's Beagle collections.

Little has been published on the contents and disposition of the plant, animal, and geological collections that Charles Darwin gathered on the voyage of HMS *Beagle*. There are many clues in the contemporary papers published on the various groups by John Gould, George Waterhouse, Francis Walker, Adam White, and Darwin himself, but little of this information has penetrated into the modern literature. Unpublished notes in the Darwin Archives at the Cambridge University Library, at Down House, and at the British Museum (Natural History) provide more clues. Examples of treasures recently unearthed are Darwin's Geological Specimen Notebooks, conveyed in 1981 from the Mineralogy and Petrology Museum to the University Library by Dr. Sandra Herbert, my finding of his Plant Notes in the Cambridge University Herbarium, and my recent discovery that the notes on Insects in Spirits of Wine, thought to have been missing from the Insect Department of the British Museum (Natural History) since 1927, are right where they should be. Information from these sources and others will be used in discussing where the specimens are now to be found and how they arrived there, with emphasis on the plants and fungi.

## Poster Session

OLSON, JERRY S. Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830. - Mapping World Vegetation for Ecosystem Cycling.

Forest clearing, cutting, and fire have decreased areas and age classes of woody vegetation and lowered global pools of phytomass and its organic carbon, nitrogen, and sulfur compared with preagriculture or preindustrial times. A computer data base helped generate color separation plates for printing a map of 44 land ecosystem complexes in seven broad groups: FOREST AND WOODLAND; INTERRUPTED WOODS; MAINLY CROPPED, RESIDENTIAL, COMMERCIAL, PARK; GRASS AND SHRUB COMPLEXES; TUNDRA AND DESERT; MAJOR WETLANDS; and OTHER COASTAL, AQUATIC, AND MISCELLANEOUS. A global estimate for C in live plants near  $560 \pm 100$  Pg ( $10^9$  tons) is far below estimates formerly used in some carbon cycling analyses. Tropical forests (1) probably already have been reduced more than is commonly realized, and (2) may never have been as widespread or massive as recently supposed.

Research supported jointly by the Carbon Dioxide Research Division, U.S. Department of Energy, under contract W-7305-eng-26 with Union Carbide Corporation and the U.S. National Science Foundation's Ecosystem Studies Program under Interagency Agreement No. DEB 77-26722.

## Contributed Papers

PRINGLE, JAMES S. Royal Botanical Gardens, Box 399, Hamilton, Ontario, Canada L8N 3H8.

- Biographical notes on two collectors cited in Hooker's Flora Boreali-Americana.

Anne Mary Perceval (1790-1876) was the daughter of Sir Charles Flower, Bt., Lord Mayor of London. She came to Quebec in 1810 when her husband was appointed H.M. Collector of Customs. The Percevals acquired a large estate with extensive woodlands in nearby Sillery, part of which is now the Bois de Coulonge. Mrs. Perceval, along with William and Harriet Sheppard, was probably recruited as a collector for Hooker's Flora by the Countess of Dalhousie. Her collecting sites included Sillery, Ste.-Foy, and Cap Rouge; recipients of specimens, besides Hooker, included Darlington, Torrey, and Schweinitz. She returned to Britain in 1829, and spent her latter years on the Isle of Lewis.

Clement Charles Todd (d. 1828), a naval surgeon, served at Kingston and in the Battle of Lake Champlain before being sent to Penetanguishene in 1819. He was already knowledgeable in botany when he was invited to collect plants for Hooker by John Richardson in 1825, when the 2nd Franklin Expedition passed through Penetanguishene. Todd collected on the Penetanguishene Peninsula and along the Severn River from 1825 through 1827. His paper on the climate of Penetanguishene includes the first publication of phenological observations in Upper Canada. He returned to London for further study in 1827, and died there while awaiting duty on H.W. Bayfield's Gulnare expedition.

RUDOLPH, EMANUEL D. Department of Botany, The Ohio State University, Columbus, OH 43210. - The role of Almira Hart Lincoln Phelps in the spread of botany in nineteenth century America.

Mrs. Phelps as a young woman came under the influence of her older sister Emma Willard, who helped form her educational philosophy, and of Amos Eaton, who helped form her botanical and scientific understanding. Feeling the lack of a suitable botanical textbook to introduce students to the subject, particularly female students who were becoming more prevalent, she wrote one, Familiar Lectures on Botany, published in 1829, using her first husband's surname. Mrs. Lincoln's Botany quickly became popular and continued to be revised and reprinted through 1875. In 1833, a second botany text for lower level students, Botany for Beginners, appeared. It too, went through many reprintings up to 1870. Mrs. Phelps' other books and writings on science and education were popular also. The botanical texts were educationally innovative in starting with flower structure using common living examples and later considering other morphological and physiological aspects of plants. The Linnean System was used to classify the "most common native and foreign" plants that were described. Clear figures, often copied from well-known authorities helped to instruct teachers and students. Because of its wide usage, even in later years in competition with the textbooks of Asa Gray and Alphonso Wood, Mrs. Phelps' books were an important factor in educating many students, especially females, in botany and inducing some of them to have a life-long interest in the science.

## MICROBIOLOGICAL SECTION

## Poster Session

TRAQUAIR, JAMES A.\*, and RENÉE B. MELOCHE.  
Research Station, Agriculture Canada, Harrow,  
Ontario, Canada NOR 1G0; SHANNON M. BERCH.  
Département d'Écologie-Pédologie, Université  
Laval, Ste-Foy, Québec, Canada G1K 7P4. -  
Endotrophic (vesicular-arbuscular) mycorrhizae  
of *Prunus persica*.

Three seedling rootstocks of peach (cv. Bailey, Harrow Blood, and Siberian-C) were compared with respect to endomycorrhizal colonization. The incidence of arbuscules and vesicles was noted in feeder roots fixed in formalin-acetic acid-alcohol (FAA) and stained with acid fuchsin. Spore frequency in nursery soil associated with these roots was determined by flotation and wet-sieving techniques. Microscopic examination of stained root segments revealed extensive colonization of the cortex by endotrophic mycorrhizal fungi. External mycelium, lobulate infection hyphae, arbuscules in various stages of development, and vesicles were evident in all three hosts. Arbuscules were observed more frequently in Bailey or Harrow Blood roots than in Siberian-C ( $p = 0.05$ ) but arbuscular frequencies in Bailey or Harrow Blood did not differ. No differences were observed between the cultivars with respect to intensity of endomycorrhizal colonization, fungal types or the number of soil-borne spores. Spore densities were high (in the order of 30-60 spores/g soil) but many of these propagules were apparently inviable. *Glomus* and *Gigaspora* spp. were distinguished on the basis of spore size and morphology.

## Contributed Papers

CAVENDER, JAMES C. Department of Botany, Ohio University, Athens, Ohio 45701 - Cellular Slime Molds of the Rocky Mountains.

Soil populations of cellular slime molds are generally smaller and less diverse in soils of Rocky Mountain forests than in eastern deciduous forests. CSM were found at all elevations and habitats sampled. Of these, which exist along an altitudinal gradient—desert scrub, pinyon-juniper, ponderosa pine, spruce-fir and tundra, the subalpine spruce-fir belt, the most humid of the forest belts in this relatively dry region, proved to have the largest and most diverse populations. Almost all sites were dominated by two species *Dictyostelium mucoroides* and *D. sphaerocephalum*. Since Rocky Mountain soils are exposed to severe environmental fluctuations these two species are the most tolerant of the dictyostelids, particularly to moisture and temperature conditions. *Dictyostelium septentrionalis* was the only rare species discovered.

GRENVILLE, D.J. and Y. PICHE. Department of Botany and Genetics, University of Guelph, Guelph, Ontario, Canada N1G 2W1  
- Sclerotial development in two ectomycorrhizal fungi, *Pisolithus tinctorius* (Pers.) Coker & Couch, and *Paxillus involutus* (Batsch) Fr.

The sclerotia of *Pisolithus tinctorius* form in an intercalary position on mycelial strands following ectomycorrhizal formation. Initiation involves

numerous outgrowths of hyphal tips that branch frequently to form a tightly knit, lenticular swelling. Initiation of sclerotia occurs on mycelial strands that have turned bright yellow. Sclerotia are also yellow until they form a hard, black, smooth rind at maturity. SEM studies show that the developing sclerotia consist of interwoven, highly branched mycelia with the external hyphae possessing clamp connections and an extracellular coating. TEM studies show a fibrillar substance between the thick walled outer hyphae which possess dolipore septi. Light microscope studies and preliminary histochemical investigations indicate that the sclerotia have an outer rind of thick-walled hyphae surrounding a medulla where lipid, phenolic compounds and other storage substances are found. Sclerotial development in *Paxillus involutus* is similar to that of *P. tinctorius*; however, formation is more rapid. Sclerotia of *P. involutus* are spherical rather than lenticular and develop from buff brown mycelial strands and remain this colour until a black rind is formed at maturity. Sclerotia of *P. involutus* will also form on culture plates. Sclerotia of both fungal species are readily produced in growth pouches in association with *Pinus strobus*. It is possible that the sclerotia of these two species can be used as germplasm sources for further study of mycorrhizal systems and perhaps for inoculation of nursery stock. Research supported by a NSERC grant to R.L. Peterson.

SINHA, ASHA. Department of Mycology and Plant pathology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi - 221005, India.

- Microbial population of litter in a tropical deciduous forest.

Microbial decomposition of litter, collected from natural forest of Varanasi, was carried out by nylon bag technique. Fungal, bacterial, and actinomycetous populations were investigated monthly. The fungi were grouped as "dominant", "common", "frequent", and "rare" depending on their percentage frequency, abundance, sporulation and time of appearance in different months. *Alternaria alternata*, *Aspergillus flavus*, *A. niger*, *Cladosporium herbarum*, *Discosia maculicila*, *Fusarium semitectum*, *Phoma hibernica*, *Penicillium citrinum*, *P. rubrum*, *Torula graminis*, *Trichoderma harzianum* and Dark sterile mycelium are recorded as dominant fungi. *Arthrobacter*, *Bacillus*, *Pseudomonas* and *Micrococcus* were found to be dominant bacteria. The maximum fungi ( $86.25 \times 10^4/g$ ), actinomycetes ( $38.75 \times 10^6/g$ ), and bacteria ( $16.87 \times 10^7/g$ ) were recorded in August and minimum fungi ( $29.5 \times 10^4/g$ ) in February, actinomycetes ( $11.36 \times 10^6/g$ ) in May and bacteria ( $31.63 \times 10^7/g$ ) in March. Monthly variation in microbial population correlated with some climatic factors like moisture content, temperature, and relative humidity.

WILL III, OSCAR H., MANFRED RUDDAT AND EDWARD D. GARBER. Department of Biology, Barnes Laboratory, University of Chicago, Chicago, IL 60637  
- Carotenes and cytochrome c in *Ustilago violacea*  
Pigmentation in the smut fungus, *U. violacea*, results from the accumulation of carotenes and/or cytochrome

c. HPLC and spectroscopy were used to characterize and quantify the carotenes in white, pink, yellow, orange and pumpkin strains of U. violacea and liquid N<sub>2</sub> spectroscopy of whole cells or alkali extracts were used to quantify the cytochrome c levels. White strains contained only phytoene and/or traces of lycopene,  $\beta$ -zeacarotene,  $\gamma$ -carotene, or  $\beta$ -carotene and  $0.15 \times 10^{-11}$  mg/cell of cytochrome c. Pink strains contained either no carotene or a mixture of colored carotenes ( $30-60 \times 10^{-12}$  mg/cell). The cytochrome c content of pink strains was about 14 times that of white strains. The yellow strain accumulated a mixture of colored carotenes at a level of  $10 \times 10^{-11}$

mg/cell and cytochrome c at a level similar to that of the white strains. The pumpkin and orange strains accumulated carotenes at a level intermediate to pink and yellow strains. The cytochrome c content in the orange and pumpkin strains was similar to the pink strains. The white phenotype results from a general lack of colored carotenes and a physiological level of cytochrome c, while the pink phenotype results primarily from cytochrome c and in some pink strains also from colored carotenes. The pumpkin and orange phenotypes result from the presence of high cytochrome c levels and colored carotenes and the yellow phenotype from low cytochrome c and colored carotenes.

## PALEOBOTANICAL SECTION

### Contributed Papers

ASH, SIDNEY. Department of Geology-Geography, Weber State College, Ogden, Utah 84408. - Contrasting floras of the Upper Triassic bentonitic and redbed lithogenetic sequences of the Colorado Plateau.

The Upper Triassic continental rocks of the Colorado Plateau region have been subdivided by Stewart (1969) into three lithogenetic sequences that reflect the origin of the strata. Distinctive and contrasting floras which also seem to reflect the origin the strata occur in the two lower sequences. The lower-most sequence, the bentonitic sequence, consists principally of variegated bentonitic claystone, clayey sandstone, and conglomerate. It is thought to have been deposited primarily in streams and lakes and on floodplains. Plant fossils are common in the bentonitic sequence and most of those which have been described from the Upper Triassic rocks in the Colorado Plateau occurred at many places in this sequence. Nearly 60 species have been described from the sequence including representatives of most major plant groups. The fossils are generally fragmentary and most have been transported prior to burial and fossilization. The leaves are usually preserved as compressions. The overlying sequence, the redbed sequence, consists mostly of reddish-brown or reddish-orange siltstone. It is thought to have been deposited in lakes and on floodplains. In contrast to the situation in the bentonitic sequence, plant fossils are rare in the redbed sequence. They are known from only four areas and only four identifiable species have been described from the sequence. Most of the fossils have not been transported and occur in the position of growth. These include Neocalamites sp., Peloudea poleonensis, and Sanmiguelia lewisii. Typically, the fossils are preserved as impressions and pithcasts.

BASINGER, JAMES F. and DAVID L. DILCHER. Dept. of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, and Dept. of Biology, Indiana University, Bloomington, IN 47405. - Fruits of *Cercidiphyllum* from the early Tertiary of Ellesmere Island, arctic Canada.

Numerous clusters of follicles have been recovered from Paleocene shales of the lower Eureka Sound

Formation, Fosheim Peninsula, Ellesmere Island, 79°47'N 85°6'W. Individual follicles are about 13 mm long and 2 mm wide, are sickle-shaped, and are arranged so that tips converge at the tops of the clusters. Clusters are globose, 15-20 mm in diameter, with a peduncle about 10 mm long. The peduncle branches a few times at the base of the cluster to produce about 15 follicles borne in a terminal position. Fruits had dehisced prior to fossilization; seeds have not been found. Dehiscence occurs on both ventral (toward center of cluster) and dorsal surfaces. The fruits are associated with a low diversity flora including leaves of Cercidiphyllum, Tilia?, Glyptostrobus, and Metasequoia. While these compact clusters of fruits resemble reproductive organs of late Tertiary, and to some degree modern, Cercidiphyllum, they are unlike the elongate, multifollicular axes typically attributed to early Tertiary (Paleocene) Cercidiphyllum. This fossil material from Ellesmere Island may represent a lineage more closely allied to the living species than the Cercidiphyllum recognized in more southerly, early Tertiary localities. It is particularly interesting that these compact fertile shoots are found at an earlier age in the high arctic area than at lower latitudes.

BEELER, HAZEL E.\* and STEPHEN E. SCHECKLER. Department of Biology, VPI&SU, Blacksburg, VA 24061. - A new Upper Devonian tree lycopod.

A new tree lycopod has been discovered in the upper Hampshire Formation (mid to late Famennian) exposed at Elkins and Valley Head, WV, and Rawley Springs, VA. Axis fragments range from 3mm-6cm in diameter, and the largest do not appear to have been at the base of the plant. Taper of axes suggests the plant was 3-6m tall. Forking is equal and mainly in the crown. Outer surface of axes is smooth, without leaf cushions, but with vertically elongated, elliptical, slightly raised leaf scars, which are sparsely spaced and in a steep spiral. The exarch xylem cylinder is smooth and lacks pith in mid-sized axes. As in most lycopods, the stele occupies only a small portion of the stem (ca. 2mm in a 14mm diameter axis). The outer configuration of the new lycopod resembles Helenia and Heleniella, which are probably decortications, and some decorticated Lepidodendropsis. The latter, however, bears its leaves in a different arrangement from the new lycopod and has a ridged xylem cylinder. Furthermore, presence of epidermis, cuticle and leaves on some axes of the new lycopod indicate that we have its true outer surface. The new lycopod

appears to have been restricted to a near-swamp community. It is rare or absent both in floodplain sheet deposits and Rhacophyton swamps. When present in the latter, it seems to have been transported only a short distance, and becomes more common in the coarsening-upward sequences produced by swamp filling. The plant also occurs in allochthonous shoreline storm deposits near Rhacophyton swamps. This new tree lycopod is significant because it occurs in the near-swamp environment rather than being dominant in the swamp community as Lower Carboniferous tree lycopods are.

BLACKWELL, WILL H.,\* WAYNE D. MARTIN<sup>1</sup> and ROBERT G. McWILLIAMS,<sup>2</sup> Department of Botany and <sup>1,2</sup>Department of Geology, Miami University, Oxford, OH 45056.  
- Algal Remains in Cryptalgal Laminated Carbonates of the Upper Middle Cambrian of Northwest Wyoming.

Cryptalgal laminites, regarded by some as a type of stromatolite, form areally extensive beds cropping out sporadically in the Rocky Mountains from northwest Wyoming to northwest Canada. At Torrey Canyon, in the northwestern part of the Wind River Basin of Wyoming, rock specimens of planar, algal laminated lithofacies were collected immediately below an edge-wise, lime pebble conglomerate in the upper part of the Park Shale Member of the Gros Ventre Formation, Upper Middle Cambrian. Thin sections of these micrites reveal preserved organic remains including: a dominant, filamentous, prokaryotic mat-former; other probable prokaryotes; and larger, possibly eukaryotic algal filaments. The algal composition is not unlike that reported for silicified, Late Precambrian Conophyton from the Soviet Union. Conophyton is locally common in the Cambrian and Ordovician of northwestern Wyoming. Regional stratigraphic considerations suggest that widespread occurrence of stromatolites and algal mats was due primarily to changes in sea level. Our studies and observations indicate that: 1) identifiable algal remains may be present; 2) stromatolitic associations such as Conophyton and cryptalgal laminites were prevalent in the early Phanerozoic; 3) the disappearance and reappearance of stromatolitic forms was due at least as much to sedimentary and eustatic change as to metazoan grazing pressure or competition; and 4) the smooth, flat, millimeter-thick sediment laminations occurring in Holocene tropical carbonate flats, as for example on northwest Andros Island, Bahamas, are precise modern analogs of the Upper Middle Cambrian cryptalgal laminites.

BRACK-HANES, SHEILA D.\*, MICHELLE J. BALLARD, and THOMAS R. LANE. Natural Sciences, Eckerd College, St. Petersburg, FL 33733. - Lycopod reproductive structures from the Late Mississippian of Georgia.

Mississippian (Chesterian) lycopod compressions from northwestern Georgia include cone fragments of Lepidostrobus, Lepidostrobo-phyllum, and isolated Echitriletes echinoi-des megaspores. Lycospora microspores of the cone have a broad equatorial flange and a punctate proximal surface. Echitriletes echinoi-des, which is abundant in the shale, is also the spore type found in the sporangia of the Lepidostrobo-phyllum compressions. Previously, the spiny megaspores have been reported from sporangia of a different

sporophyll, Lepidostrobo-phyllum fimbriatum. The Georgia Lepidostrobo-phyllum is smaller with a distinctively narrow lamina that has entire margins.

BRACK-HANES, SHEILA D.\* and ALICE PERUS-SAULT. Natural Sciences, Eckerd College, St. Petersburg, FL 33733. - A seagrass compression from the Middle Eocene of Florida.

The Avon Park Limestone (Claiborne) contains a marine flora with several distinctive seagrasses. Most prominent among them is one that closely resembles Thalassia (turtle grass of the Hydrocharitaceae family) in its morphology. There are certain features, however, such as a dark dorsal band on its leaves in the region of its sheath, that is characteristic of another seagrass, Posidonia (Potamogetonaceae family). The dark band in Posidonia represents a heavy deposit of tannin cells in the leaf-sheath area where the leaf is contiguous with its sheath. In Posidonia, a ventral ligula with numerous tannin cells, also occurs in the region of the dark band. The Avon Park seagrass is believed to be a ligulate plant of the Potamogetonaceae family that, until now, has been unknown in Eocene rocks.

BURNHAM, ROBYN J. Department of Botany KB-15, University of Washington, Seattle, WA 98195.  
- Diversification and stable distribution with respect to temperature in early Tertiary Ulmoideae of western North America

Appearance and major morphological diversification of each of three genera of the Ulmoideae (Ulmaceae), Ulmus, Zelkova, and Chaetoptelea, follow the same pattern during the early Tertiary of western North America. Each genus is represented by a homogeneous morphospecies first occurring in the Paleocene or early Eocene, followed by a middle to late Eocene diversification. The diversifications produce distinctive new morphological species within the same basic organizational plan recognized today for each genus. The initial appearance of new forms occurs during or immediately following periods of inferred climatic instability in floras indicating less equable conditions. Superimposed on the patterns of diversification are indications of consistent distribution with respect to temperature of each genus throughout the early Tertiary that are comparable to the climatic ranges of the genera today. Species of each genus, as a group, contribute to specific physiognomic forest types and to floral assemblages that suggest specific temperature parameters. Species of Ulmus and Zelkova delimit the widest temperature and geographic ranges of the subfamily, occupying modern habitats in notophyllous broadleaved evergreen forests through low montane conifer forests of Asia. The same ranges are indicated by occurrences in early Tertiary floras. The monotypic Chaetoptelea is restricted today to paratropical and notophyllous broadleaved forests of Central America and apparently has been restricted to these physiognomic forest types since the Paleocene.

CHITALEY, SHYA. The Cleveland Museum of Natural History, Cleveland, OH 44106  
- Cones from the Cleveland Shale.

Two well preserved compressed Lycopoid cones are described in this paper. Both are from the dig of the

I-71 Interstate passing through Cleveland of Ohio at the intersection of I-71 and West 130th Street, exposing the Black Cleveland Shale. They are studied under low and high magnifications for their morphology and structure after clearing and macerating with hydrofluoric acid.

The Cone A is elongated, exposed in part and counterpart, showing a central axis with whorls of sporophyll/ sporangium complexes. It measures 11.7 X 4.5 cm; axis 0.6-1 cm wide and the strap shaped sporophyll/ sporangium complex 1.7 X 0.3 cm.

The Cone B is ovate showing a portion of central axis in the middle and at either ends sporophyll/ sporangium complexes arranged in a shallow helix around the axis. It measures 13 X 5.3 cm; axis 1 cm; sporophyll/ sporangium complex 1.2 X 0.2 cm. Miospores are of two sizes in both A and B. The cones are compared with the known ones for their affinities. Cone A shows greater resemblance to *Lepidostrobus gallowyi* than the B. The presence of such big arborescent cones in the Upper Devonian Cleveland Shale is of high significance.

CICHAN, MICHAEL A. Department of Botany, The Ohio State University, Columbus, OH 43210. - The vascular cambium in

Carboniferous plants: *Arthropitys communis*. Developmental patterns in the vascular cambium of *Arthropitys communis*, a Carboniferous arthrophyte, are characterized through an analysis of structural changes that occur in the secondary xylem. By examining cell lineages in tangential sections and using an equation that predicts the minimum rate at which new initials are added to the cambium, it is shown that circumferential enlargement of the layer occurred by an unusual mechanism involving both cell division and enlargement. Ray initials were added to the cambium at a relatively high rate by the division of existing ray initials. New fusiform initials were formed at relatively low rates, and preliminary evidence suggests that the process was accomplished, at least in part, by the conversion of ray initials to fusiform initials. With respect to cell size, there is a gradual centrifugal increase in the length and tangential diameter of the fusiform cambial elements. A similar developmental increase is observed in the tangential size of ray initials. A general comparison of the pattern observed in *A. communis* with that found in other Carboniferous arthrophytes, while illustrating the distinctive nature of the cambium in this group, documents the occurrence of diverse developmental regimes in these evolutionarily primitive plants.

CICHAN, MICHAEL A\* and THOMAS N. TAYLOR. Department of Botany, The Ohio State University, Columbus, OH 43210. - An alternate method for determining tracheid length in petrified wood.

To date, studies of the anatomy of fossilized wood from vascular cryptogams and gymnosperms have generally neglected the length of the tracheary elements. This is due primarily to the fact that, unlike the wood of living plants, petrified wood is not amenable to maceration procedures. Moreover, the unusual length and often sinuous course of the tracheids generally precludes direct measurement of the cells in longitudinal sections.

In this paper, a method is presented which allows estimates of tracheid length to be made by analysis of intersected cells in cross section. Using a model which simulates the organization of tracheids in a hypothetical tangential section of wood, an equation is derived which relates cell length to the ratio between the number of intersected shafts and apices observed in cross section and the length of the tracheid apex. It is determined a priori that the accuracy of the length estimates obtained using this method will vary in accordance with the general features of the area of wood being analyzed and morphological variability in the component tracheids. Use of the technique is demonstrated in an analysis of wood from the anatomically preserved Carboniferous arthrophyte *Sphenophyllum plurifoliatum*, a plant known to possess extremely long tracheids. The lengths obtained using this method correspond closely to those derived by indirect measurement, and it is concluded that the technique is a valuable tool in characterizing the length of cells which, for various reasons, can not be measured directly.

COSTANZA, SUZANNE H. Department of Botany, University of Illinois, Urbana, Ill. 61801 - Comparison of two Pennsylvanian coal swamp cordaites.

Two distinct Euramerican Pennsylvanian coal swamp cordaite genera, *Mesoxylon* and *Cordaixylon* (previously *Pennsylvanioxylon*) differ in several ways. *Mesoxylon* primary xylem strands, radially narrow and tangentially broad, are indistinct. *Cordaixylon* primary xylem is clearly defined, with strong pithward projection and lateral edges. In woody *Mesoxylon*, the originally single leaf trace divides into two at the inner xylem margin, but in equivalent *Cordaixylon* leaf traces first divide in the cortex. Small branch traces, usually paired, fuse in the cortex in *Mesoxylon* but remain separate in *Cordaixylon*. *Mesoxylon* leaves are probably inserted in complex multiple spirals whereas *Cordaixylon* leaves follow a single spiral. Associations of ovules with other organs are strongly supported by repeated occurrences of single-ovule floras. The plant producing *Mesoxylon* stems most probably produced *Gothania* reproductive shoots, *Mitrospermum* ovules, and thick leaves such as *Cordaite felicis* with strong interveinal sclerenchymal bands. The *Cordaixylon* plant produced *Cordaianthus* reproductive shoots, *Cardiocarpus* ovules, and thinner leaves which may or may not have strong interveinal sclerenchyma. Because of small stem size, and adventitious roots and buds, coal swamp species in these two genera are reconstructed as small trees or viny shrubs. The small stems contrast with large trunks from other depositional settings, such as French Stephanian Grand' Croix freshwater swamps. The size difference between in-swamp and out-of-swamp, lowland plants is also seen in lycopods. Thus, although coal swamps were areas of accumulation, they may not have been optimal for individual plant growth.

CRABTREE, DAVID R. Department of Botany, University of Montana, Missoula, MT 59812 - A regional fern flora from the Albian (Cretaceous) of Montana, Idaho and Wyoming.

A Lower Cretaceous (late Albian) regional fern flora is reported from Montana, Wyoming and Idaho. Members of the Schizaeaceae, Gleicheniaceae, Cyatheaceae and Polypodiaceae are present. The assemblages are found

## 70 Paleobotanical Section

in rocks interpreted as paludal. Several of the ferns exhibit distributions across North America and Europe. They apparently represent a portion of a Cretaceous fern assemblage that was widely successful in lowland and deltaic environments. Several of the ferns reported here have been inconsistently classified in previous reports. Attempts are made to clarify the distribution and taxonomy of Gleichenia gracilis, Anemia dicksonianum, Ruffordia goepperti, and Onychiopsis psilotoides.

CRANE, PETER R. Department of Geology, Field Museum of Natural History, Lake Shore Drive, Chicago, IL 60605-2496

### - Heterophylly in Paleocene Lauraceae

A suite of fossil leaves from the Reading Beds (Upper Paleocene) of southern England contain distinctive and abundant, spherical resin-bodies in the leaf mesophyll. The morphology and major venation of these leaves may be trilobed and palactinodromous, simple and pinnate, or simple and acrodromous. Simple and trilobed leaves yield identical cuticles, and are interpreted as variants from a single heterophyllous species. Impressions of similar fossil leaves have been reported from the Paleocene of northwest Greenland, and Menat, southern France. Characters of gross morphology and major venation indicate a relationship to the Lauraceae, which are known from fruit remains to comprise a major component of the British early Tertiary flora. Three extant species of Sassafras and one extant species of Lindera display heterophylly similar to that in the fossil leaves. The resin bodies in the fossil are interpreted as the remains of ethereal oil cells and the major cuticular characters are similar to those of many extant Lauraceae. However, details of the fossil cuticle show no close similarity with any living species and provide no evidence for confident assignment to either Lindera or Sassafras. The fossil leaves are referred to Lauraceaeaphyllum stenolobatus Koch. Details of morphology, particularly in the trilobed leaves, are also different from "mature" leaves of extant species and most closely resemble seedling leaves of Lindera triloba. Trilobed leaves more closely comparable in morphology to "mature" leaves of Lindera and Sassafras appear later in the fossil record.

CREPET, W. L.\* and MICHAEL S. ZAVADA. Biological Sciences Group U-42, University of Connecticut, Storrs, Ct. 06268 and Department of Biology, Indiana University, Bloomington, Ind. 47405 - Quercoid catkins from the Middle Eocene.

Apparently lax catkins of small florets have been discovered from the Middle Eocene Claiborne Formation. Floral morphology is suggestive of affinities with the subfamily Quercoidae of the Fagaceae. Pollen, a good diagnostic character at the subfamily level in the family, is tricolporate and is similar to the pollen of the Quercoidae in P/E ratio and in size. Ornamentation, also a good diagnostic feature, is more typical of the subfamily Castaneoideae. These are the oldest unequivocally quercoid fossils and their significance is evaluated in the contexts of the subfamily, family, and fossil record.

DAGHLIAN, CHARLES P. Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019

### - Epilobium pollen from the Oligocene of New Zealand.

Pollen of Epilobium has been reported previously from the Oligocene of New Zealand but was considered by earlier workers to be a Recent contaminant. New material from the Pomahaka Formation (Late Oligocene) of New Zealand provides evidence that Corsiniipollenites epilobioides is not a contaminant. Combined LM, SEM and TEM observation of this palynomorph indicates it is a member of the Onagraceae on the basis of its characteristic wall structure. The fossil grains can be allied most closely with Epilobium on the basis of exine structure, particularly the ektexine-endexine relationship, exine sculpture, aperture configuration and gross form. This species of Epilobium in the Late Oligocene may or may not have given rise to the 46 native species of the genus in Australasia, but suggests that some of these species may have had a much longer period of residence in the region than previously recognized. This new record is important in interpreting the history and biogeography of Epilobium and of the Onagraceae.

DELEVORYAS, T.\* and R. C. HOPE. Department of Botany, University of Texas, Austin, TX 78712 and Department of Geology, Campbell University, Buies Creek, NC 27506. - Further notes on the late Triassic conifers Compositrobus neotericus and Voltzia andrewsii.

In the original description, ovulate cones of Compositrobus neotericus Delevoryas and Hope were reported to have ovuliferous scales with two ovules borne on the upper surface of each. Although most ovuliferous scales were preserved without attached ovules, two distinct scars are present on each, suggesting a pair of ovules. On the basis of a single ovuliferous scale with attached ovules, the reconstruction showed the two flattened ovules borne on edge, with flat faces parallel to each other. Additional material confirms the presence of two ovules per scale, but the ovules appear to have been borne with flat faces resting on the ovuliferous scale. The coeval cone of Voltzia andrewsii Delevoryas and Hope had lobed ovuliferous scales, but no subtending bracts had ever been detected. It is now demonstrated that a small, tapered bract subtended each scale. Immature cones of V. andrewsii also contribute information about cone ontogeny.

DIMICHELE, WILLIAM A. Botany Department, Univ. of Washington, Seattle, WA 98195  
Timing and controls of diversification in the Carboniferous Lepidodendrales

Phylogenetic analysis of the Lepidodendrales, subsequently combined with stratigraphic data provide the basis for explaining the timing of generic diversification and the relative species diversity of each genus. The following patterns are observed: 1. Paralycopodites is both the oldest and has the fewest derived character states of the group. It occurs

initially in a diversity of ecological settings, later is ecologically narrow, consists of few species, and possibly includes species ancestral to three other genera in the Mississippian. 2. The only major adaptive radiation occurred in the Mississippian, shortly after the appearance of Paralycopodites. 3. Three of the subsequently appearing genera, Sigillaria, true Lepidodendron, and "Lepidodendron" (*sensu* L. vasculare), consist of numerous species that occur in relatively heterogeneous ecological settings, and contain the probable ancestors of some taxa above the species level. 4. Lepidophloios consists of few species with narrow ecological tolerances, and was apparently ancestral to no superspecific taxa. These patterns suggest that the major delimiters of the generic adaptive radiation were increased morphological and ecological specialization of the newly appearing forms, preempting 'adaptive space'. Increased architectural complexity may also be important in the limiting the magnitude of actual and detectable morphological divergence in speciation.

FARABEE, MICHAEL J.\* Department of Botany & Microbiology, University of Oklahoma, Norman, OK 73019. JAMES E. CANRIGHT Department of Botany & Microbiology, Arizona State University, Tempe, AZ 85287. - A new genus of dispersed fossil pollen from the Upper Cretaceous of North America.

A new genus of dispersed fossil pollen is described from Maestrichtian deposits in the Aquilapollenites and Normapolles phytogeographic provinces in North America. These deposits had lithologies ranging from shale to lignite, were widely separated geographically, and had characteristic Maestrichtian palynofloras. The genus occurs in the Lance Formation of Wyoming, the Owl Creek Formation of Kentucky, the Prairie Bluff Chalk Member of the Selma Group in Alabama, and an unnamed lignite from Arkansas. The genus is characterized by its subspherical amb, predominantly polar compression, hexaportricolpate apertures, and an extexine composed of baculate sculpture elements forming a coarse reticulum (lumen sizes up to 2 micrometers) with lumen sizes decreasing toward the colpi margins. The combination of these characters distinguish this new genus from previously described dispersed pollen genera. The same species occurs in all four deposits, and thus is a useful tool for correlating deposits between the distinct phytogeographic provinces. The precise botanical affinity of the genus is most likely with some extinct group of the Santalales, possibly with precursors to some of the Olacaceae.

GENSEL, PATRICIA G. Biology Department, University of North Carolina, Chapel Hill, NC 27514 - A new, anatomically complex plant from the Early Devonian of Gaspé.

Compressions, impressions and permineralizations were found of an apparently new plant from the Early Emsian Battery Point Formation, Gaspé, Quebec which most closely resembles the trimerophytes in vegetative morphology but exhibits anatomy more comparable to Middle Devonian plants such as Aneurophytales or Iridopteridales (*sensu* Stein, 1982). Major axes are 0.7-1.0 cm wide and divide isotomously at least twice in a 15 cm distance. Each resultant axis may also divide anisotomously to produce spirally arranged lateral branches. These in turn divide one to several times, ending in recurved tips. All axes are covered with delicate hairs 0.3-0.6 mm long.

Regions of axes on compressions are permineralized with pyrite and limonite; other permineralized axes occurred in nodules. Anatomy of main axes consists of primary xylem in the form of a deeply three-lobed protosteles; one protoxylem area occurs near the end of each lobe and in the center. Maturation is mesarch. Elliptical lateral traces are produced by 1) tangential enlargement of a lobe tip, first to one side and then the other; 2) enlargement of protoxylem, and 3) separation of outer part of protoxylem and associated metaxylem.

While superficially similar to certain Middle Devonian Aneurophytales, the new plant differs in lacking secondary xylem, having fewer protoxylem areas, and a different mode of lateral trace formation. It differs from Iridopteridales in similar features. However, it demonstrates a much greater level of histological complexity than has been known to date among Early Devonian plants, and might represent a precursor to some of the above Middle Devonian forms.

GRAHAM, ALAN. Department of Biological Sciences, Kent State University, Kent, Ohio 44242- Miocene Communities from Costa Rica.

A hallmark of tropical biotas is their diversity. The refuge theory of Haffer explains this diversity by assuming past climatic changes that periodically restricted the rain forest to isolated refugia, followed by sea-level and climatic changes that allowed these elements to expand and coalesce into the vegetation presently occupying the Amazon Basin. Since paleobotanical data is not presently available directly from the basin, the theory depends on information from adjacent regions. van der Hammen has documented climatic and vegetation changes from high altitude lakes in Columbia, and data from the uppermost Miocene Paraje Solo formation in Veracruz, Mexico showed that in one region where rain forest exists today, it was absent or poorly represented in the past. New supporting data from Miocene microfloras in Costa Rica reveal a temperate community of Podocarpus and Quercus, presently found at higher altitudes in the Talamanca Range, while elements of the rain forest are absent or poorly represented. These results are consistent with those previously reported from Veracruz and Colombia. Until data directly from the basin, as at Rondonia, are more complete and better dated, the widely accepted refuge theory continues to depend on information from these peripheral regions for evaluation.

GROTE, PAUL J.\* and DAVID L. DILCHER. Department of Biology, Indiana University, Bloomington, IN 47405. - Investigations of angiosperms from the Eocene of North America: A five carpellate fruit. Angiosperm fruits from the middle Eocene Claiborne Formation of western Kentucky and Tennessee have been studied. About 170 fruits of one similar type from several clay pits have been examined morphologically. The fruits consist of 5 fused, superior carpels and are terminal on short, fragmentary woody axes. These fruits are compressed, mostly laterally, and are 10 to 23 mm. wide by 9 to 18 mm. high. They are surrounded by 5 woody, imbricate sepals. The sepals cover the fruit almost entirely when immature and about 1/3 when mature. Immediately subtending the sepals are 2-4 helically arranged bract scars. The fruits are woody, divided into 5 distinct locules, and dehisce loculicidally,

## 72 Paleobotanical Section

rarely breaking free to expose a central column. Each carpel contains one apparently anatropous seed. The seeds are pyriform (6x8 mm.) and are borne on axile placentae. The surface of each seed is papillate. The carpels have a thin outer covering which, when preserved, is brittle and frequently broken away to expose a woody mesocarp with a reticulate surface. An endocarp can be differentiated toward the inner surface of the mesocarp surrounding each seed. These fruits appear to have an affinity with the Theaceae.

HAMER, JON J. Department of Botany, Ohio University, Athens, Ohio 45701 - A permineralized sporangial fructification from the Upper Pennsylvanian of the Appalachian Basin.

Several specimens of a new type of sporangial fructification have been discovered in coal balls from the Duquesne Coal near Steubenville, Ohio. In the largest specimen sporangia are borne terminally on up to two orders of branching axes. Penultimate axes branch pinnately to produce irregularly-branched ultimate axes. Sporangial wall cells are of a single type and show no specialization for dehiscence. Spores are radial and trilete, and most similar to the spore dispersal genus Dictyotriletes. The specimens are compared to Sclerocelyphus Mamay and to other Paleozoic fructifications of uncertain affinities.

JOHNSON, NORMA G.\*, ALFRED TRAVERSE and PAUL K. STROTHER. Department of Biology, Pennsylvania State University, University Park, PA 16802 and Department of Geology, Dickinson College, Carlisle, PA 17013 - Plant microfossils from the Lower Silurian Tuscarora Formation at Mill Hall, Pennsylvania  
A 200 meter thick section of the Lower Silurian Tuscarora Formation near Mill Hall, Pennsylvania, yields palynomorphs such as Tetraedraletes and Nodospora, as well as dyads and probable diacrodoid and sphaeromorph acritarchs. A series of time-lapse photographs shows significant changes in the spore morphology of Nodospora spp. during oxidation with chlorine bleach, apparently indicating that species of Nodospora previously thought to be distinct are based on natural or laboratory-induced differences in level of oxidation. Large (3/4 mm) pear-shaped spore clusters occur as megascopic fragments on shale surfaces. Studies using light and scanning electron microscopy show that these large spore clusters are composed uniformly of Tetraedraletes medinensis. These plant microfossils were presumably deposited in a near-shore or fluvial environment. No forms known to be marine have been found in the Mill Hall samples, and the flora compares favorably with an undisputedly non-marine section of the Tuscarora Formation from Waggoners Gap, Pennsylvania.

KASPER, JR.\*, ANDREW E. AND WILLIAM H. FORBES. Department of Botany, Rutgers University, Newark, N.J. 07102 and Division of Mathematics and Science, University of Maine, Presque Isle, Me. 04769. - An early occurrence of Psilophyton from the Upper Silurian/Lower Devonian Fish River Lake Formation in northern Maine.  
Plant remains assignable to Psilophyton from the Fish River Lake Formation in northern

Maine may represent one of the earliest occurrences of the genus to date. The Fish River Lake Formation was named and described by Boone in 1970. It contains the unusual association of a continental flora with a marine fauna. The age determination based on several faunal collections is late Silurian to early Devonian--the upper limit being New Scotland, i.e., Helderberg (=Gedinnian/Siegenian) age. Three different localities have yielded compression specimens of axes bearing clusters of sporangia. Plants from one locality have unornamented and vertically ribbed stems up to 3 mm wide. They branch pseudomonopodially and the laterals undergo several dichotomies ending in recurved branchlets bearing clusters of sporangia. The sporangia are pendent, narrowly elliptical, paired and 3-5 mm long. Plants from another site likewise have unornamented and ribbed axes but are much smaller--1.5-2 mm wide. Branching is pseudomonopodial and the ultimate branchlets bear minute paired sporangia 2-2.5 mm long. The former species is compared to Dawsonites arcuatus, the latter to Psilophyton dapsile. Most well-documented occurrences of Psilophyton are Emsian to Eifelian in age.

KOVACH, WARREN L.\* & DAVID L. DILCHER. Indiana University, Bloomington, Ind., 47405. - A new mid-Cretaceous angiosperm fruiting axis.

A new type of angiosperm reproductive axis has been found in the mid-Cretaceous sediments of the Dakota Formation in west-central Kansas, thus adding to the diversity of angiosperm reproductive structures known from this time. The largest axis fragment we have is 15 cm long; the entire axis may have been longer. These reproductive axes are racemes which bear numerous helically arranged fruiting structures (4-5 per cm). In some specimens, many of these fruiting structures have been shed and only the scars remain. Each of these fruiting structures consists of a pedicel (4 x 0.5 mm) which arches distally from the main axis, terminating in a spherical receptacle (1 mm diameter) upon which are borne approximately 35-50 small, helically arranged carpels. Each carpel is approximately 2 mm by 0.7 mm and is borne on a 1 mm stalk. The carpels appear to have an abaxial vein with a closed adaxial suture extending most of the carpel length. Each fruit, as far as can be determined at present, appears to bear a single seed, and the entire fruit seems to be deciduous at maturity. The longest axis fragment we have bears an estimated 2,700 fruits. Each gynoecium is subtended by one whorl of about ten very small, rounded scars. This angiosperm reproductive material has features similar to some families of presumed primitive dicotyledons and monocotyledons.

KURMANN, MARIE H. Department of Botany, The Ohio State University, Columbus, OH 43210. - The ultrastructure of pollen extracted from Boulaya fertilis.

The genus Boulaya (Carpentier) was characterized in detail by Halle in 1933 for impression-compression specimens of pollen organs associated with the medullosan pteridosperms. Specimens are pyriform and consist of several fused sporangia that may extend up to 2.0 cm in length. Well-

preserved specimens possess "teeth" that probably correspond to the free ends of the pollen sacs. The specimens used in this study were borrowed from the British Museum (Natural History) and appear to consist of a variable number of sporangia, with 8 being the most common number. Pollen grains are of the Monoletes type and range from 230-280  $\mu\text{m}$  in length. On the proximal surface is a monolete suture; distally the grains possess two longitudinal grooves. The sporoderm is two parted consisting of a homogeneous nexine with conspicuous lamellae, and an outer alveolate sexine up to 6  $\mu\text{m}$  in thickness. In this study the ultrastructure of the pollen is compared to other Monoletes-type grains extracted from pollen organs of the Halletheca and Aulacotheca morphological types.

LA PASHA, CONSTANTINE A. Department of Botany, University of Montana, Missoula MT 59812.  
- Rhombostrobus cliffwoodensis - a taxodiaceous seed cone from the Upper Cretaceous of New Jersey.

Description of Rhombostrobus cliffwoodensis was originally based on a single fragmentary pyritic seed cone. A new pyritic specimen of a more complete cone from the Magothy Formation, Cliffwood, New Jersey adds to the understanding of this species. The new cone is 3 cm diam and at least 4 cm long and lacks apex and base. The axis is 10-12 mm diam. The pith is 4.5-5.0 mm diam and is composed of 28-40  $\mu\text{m}$  diam parenchyma cells. Xylem forms a cylinder 0.8-1.1 mm thick and lacks resin canals. Tracheids of the vascular cylinder are uniform, slightly rounded, 9-18  $\mu\text{m}$  diam, and form radial files. The cortex is 1-2 mm thick and has a single ring of resin canals surrounding the xylem. Bract-scale complexes that are 3 mm thick, 8 mm wide, and 10 mm long are inserted normal to the axis in a helical arrangement. The complex trace is adaxial to the single row of major resin canals in the complex, and forms a broad band or separate bundles. A single resin canal enters the complex from the cortex and divides distally. Two winged seeds are produced in shallow depressions on the adaxial surface of the complexes.

The new material clarifies some of the details of the cone axis and bract-scale complex vasculature. This information allows more precise comparisons with other members of the Taxodiaceae. These comparisons confirm the previous interpretations of the relationship of this species to other members of the Taxodiaceae. Rhombostrobus cliffwoodensis combines features of seed cones typical of Sequoia with those typical of Cunninghamia.

LEARY, RICHARD L. Geology Department, Illinois State Museum, Springfield, IL 62706. - New fossil algae from Valmeyeran (mid-Mississippian) strata of Illinois.

Two previously unknown algal forms are preserved as carbonaceous films and impressions in basal St. Louis Limestone (Valmeyeran) of Jersey County, Illinois. One form consists of broad (1.5 cm) branching thalli with papillae ca. 1 mm in diameter. Although none of the characteristics used to classify extant algae (cellular structure, pigment, reproductive cycles, food storage substances, etc.) are preserved, these algae are thought to belong to Rhodophyta (red algae) and have morphologic similarities with some species of Gigartinales.

A second form is by far the most abundant and best preserved. It consists of elongate blades up to 6.8

cm long, 1 cm wide, with rounded apices and tapered bases. The blades were probably inflated and the bases frequently had pneumatocysts 1 mm in diameter; as many as 7 pneumatocysts were observed on a single blade. The blades were attached spirally to stipes up to 0.9 cm in diameter. The stipes bifurcated dichotomously. They were probably attached to an expanded holdfast. This algal form has similarities with certain Phaeophyta (brown algae), in particular Laminariales such as Macrocystis.

The fossils are abundant in several quarries in western Illinois - eastern Missouri. The algae are associated with conularia, an animal with a cone-shaped exoskeleton. The algae and conularia probably grew in shallow marine water on the eastern flank of the Ozark Dome. This region would have been at ca. latitude 20° south during Valmeyeran time.

LESNIKOWSKA, A. D.\* and M. A. MILLAY. Botany Department, University of Illinois, Urbana, IL 61801, and Botany Department, University of Maryland, College Park, MD 20742. - Cladistic analysis of fossil and extant marattialeans ferns.

A preliminary cladistic analysis of living and fossil marattialeans ferns has revealed a pattern of relationship that serves to indicate areas of future research. WAGPROG was used to construct a consensus tree for 38 taxa based on 38 characters. The analysis was rooted using the ferns Musatea (Zygopteridales) and Ankyropteris (Filicales) as the outgroup. The extant taxa were linked together in the middle of the cladogram near Millaya and Eoangiopteris while the most derived Paleozoic taxa occurred in the Latifolia and Minor groups of Scolecopteris. Some examples are noted in which parallelisms or reversals in several characters are required, suggesting that at least some of the character states of some of the OTUs involved are not homologous. In one example discussed, the cladogram suggests the simultaneous evolution of a suite of vegetative characters in the ancestor of the extant taxa, together with several reversals in synangium characters. A more parsimonious explanation would be provided by the occurrence - currently unknown - of non-arborescent members of several Paleozoic lineages. Without such a hypothesis such marattialeans, if they exist, might not be recognized. Thus the hypotheses represented by the cladogram provides a conceptual framework for the integration and evaluation of new information as well as indicating areas of future research.

MAHLBERG, PAUL G.\*, AND DONALD W. FIELD. Department of Biology, Indiana University, Bloomington, IN. 47405. - Fossil laticifers from Eocene brown coal deposits of the Geiseltal.

Cellular remains from brown coal deposits of the Geiseltal, near Halle, were determined to be fossilized nonarticulated laticifers. The thick mats of intact cells consisted of strands of rubber. These cells, often with cell wall remains surrounding the strand of rubber, retained a tubular shape during preservation. Small holes, possibly artifactual, occurred at irregular intervals along the surface of some of the cells. The laticifers viewed in trans- or longitudinal section were composed of a dense, yet poriferous, isoprenoid content originally present in the cell. The porous interstices represented areas of protoplasm, now absent. Various configurations in the rubber, as spherical surfaces, represented

surface images, in negative relief, of former nuclei and organelles. The laticifer axes possessed branches of various configurations comparable in morphology to those of laticifers in extant plants. Acetone extracts of the laticifer contents, analyzed by gas-liquid chromatography, demonstrated the presence of several triterpenoids which formed a characteristic profile for these remains. This profile resembled the triterpene profiles from latex of extant Euphorbia where they represent a fingerprint for a taxon. The cellular morphology and triterpenoid profile of these fossil laticifers may be employed effectively as markers, in comparative studies with extant plants, to identify the species of origin of these laticifers.

MANCHESTER, STEVEN R. Department of Geology, Indiana University, Bloomington, IN 47405 - Eocene fruits, wood and leaves of the Fagaceae from the Clarno Formation of Oregon. The Middle Eocene Nut Beds locality of the Clarno Formation in central Oregon has yielded a variety of fagaceous remains, including the earliest known acorns, two types of wood and two types of foliage. The acorns, preserved as casts, are longitudinally striate rounded nuts 13-15 mm in diameter and about 18 mm long, capped by a basal involucre covering about 1/3 of the nut. Similar acorns occur today in both Lithocarpus and Quercus. Silicified wood of Quercinium crystallifera Scott & Wheeler is semi-ring-porous and has large vessel elements, vasicentric tracheids and both uniseriate and large aggregate rays. This wood is anatomically similar to that of extant Quercus and Lithocarpus. The other wood, Fagaceoxylon ostryopoides Scott & Wheeler, is characterized by diffuse-porosity, pores in radial multiples and in flame-like tracts, vasicentric tracheids and exclusively narrow, but sometimes aggregate, rays. Although identical anatomy has not been observed in modern species, the wood most closely resembles that of extant Castanoideae. The two types of leaves both have evenly spaced craspedodromous secondary veins leading directly into simple teeth with shallow (2-3 mm) sinuses and closely spaced percurrent tertiary veins. In one type the teeth are gently rounded and non-spinose, suggesting affinity with Quercus. In the other type the teeth are spinose, as in some modern Quercus and Castanoideae. Together, these fossils document at least two distinct but sympatric fagaceous genera in the Clarno flora.

MANCHESTER, STEVEN R. Department of Geology Indiana University, Bloomington, IN 47405 - Fruits and seeds of Tapiscia (Staphylaceae) from the Middle Eocene of Oregon. Silica casts of fruits and seeds representing Tapiscia are common in collections from the Middle Eocene Nut Beds locality of the Clarno Formation in central Oregon. The seeds are subglobose, 4-5 mm long, 3-4 mm wide, rounded dorsally and basally, pointed at the micropylar end and concave ventrally. The ventral side is dominated by a circular, recessed chalazal scar, 1.2-1.8 mm in diameter. The exterior of the seed is longitudinally striate. The fruits are globose, about 6 mm long and 5 mm wide, with a pericarp of uniform thickness covering the seed and having a finely verrucate surface. In the features

observable, the specimens are almost indistinguishable from those of extant Tapiscia sinensis Oliv. Although the single extant species of Tapiscia is confined to China, this North American occurrence supplements those recognized in England and Germany indicating that Tapiscia, like other modern genera of the Staphylaceae, was geographically widespread in the early Tertiary.

MAPES, GENE. Department of Botany, Ohio University, Athens, OH 45701 - Permineralized Lebachia pollen cones.

Permineralized conifer pollen cones conforming to Lebachia Florin are described from Hamilton, Kansas. The fossiliferous limestone occurs in an Upper Pennsylvanian/Lower Permian channel deposit in the Virgilian Shawnee Group. Cuticle from the cones has 1-2 broad parallel bands of stomata, marginal uniseriate hairs, and papillae. Pollen cones are compact, ellipsoid to cylindrical, and borne as single terminal units on leafy lateral or ultimate branches. Mature cones average 0.6 cm wide x 2.0 cm long, though some are up to 10 cm. Cone organization is simple, not compound. Sporophylls are spirally arranged on non-woody axes, avg. 0.1 cm diam. Individual sporophylls display an attenuated tip, entire-dentate margin, and distinct abaxial heel; each sporophyll bears an adaxial cluster of approximately 5-10 elongate pollen sacs containing Potonieisporites grains. Sporangial walls average 1-2 cells thick with no specialized cells for dehiscence. Although Lebachia pollen cones have been previously interpreted as Pinus-like, with two abaxial sporangia, the Hamilton Lebachia cones are more comparable to certain Mesozoic voltzialean taxa such as Darneya Schaarschmidt and Maubeuge emend. Grauvogel-Stamm. The structure of these Lebachia clarifies our understanding of conifer phylogeny and indicates that pinaceous pollen cone organization is not as primitive as currently believed.

MAPES, G.\* and R.H. MAPES. Department of Botany and Department of Geological Sciences, Ohio University, Athens, OH 45701 - Distribution of Mississippian age plants in the Fayetteville Formation.

Permineralized and compressed plants from the Fayetteville Formation in Arkansas fill an important gap in paleobotanical characterization of North American upper Mississippian strata. The Fayetteville plants are most comparable to Lower Carboniferous taxa from Czechoslovakia, England, and Scotland. Ammonoid cephalopods from Fayetteville Fm. confirm Middle Chesterian age and European biostratigraphic equivalence to E<sub>1</sub>, Pendleian Stage, Namurian A. In northern Arkansas, the Fayetteville outcrops along an east-west trend; the lower portion is thick black shale with an excellent invertebrate fauna and permineralized flora. In northwestern Arkansas, the upper Fayetteville Fm. includes the deltaic Wedington Sandstone Member with interbedded coals and terrestrial shales. The Wedington compression flora contains in situ root traces and casts, large radial seeds, arthropytes, lycopod branches and cones, fern and seed-fern foliage, and lyginopterid fertile axes. Permineralized plants are from the lower Fayetteville Fm. and include lycopod branches, roots, and cones, lyginopterid, calomopityean and medullosan seed-fern axes, coenopterid fern petioles, and arthropytes. Lateral floral distribution varies quantitatively and

qualitatively: lycopods diminish in numbers, east of the delta, as total diversity and numbers of gymnosperms remains increase. Paleofloristic interpretations are hampered by differential preservational modes, but several lines of evidence, including paleocurrent data, suggest the Wedington deltaic system influenced plant transport and subsequent distribution along the southern flanks of the Ozark dome during early Upper Carboniferous time.

MELCHIOR, Robert C.\* and HALL, John W., Dept. of Biology, Bemidji State University, Bemidji, MN 56601 and Dept. of Botany, University of Minn., 220 Biological Sciences Center, 1445 Gortner Ave., St. Paul, MN 55108 - Geological observations on the occurrence of some Paleocene Megaspores and allied forms.

An analysis of the sedimentology of the Wannagan Creek Site (Paleocene, North Dakota) has contributed to an understanding of the modes of occurrence of Dictyothylakos Horst, Minerisporites mirabilis (Miner) Potonie (i.e. Isoetites horridus (Dawson) Brown and Azolla stanleyi Jain and Hall). The stratigraphy of the site consists of three units, 1) a lower sandy silt representing deposition by a slow moving stream, grading into 2) an overlying black organic shale suggesting lacustrine sedimentation, and 3) an upper, disconformable graded siltstone indicating a crevasse splay. The sequence is characteristic of a chute cutoff which was gradually isolated to become a lake that was ultimately filled by an overbank crevasse splay. Dictyothylakos, which is interpreted as a hydrophytid (caddisfly) larval feeding device, is restricted to the stream deposit. M. mirabilis is found predominantly in the lake deposit as is A. stanleyi although reduced populations of both types are also found in the upper (gradational) beds of the stream deposit as well. Megafossils of I. horridus are found presumably in place in the upper stream deposit in water less than 1 m deep. Vegetative remains of A. stanleyi from the site bear anomalous megaspores, without float apparatus, that resemble megaspores of Salvinia, and M. mirabilis exhibits a high degree of variability. These phenomena could conceivably lead to errors in identification and paleoecological interpretation.

MICKLE, JAMES E.\* and RICHARD L. LEARY. Illinois State Museum, Springfield, IL 62706. Aulacotheca from the Early Pennsylvanian of the Illinois Basin. Compressed synangia referable to the medullosan pollen organ Aulacotheca have been discovered in Early Pennsylvanian sediments from Rock Island Co., IL. Specimens were recovered from channel fill shales containing floral elements suggesting an upland environment. Based on synangial size and morphology, sporangial number, and prepollen type, two distinct, new forms are recognized. Synangia of the first form are 11-17 X 2.5-4.0 mm and have 4-6 sporangia. Free sporangial tips are acutely pointed. Dehiscence is through a longitudinal slit to the inside of the synangium. Prepollen averages 181 X 129  $\mu$ m and has a monolet suture with median deflection. Sexine on proximal and distal surfaces shows narrow, closely-spaced, anastomosing inpockets; distal and lateral walls are separated by a deep, encircling fold. Synangia of the second form are 21-29 X 3.8-5.5 mm and apparently have 4 sporangia. Distally, free sporangial tips have a narrow extension, giving a mucronate appearance. Features of these synangia suggest that greater morphological

diversity in synangial and pollen structure occurs in Aulacotheca and the medullosan pteridosperms than previously recognized.

MILLAY, M.A.\* and J. GALTIER. Botany Department, University of Maryland, College Park, MD 20742 and Lab de Paléobotanique et Evolution des Végétaux, Université des Sciences et Techniques du Languedoc, Place E. Bataillon, 34060 Montpellier Cedex, France. - A species of *Scolecoperis* (Marattiales) from Grand' Croix (France) resembling Renault's *Ptychocarpus*.

A new species of *Scolecoperis* is described from silicified permineralizations from the Stephanian of Grand' Croix (France). Material consists of radial synangia attached to poorly preserved pinnules. Synangia are circular in cross section (average 0.8 mm diam and 1.0 mm long) and composed of 4-7 sporangia that surround a central cellular area in the basal one half. Sporangia are tubular (0.25 mm diam) and taper distally into deltoid tips that close off the synangium interior prior to dehiscence. Spore release involves the lateral separation of sporangia distally and the rupture of cells along the inner sporangium midline. Outer facing walls are parenchymatous with a distinctive epidermis. Synangial pedicels are short, parenchymatous, and broad (0.6 mm diam), with a central area of thick walled cells. Pinnule margins are entire, downturned, and extend to near the synangium apices. Spores are reniform (average 22 x 13  $\mu$ m), monolet, and have an ornamentation of small irregular grana. Comparisons are made with material from Autun described by Renault under the name *Ptychocarpus* Weiss, and previously only illustrated in line drawing form. Examination of Renault's specimen suggests the possible identity of these two forms. The new species is most similar to *Scolecoperis altissimus* and *S. altus*, but differs from these species in pinnule morphology and possession of a broad pedicel.

MILLER, CHARLES N., JR. Department of Botany, University of Montana, Missoula, MT 59812. A new species of *Pinus* based on seed cones from the Late Cretaceous of New Jersey.

The new species is based on two specimens of semi-fusoid cones from the Magothy Fm. (Santonian - Campanian) exposed at the classic Cliffwood locality on Raritan Bay. The cones are ovoid-conical and are 3-4.5 cm. long by 2.2-2.3 cm. at their widest diameter. The ovuliferous scales are up to 9 mm. wide and are 12 mm. long. The scale apex is inflated and terminates in a rhomboidal apophysis that has a centrally located umbo. There is no evidence of a spine on the umbo. Several anatomical features further support the assignment of the new species to *Pinus*. These are the union of the vascular traces to each bract and associated scale where they diverge from the vascular cylinder of the cone axis, the restriction of the resin canals of the scale base to tissues abaxial to the vascular strands, and the separation of the scale and subtending bract so that they are free marginally before they are medially. These anatomical features occur in combination with inflated scale apices only in cones of *Pinus*. Within this genus the fossil cones compare most favorably with cones produced by species of the Subgenus *Pinus*. The parenchymatous construction of the cortex of the cone axis in the fossils precludes assignment of the new species to the subsections *Contortae*, *Oocarpae*, or *Sylvestres* of the Section *Pinus*. Thus, the fossil cones belong to one of the remaining subsections of

## 76 Paleobotanical Section

the Section *Pinus* or the Section *Ternatae*. However, our knowledge of the comparative cone anatomy of modern species of these taxa is insufficient to permit a more precise identification of the fossil within this group.

NIKLAS, KARL J. Division of Biological Sciences, Cornell University, Ithaca, NY 14850. - Evidence for a conducting strand in non-vascular land plants from the early Silurian (Llandoveryan) of Virginia.

Data are presented for elliptical, bifurcate, to irregular compression fossils of Llandoveryan age from the Massanutten Formation of Virginia. The fossils range from 0.45 to 10 mm in diameter ( $1.32 \pm 0.51$  mm,  $n = 122$ ). Maceration of compressions  $\leq 2.4$  mm in diameter yield surficial cellular remains, while larger compressions yield smooth walled and banded tubular elements. Strands of cells, internal to surficial cellular outlines, were isolated from large compressions. SEM of cellular strands reveal peripheral smooth walled tubes ( $17 \pm 6.9$   $\mu\text{m}$  in diam.), with hemispherical or conate end walls, surrounding banded tubes ( $16.8 \pm 2.1$   $\mu\text{m}$  in diam.)

A  $\delta^{13}\text{C}$ -value of  $-25.6$  determined for duplicate samples is consistent with a terrestrial origin of the organic material. The influence of methanogenic bacterial action attending or following burial cannot be ruled out, however.

The anatomy and morphology of the cellular strands found in these Massanutten fossils is inconsistent with those of present-day moss hydromes, but shares features with the conducting strands of some early Paleozoic plants.

PIGG, KATHLEEN B. \* and GAR W. ROTHWELL, Department of Botany, The Ohio State University, Columbus, Ohio 43210, and Department of Botany, Ohio University, Athens, Ohio 45701. - Development and surface configurations of the Paleozoic isoetalean Chaloneria.

A large number of lycophyte stems have been observed on split surfaces of coal balls from the Duquesne Coal, outcropping west of Steubenville, Ohio. Surface features conform closely to several genera including *Chaloneria*, *Asolanus*, *Stigmaria*, and *Knorria*. When sectioned, all of the specimens have been found to represent different developmental stages and decortication levels of *Chaloneria comosa* Pigg and Rothwell. When the stem surface and leaf bases are present the specimens may be identified as *Chaloneria*, but when the leaf bases are absent or abraded a *Stigmaria*-like configuration is produced. If the specimen splits midway through the cortex of a stem with secondary cortical development an *Asolanus* configuration results, but if the split occurs at the level of the periderm a *Knorria* pattern is produced. The various specimens provide a basis for characterizing secondary cortical development in *Chaloneria*, and for comparing it to similar development in *Isoetes*. The material also allows for more precise interpretation of the affinities of *Asolanus* and other poorly known Carboniferous lycophytes such as *Cyclostigma* and *Bothrodendron*.

POSNICK, ALLAN E., ANDREW E. KASPER, JR.\* AND WILLIAM H. FORBES. Department of Botany, Rutgers University, Newark, N.J. 07102 and Division of Mathematics and Science, University of Maine, Presque Isle Me. 04769. - Plant fossils of *Barinophyton richardsonii* from the Upper Devonian Perry Formation of eastern Maine.

New collections from the Upper Devonian Perry Formation in eastern Maine have resulted in a better understanding of the morphology of *Barinophyton richardsonii* (Dawson) White, 1905. *B. richardsonii*, the type species of the genus, is based on only a few fragmentary specimens and is known solely from the Perry Formation. The original specimens were first assigned to *Lepidostrobus* then *Lycopodites* by Dawson (1861, 1863). In 1905 White established a new genus, *Barinophyton*, for the material. The fossils are preserved as compressions and show fertile axes bearing strobili. The largest specimen, although incomplete, is 12 cm long and bears 12 strobili. The plants consist of unornamented and unbranched axes 5-6 mm wide. The sessile strobili are attached alternately and distichously along the axes, lie at a  $45^\circ$  angle, and are spaced 7-8 mm apart. The largest strobilus, although incomplete, is 3.4 cm long. The strobilar axis bears numerous appendages and sporangia on its adaxial surface. In strobili compressed in adaxial-abaxial orientation two rows of appendages are evident. The new collections have provided the most complete fertile specimen to date. It is speculated that the Barinophytales arose from zosterophyllophyte ancestors.

RETAILLACK, GREG. J. Department of Geology, University of Oregon, Eugene, Oregon 97403

- Factors in the origin of North American prairie. The fossil record of prairie vegetation is poor, because of its usual dry and well-drained habitats, in which plant fossils are seldom preserved. The development of prairie during the Tertiary has been interpreted from fossil phytoliths and other hard parts of plants, as well as from fossil mammalian remains. Fossil soils are additional evidence for the timing and factors involved in the origin of prairie vegetation.

A sequence of Late Eocene and Oligocene, fossil soils in Badlands National Park, South Dakota, is evidence of change from woodland (on paleudalf fossil soils), to savanna (on andic ustochrepts) dissected by streamside gallery woodland (on paleustalfs) and finally to prairie (on calciorthis and ustollic eutr-andepts). Prairie vegetation appeared by the time climate had dried to semiarid, as interpreted from calcic horizons at shallower depth, less clay, lower quartz/feldspar ratios and hues changing from reddish to yellowish in fossil soils stratigraphically higher in the sequence. Increased openness of vegetation appears to have corresponded to increased rate of sediment accumulation, perhaps an indication of a more unstable landscape. Fire does not appear to have been important in the development of prairie from savanna, because charcoal is preserved even in well-drained soils, and none was found in the fossil soils. Grazing activity is unlikely to have been important for the appearance of prairie, because changes in

associated mammalian fossils are minor compared to changes at other stratigraphic levels, and because the fauna remained savanna-adapted. Plant competition was probably unimportant for these early, aridland prairies, because patterns of root traces, peds and cutans in their fossil soils are indications that herbaceous plants were generally well-spaced.

RIGGS, SUSAN D. Department of Botany, Ohio University, Athens, Ohio 45701 - A complex cone of putative sphenophyllalean affinities from the Upper Pennsylvanian of the Appalachian Basin.

A cone with whorled appendages and distinctive monolete spores has been discovered in coal balls from the Duquesne Coal west of Steubenville, Ohio. The cone is up to 13.5 mm in diameter and has a distinctly triangular axis in internodal regions. Near the base the axis has a triarch, exarch protosteles approximately 0.5 mm in diameter. Distally the metaxylem is not differentiated at the center, such that there are three exarch bundles. Approximately six appendages diverge at each node. Most of these are slender, but a few are flattened and bract-like at the base. Distally, all appendages branch to produce terminal sporangia, slender spine-like tips, or both. The sporangia are spheroidal, 0.6-0.8 mm in diameter, and have a thin wall. In section view the wall cells form a uniseriate palisade. There is no obvious dehiscence mechanism. Spores have distinctive large ridges that are interconnected by smaller ridges, and are similar to Striatosporites Bhardwaj and Columnisporites Peppers. Among presently known sphenophyllalean cones the specimen compares most favorably with the Upper Devonian Eviostachya Leclercq.

RISCHBIETER, MICHAEL,\* BEN M. STIDD and TOM L. PHILLIPS. Dept. of Biological Sciences, Western Illinois University, Macomb, IL 61455 and Dept. of Botany, University of Illinois, Urbana, IL 61801.--A new seed fern pollen organ from the Pennsylvanian of Kentucky.

A new seed fern pollen organ is present associated with vegetative remains of Schopfiastrum in coal balls collected at the Providence, Kentucky, locality. Sporangia are clustered in groups of 7-9, connate basally but separated for most of their length. The bulk of the sporangium wall is composed of a prominent layer of elongate thick-walled cells covered by a uniseriate epidermis. Sporangial tips are beaked and composed of the thick-walled cells. The synergia are vascularized but the course of the vascular tissue is not yet determined. Pollen is of the lyginopterid type, 30  $\mu$ m in diameter and trilete. The exine is alveolate/tectate with a prominent nexine; surface ornamentation is densely verrucate/rugulate.

ROBERTSON, EDDIE B. Phillips Petroleum Company Bartlesville, Oklahoma 74004 - Paleocene palynology of the Missouri Breaks.

Pollen and spore assemblages are established for the Paleocene deposits exposed along the Missouri Breaks of western North Dakota. A sequential series of sections sample Maastrichtian to Early Eocene sediments along the valley of the Little Missouri River. Sections are taken from the Hell Creek, Tullock, Lebo, Tongue River, Sentinel Butte and Golden Valley Formations. The assemblages are established using a com-

bination of fossil indices and agglomeration techniques. The assemblages of the Paleocene of the Williston Basin in western North Dakota are unique. They show a close relationship to those described by Leffingwell in the basins to the south and to a lesser extent to the palynofloras described by Rouse from the Paleocene of western British Columbia.

ROTHWELL, G.W. Department of Botany, Ohio University, Athens, Ohio 45701 - An indusiate filicalean fern with gradate soral development from the Upper Pennsylvanian of the Appalachian Basin.

A large number of indusiate sori occur on the abaxial surface of pinnules produced by an Anachoropteris clavata-type frond. The indusium is cyatheoid, either completely enclosing the sporangia or open at the apex. Sporangia are attached to an elongated and vascularized hymenophylloid receptacle that is oriented parallel to the pinnule surface. Individual sporangia have a bi- or triseriate ring-like annulus and a narrow stalk. In some specimens all the sporangia are located close to the receptacle, while the terminal sporangia of others have much elongated stalks. Still other sori lack sporangia in the apical region, and this range of variability provides the basis for interpreting gradate development. Spores are radial and trilete with concave inter-radial sides, and exhibit spinules on both proximal and distal surfaces. Material of this type expands our knowledge of variability within the most primitive filicaleans, and provides an additional basis for interpreting evolutionary radiation within the group.

ROTHWELL, G.W. Department of Botany, Ohio University, Athens, Ohio 45701 - Functional morphology in ovule development, and the evolution of gymnospermous reproduction.

Lagenostomalean ovules are the best currently available evidence for interpreting reproductive biology among the most primitive gymnosperms. Different species show a greater degree of structural variability than generally recognized, but common features of the pollen chamber unite them into a single group and indicate a monophyletic origin of seed plants. Similarities in pollen chamber structure and function have been obscured by a morass of conflicting and inconsistently applied terms that refer to the various parts. Although specimens typically show a narrower range of ontogenetic variability than do other Paleozoic ovules, a comparison of different species and the discovery of ovules in both earlier and later stages than generally encountered now provide a basis for interpreting many features of lagenostomalean reproduction. The differences exhibited by other Paleozoic ovules provide a basis for recognizing the occurrence of trigonocarpalean reproduction at the base of the Namurian, cardiocarpalean reproduction at the base of the Westphalian, and conifer type reproduction by Westphalian D.

SCHECKLER, STEPHEN E.\* and JAMES F. BASINGER. Dept. Biology, VPI&SU, Blacksburg, VA 24061 and Dept. Geol. Sci., Univ. Saskatchewan, Saskatoon S7N 0W0. - Late Devonian Archaeopteris fissilis from north-easternmost Laurentia, eastern Yukon, Canada. Lower Earn Group turbidites yield an A. fissilis (99%) flora. This is its first record in North Amer-

ica; *A. fissilis* is found elsewhere only at Ellesmere and Donetz. Other floral elements are *A. macilenta*, an herbaceous lycopod, and a possible aneurophytalean. These and associated conodonts support an early-mid Frasnian age. *Archaeopteris fissilis* bears crowded helices of decurrent leaves on all branches. Non-laminate leaves are 2-3 times forked, planated, and are smaller distally. Those on penultimate branches are 2-2.5 cm long while sterile leaves on the 2-ranked ultimate branches are 0.8-1.2 cm long. Portions of 18 fertile strobili show that fertile leaves are smaller (0.8-1 cm long), bear dense clusters of sporangia (1.8-2 mm, but up to 3 mm long by 0.6-0.7 mm wide) on the upper surface, and that *A. fissilis* is heterosporous and monoecious. Two incomplete strobili show that most fertile leaves are unisexual. All but the distal few are megasporangiate. Megasporangia contain 32-64 megaspores (190-220  $\mu\text{m}$ , but up to 280  $\mu\text{m}$ ). Microsporangia are similar in size, but contain hundreds of 70-80  $\mu\text{m}$  microspores. Penultimate and ultimate branch anatomy is similar to other *Archaeopteris*. These data support retention of *A. fissilis* in *Archaeopteris* and suggest that leaf lamination is insufficient to distinguish this genus from *Svalbardia*. Although *A. fissilis* suggests the origin of laminate leaves of *Archaeopteris* from non-laminate precursors, this condition may relate more to its ecology. Yukon, Ellesmere, and Donetz are all at reconstructed Frasnian paleolatitudes of 30° N, a desert latitude. This suggests that *A. fissilis* leaves may have been reduced for xeric adaptation, rather than retaining the ancestral condition of older progymnosperms.

SCHOPF, J. WILLIAM\* and ROBERT MIKAWA. Department of Earth and Space Sciences and Institute of Geophysics and Planetary Physics, University of California, Los Angeles, CA 90024. - Precambrian stromatolitic microbiotas of the Gaoyuzhuang Formation of northern China.

Two communities of diverse, well-preserved, fossil prokaryotic microorganisms have been detected in petrographic thin sections of carbonaceous cherts from the 1,400-1,500 Ma-old Gaoyuzhuang Formation at the stratotype section of the "Sinian Suberathem" near Jixian, 100 km east of Beijing, in northern China. One of these communities is preserved in bedded, essentially flat-laminated, stromatolitic chert; the other occurs in silicified conical stromatolites of the forms *Conophyton cylindricum* and *C. garganicum*. These newly discovered microfossils comprise two of only a very few permianized microbiotas now known from the Precambrian of China and are among the first such fossil biocoenoses to be detected in the Sinian stratotype section. Comparison of the two assemblages is of considerable biostratigraphic interest, providing an unusual opportunity to assess the role of environment and ecologic setting in influencing the biologic composition and diversity of similarly aged and comparably preserved Precambrian microbial assemblages of this type.

SCHWARZWALDER, ROBERT N. Department of Biology, Indiana University, Bloomington, IN 47405. - The use of multivariate statistics in paleosystematics.

Classification systems of fossil plants are often inadequate, especially in cases of problematic groups or when the characteristics available for analysis are of unknown phylogenetic significance. Fossil taxa are often erected from small groups of

specimens without sufficient attention to variation among and between taxa. The resultant classification schemes contain species which represent points on a structural continuum and are established by arbitrary criteria, such as differences in size or variations in shape, which subdivide the specimens but may or may not have any real significance. The use of multivariate statistics can facilitate paleosystematic studies by: providing a determination of continuous versus discrete variation in characters; ascertaining the most useful characteristics for classification of specimens; and, providing hierarchical groupings of taxa. Using sandstone impressions from the Dakota formation of Kansas and Nebraska, three multivariate statistical methods - discriminant analysis, cluster analysis, and multidimensional scaling - have been applied and evaluated as paleosystematic tools. Multivariate statistics, mostly cluster analyses, have been previously utilized in paleobotanical studies; however, despite their potential these methods have not enjoyed widespread acceptance in the field. Phenetic systems can provide meaningful hierarchical classification systems, and while they may require additional analysis before phylogenetic conclusions may be drawn, they are consistent with the form taxon concept commonly utilized in paleobotany.

SHEN-MILLER, J.\*, J. WILLIAM SCHOPF & R. BERGER. Department of Chemistry and Biochemistry, and Institute of Geophysics and Planetary Physics, Univ. Calif., Los Angeles, CA 90024 - Germination of a ca. 700 year-old lotus seed from China: evidence of exceptional longevity of seed viability.

In 1952, seeds of the sacred lotus (*Nelumbo nucifera* Gaertn.) were collected by Chinese scientists from silt 1-2 m below the surface of an ancient dried pond at Paozi Tun Village in Xinjin County ("Pulantien"), Liaoning Province, P.R.C. In 1955, studies at the Beijing Botanical Garden demonstrated that these seeds were viable; one of the plants then germinated was still growing when we visited Beijing in 1982. Analyses in 1975 at the Institute of Archeology in Beijing yielded a radiocarbon age of 915±80 years for a pooled sample of these seeds untested for viability. Xinjin seeds were provided us by Zhang Yi-jun of the Beijing Botanical Garden. An initial study was carried out on two seeds (X-1 and X-2), characteristics of which are compared below with those of a seed (M-1) from modern progeny of Xinjin lotus, obtained from H. V. Wester of the National Park Service, Washington, D.C.

	X-1	X-2	M-1
Length (mm)	17.0	15.5	17.0
Girth (mm)	8.5	8.0	9.0
Dry Weight (g)	0.69	0.83	0.94
Appearance	shiny	shiny	dull
Germination Time (d)	no	yes, 6	yes, 4

Seeds were germinated in the dark; X-2 was immediately dried in an oven (110 C, 24 h) and stored in a desiccator. Subsequent radiocarbon dating yielded an age for this seed (UCLA-2387B) of 705±165 years. This appears to be the oldest viable seed for which a radiometric age has been directly determined. Comparisons of two more ancient seeds with those of modern Xinjin lotus are in progress.

SMOOT, E.L. Department of Botany, The Ohio State University, Columbus, OH 43210. - Phloem anatomy and trends of specialization in the Pennsylvanian seed fern *Medullosa*  
Stems of the seed fern *Medullosa* with well-preserved phloem are described from coal ball

specimens ranging in age from early/middle to late Pennsylvanian. Phloem appears to be continuous with the vascular cambium region and completely surrounds the vascular segments ("steles") of the stem. The zone of secondary phloem shows anatomical differences between the innermost phloem cells (presumably functional phloem) and the cells at the periphery of the zone (non-functional phloem). Groups of crushed cells, including some fibers, are present just outside the secondary phloem and may represent the remnants of primary phloem. Secondary phloem consists of groups of alternating tangential bands of fibers, sieve elements and axial (phloem) parenchyma, separated by phloem rays. Rays vary in height, but are generally high, and average 5-6 cells in width. The rays are dilated toward the periphery of the phloem tissue. Sieve elements are extremely long, thin-walled, and exhibit crowded sieve areas on the radial walls. Sieve areas are oval, approximately 8 x 28  $\mu\text{m}$  with numerous sieve pores, and some appear to show signs of callose deposition. The phloem anatomy of *Medullosa* is quite similar to that described for *Callistophyton*, and can be compared with other Carboniferous seed ferns. Phloem anatomy in several Pennsylvanian age plant groups is briefly summarized, and possible trends of specialization in phloem tissue are discussed.

STARK, DIXIE SUE PATTEN. Department of Botany, University of Montana, Missoula, MT 59812.  
- A new species of pinaceous cones from the Tertiary of Maryland.

Description of a new *Pityostrobus* species is based on a single specimen from an exposure of the Miocene Calvert Formation on Chesapeake Bay in Calvert County, Maryland. The cone is barrel-shaped, 6.8 cm long, and 4.0 cm in diameter. Numerous ovuliferous scales are spirally arranged around the central axis. They are approximately 2 cm long and 1 cm wide. The inflated scale apices and the pattern of vascular trace divergence into the bracts and scales are consistent with the genus *Pinus*, but the thin, frequently-dissected vascular cylinder is atypical. The combined presence of features of other Recent genera such as *Cedrus* and *Abies* dictates assignment of the fossil to the genus *Pityostrobus*. Comparison of the specimen with 19 known species of *Pityostrobus* indicates that it represents a new species. The structure of the cone is inconsistent with the Miocene age of the Calvert Formation and it is likely that the fossil was reworked from older sediments.

STEIN, WILLIAM E.† and CHARLES B. BECK. Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109. - Triloboxyton (*Aneurophyton hallii* Arnold) *arnoldii* Matten from the Middle Devonian of New York.

Although several aneurophytalean taxa with three-ribbed steles have been proposed, clear and consistent anatomical distinctions between them have yet to be determined. Reasons for this include the fact that many new specimens show significant variability in the co-occurrence of defining features, and that type specimens are often among the most poorly understood specimens. As part of a comprehensive analysis of large axes attributed to the genus *Triloboxyton* from marine sediments in western New York, we have re-studied type material of the poorly known *T. arnoldii*. The main axis consists of primary xylem surrounded by

very extensive secondary tissues. The heterogeneous cortex, consisting of parenchyma, fibers, and clusters of sclereids, provides evidence of sustained growth or secondary modification. At the periphery, bundles of fibers are associated with short, dark-filled sclereids, and are separated by regular arrays of thin-walled cells. There is a possible epidermis several cell layers thick. A periderm borders shallow fissures in the axis interpreted to be of biological origin. Traces, circular in transverse section, are borne in subopposite pairs from each primary xylem rib. Distally, each trace divides once. Two closely related taxa, *Reimannia* and *T. ashlandicum*, provide different models for what the primary body in *T. arnoldii* might have been like. From these initial conditions, different patterns of subsequent development are suggested. Difficulties in interpretation persist. If, however, more than one developmental sequence could be demonstrated in these forms, then we might have a useful key to more natural taxa in the group.

STOCKEY, RUTH A. Dept. of Botany, Univ. of Alberta, Edmonton, Alberta, CANADA T6G 2E9. - Fossil conifers of the northern Yukon, Old Crow Basin.

Large numbers of conifer cones with associated wood have been found in alluvial sediments of the Old Crow - Blue Fish Basin in the northern Yukon. Early studies of the section known as "12 mile bluff" suggest a Late Quaternary age. Recent studies of the bryophytes and palynology indicate an older age, possibly Miocene. Three types of ovulate pinaceous cones have been identified corresponding to the genera *Pinus*, *Picea*, and a third small cone representing *Tsuga* section *Hesperopeuce* or *Larix*. The relatively unaltered remains were removed from a clay matrix, washed, dehydrated and embedded in bioplastic or glycol methacrylate for sectioning. Cylindrical *Picea* cones, 7 - 11.2 cm long X 2.1 - 2.8 cm wide, have a bluntly rounded base and a slightly acute apex. The parenchymatous pith is surrounded by a narrow vascular cylinder that is interrupted between the ovuliferous scale and bract traces. Surrounding the vascular cylinder is a parenchymatous cortex containing a ring of conspicuous resin canals. Vascular traces to the bract and ovuliferous scale arise separately from the axis stele with the resin canal system adaxial to the scale trace. The cones are compared to *P. banksii* Hills & Ogilvie from the Beaufort Fm., *P. anadyrensis* Kryst. from Siberia, and *P. diettertiana* Miller from the Oligocene of Montana. *Pinus* cones, 7 - 10.1 cm long X 1.7 - 2.3 cm wide, have helically arranged cone-scale complexes each bearing 2 ovules. A parenchymatous pith is surrounded by a narrow vascular cylinder with few resin canals. Vascular traces arise as a single unit. The resin canal system in the scale is abaxial to the vasculature. These cones are compared to *P. itelminorum* Vassk. from the Quaternary of Siberia and *P. avonensis* Miller from the Oligocene of Montana. Identification of these remains has added to our knowledge of the age of the sediments and provides important information with respect to the paleoecology of the basin.

STROTHER, PAUL K.\*, NORMA G. JOHNSON and ALFRED TRAVERSE. Department of Geology, Dickinson College, Carlisle, PA 17013 and Department of Biology, Pennsylvania State University, University Park, PA 16802  
- Morphology and phylogeny of Silurian spore tetrads.

Spore tetrads from the Llandoveryan (lower Silurian) Tuscarora Formation in Pennsylvania and elsewhere can be placed into three morphological categories. *Nodospora* tetrads have two mutually perpendicular axes of symmetry, but the tetrads do not break up into individual spores. *Tetraedraletes* consists of four spores arranged at the apices of a tetrahedron which are characterized by thickened contact rings. Both *Nodospora* and *Tetraedraletes* possibly represent meiotic products of sporogenesis. Other tetrads are

not characterized by symmetric aggregates of spores; they are defined as four spores occurring within a membranous sac. Of these three configurations only the Tetrahedraletes-type is strictly morphologically analogous to embryophyte sporogenous tetrads. Our studies suggest that Tetrahedraletes is a probable derivative of plants which were ancestral to the spore-bearing embryophytes.

STROTHER, PAUL K.\* and CECILIA LENK.  
Department of Geology, Dickinson College,  
Carlisle, PA 17013-Eohostimella is not a plant.

A detailed palynological investigation of the matrix surrounding Eohostimella heathiana (Schopf) revealed an allocthonous assemblage of organic fragments of mixed origin. This presumably upright axial Silurian plant (Llandoveryan C3 to C5 age) occurs in the Frenchville Formation which is considered to be part of a proximal turbidite sequence. Based on our palynological findings, the general geology, the paleoecology of immediately conformable beds and the morphology of the fossil, we conclude that Eohostimella is probably a worm tube and not a plant.

STUBBLEFIELD, SARA P.\* AND THOMAS N. TAYLOR.  
Department of Botany, The Ohio State  
University, Columbus, OH 43210. - Host-pathogen interaction in an Upper Carboniferous gymnosperm.

Evidence of a pathological relationship in the gymnospermous pollen cone Lasiostrobus polysacci is discussed. Specimens are preserved by calcareous cellular permineralization, and were collected at the well known Berryville coal ball locality (Upper Pennsylvanian). Broad regions of cortical parenchyma in the axis of the cone show evidence of fungal invasion including disruption of host tissues, branching septate hyphae, and spherical bodies. Cortical cells often contain smaller spheres which sometimes appear spore-like in transmitted light. When viewed with scanning electron microscopy these spheres consist of bubble-like projections from the inner surfaces of the host cell walls. They are globular to elongate, and may occur singly or in large groups. Such structures resemble the callosities often formed in response to fungal invasion in a number of extant plants, and may stop or retard mycelial penetration. It is difficult to determine the time of fungal invasion when dealing with fossilized organisms. Consequently, the present material is particularly interesting since it provides evidence of a host response.

TAYLOR, THOMAS N.\* AND KENNETH L. ALVIN.  
Department of Botany, The Ohio State University,  
Columbus, OH 43210 and Department of Pure and Applied Biology, Imperial College of Science and Technology, London, England. - The ultrastructure of Classopollis pollen.

One of the most unusual pollen types in Mesozoic sediments is the genus Classopollis. This broadly defined taxon ranges from the late Triassic into

the Cretaceous (Turonian), and includes spherical grains with a sub-equatorial rimula. On the proximal pole is a trilete mark, and on the distal surface a thin area in the sporoderm termed the cryptopore. Ultrastructural studies of Classopollis have been completed on grains extracted from the pollen cone Classostrobus comptonensis collected from the upper Wealden of the Isle of Wight, England. The mature nexine is composed of approximately 20 electron-dense lamellae, each about 10 nm thick. The sexine component of the sporoderm consists of four ( $S_{1-4}$ ) easily recognizable layers, with the most prominent zone formed of coarse, inwardly-tapering elements. The  $S_2$  layer is uniformly thickened throughout the wall, except in specialized areas (e.g., trilete, rimula, cryptopore) where it thins. The remaining wall layers include the spinules that ornament the surface and a uniform series of small spaces associated with the spinule bases. Grains extracted from less mature pollen cones provide an opportunity to trace some developmental stages in Classopollis sporoderm ontogeny, and to compare these stages with those of selected extant gymnosperm pollen types.

Taylor, Thomas N.,\* Edith L. Smoot and T. Delevoryas, Department of Botany, The Ohio State University, Columbus, OH 43210 and Department of Botany, The University of Texas, Austin, TX 78712. - Structurally preserved plants from Antarctica: A Triassic cycad stem. Vegetative remains assignable to the Cycadales are described from the Fremouw Formation (Triassic) of the Transantarctic Mountains. Specimens consist of well-preserved stem segments approximately 5 cm in diameter and associated petioles. In transverse section, the vascular cylinder consists of endarch primary bundles and radial files of small, presumably secondary tracheids with scalariform pits. The large, parenchymatous pith region is continuous with the cortical parenchyma, and contains numerous mucilage cells. Some phloem is preserved and there are regions in the stem where periderm is conspicuous. Traces to the petioles arise in a helical pattern and some assume a characteristic girdle configuration in the cortex. The presence of many small roots with diarch primary xylem suggests that the specimens may represent basal regions of the plant. The plants from Antarctica are compared to other anatomically preserved cycad stems of Mesozoic and Tertiary age (e.g., Menucoa, Fascivarioxylon, Michelilloa, Lyssoxylon) as well as with several extant cycads.

TIDWELL, WILLIAM D.\*, ROSS E. JONES, AND LEE PARKER. Department of Botany and Range Science, Brigham Young University, Provo, UT 84602, Brightwater Road, Blackmans Bay, Tasmania 7152, Australia, and Biological Science Department, California Polytechnic State University, San Luis Obispo, CA 93407. - A new species of Cibotiocaulis from Tasmania, Australia.

A petrified tree fern stem representing a new species of Cibotiocaulis was collected from the same locality in Tasmania as Cibotium tasmanense which was described by Gould (1972). The petrified specimens of

Cibotiocaulis are 11 cm. in diameter and consist of a stele surrounded by leaf traces and roots. The pith region is filled with numerous medullary bundles. The structure of the meristelic margins at the leaf gap and the mode of the parting of the leaf-traces are somewhat similar to those of living Cibotium barometz. The formation of the leaf trace is by gradual bulging outward of the stelar ring which broadens in its outer portion into a somewhat omega shape. The trace remains intact rather than dividing into a series of bundles as in the Upper Jurassic Cibotiocaulis tatei Ogura from Korea. The configuration of the traces in the petiolar bases of the Tasmanian specimens also differs from those in C. tatei. The traces of the Tasmanian specimens are similar to those in the Dicksoniaceae, whereas traces of C. tatei are more cyatheacean. Numerous root traces occur, but only outside of the stele in the cortical region. These specimens will be compared to living members of the Dicksoniaceae and Cyatheaceae and to the fossil genus Cyathocaulis.

TRIVETT, M.L.V.C. Department of Botany, Ohio University, Athens, Ohio 45701 - Pollen cones of a mesarch cordaitan from the Upper Pennsylvanian of the Appalachian Basin.

Mesoxylon stems of the Mesoxylopsis-type bear leaves assignable to Cordaites felicis and a new species of Gothania pollen cones that are attached as axillary branches. Pollen sacs contain prepollen assignable to Sullisaccites Millay and Taylor, and establish the natural affinities of this spora dispersae genus. The cones occur either singly, or as one of a pair of branches. In the latter case, the other branch is a vegetative bud. Cones consist of bilaterally symmetrical primary axes bearing numerous four-ranked bracts in the axils of which are fertile secondary shoots. The secondary axes have up to 25 helically-arranged vegetative and fertile scales. Fertile scales are confined to the apical region and terminate in four elongate pollen sacs that are arranged in a linear fashion. In immature specimens, the vegetative scales are tightly imbricate, completely enclosing the fertile tip. However, the pollen sacs of mature specimens extend well beyond the vegetative zone, and appear as large masses on coal-ball surfaces. This is the second cordaitan to be characterized from the Steubenville assemblage, and it demonstrates that the entire plant can not be recognized from single or isolated vegetative organs.

Upchurch, G.R. Division of Paleobotany, W-312 MNH, Smithsonian Institution, Washington, D.C. 20560 - Ficophyllum leaves from the Lower Cretaceous Potomac Group: Evidence for possible affinities with Magnoliales and Austrobaileyaceae.

Reinvestigation of upper Zone I (Aptian?) angiosperm leaves belonging to the genus Ficophyllum corroborates previous ideas on possible affinities to Magnoliales, but also shows the presence of many features typical of Austrobaileyaceae. These leaves are large and have a midrib comprised of numerous anastomosing strands, as in certain primitive Magnoliales. Their irregular pattern of festooned brochidodromous 2° venation is suggestive of Winteraceae, but the basal 2° veins are oriented at a lower angle than the others in a manner characteristic of Austrobaileyaceae and other Laurales. The 3° venation is random reticulate, as in many Magnoliales, and its higher order venation has a suite of features most suggestive of Magnoliaceae and Austrobaileyaceae. The 4° and 5° veins are retic-

ulate, with a tendency towards orthogonal rooting, and are thin for a leaf of large size. The areolation tends towards 4-sided and in some regions the areoles are elongate at right angles to the midrib. Freely ending veinlets generally are unbranched and occur in less than 50% of the areoles. The higher order venation of Magnoliaceae differs from that of the fossil only by its more numerous and more branched freely ending veinlets, while that of Austrobaileyaceae lacks 5° veins and has larger, more elongate areoles. Stomatal features are preserved on some cuticles and the suite of characters is most similar to that of Austrobaileyaceae. According to many neobotanical systems of classification this leaf would represent a very primitive angiosperm. However, its occurrence with angiosperm leaves that possess only 3 well-developed orders of venation suggests that Ficophyllum may be more advanced than some Zone I forms.

Upchurch, G.R. Division of Paleobotany, W-312 MNH, Smithsonian Institution, Washington, D.C. 20560 - The cuticular anatomy of "platanoid" leaves from the Lower Cretaceous Potomac Group.

Studies of Cretaceous angiosperm leaf architecture have provided evidence for a group of leaves with affinities to Platanaceae known as the "platanoids". Additional evidence comes from the cuticular anatomy of platanoid leaves from upper Subzone II-B (or Albian) of the Potomac Group. In every species the stomatal complex ranges from paracytic to laterocytic and weakly cyclocytic. Some of the subsidiary cells form from the 2° division of neighboring cells. Platanaceae are similar except that they lack paracytic stomata and all of their subsidiary cells arise through 2° divisions. In addition, the fossil leaves possess hair bases identical to those in extant Platanus or hair bases and secretory cells that appear to be homologous. In Platanoid #1 there are secretory cells and hair bases that intergrade with them. The secretory cells range from dome-shaped to bulbous and are variably positioned with respect to the adjacent cells. The hair bases have foot cells that are identical to some secretory cells except that each bears an apical hair abscission scar. In Platanoid #2 there are only dome-shaped secretory cells, which unlike those in Platanoid #1 are always positioned over the junction of two or more cells. In Platanoid #3 there are only hair bases of the Platanus type, which resemble those of Platanoid #1 but are always positioned over the junction of two or more cells. Identical hair bases occur on an associated inflorescence that consists of an axis bearing heads, as in some Platanaceae. Hence, the cuticular anatomy of Potomac Group platanoids, along with the closer resemblances shown by Late Cretaceous platanoid cuticles with modern Platanaceae, support the concept that the Potomac Group platanoids belong to the complex from which extant Platanaceae are derived.

Upchurch, G.R.\*, L.J. Hickey, and K.J. Niklas. Division of Paleobotany, W-312 MNH, Smithsonian Institution, Washington, D.C. 20560, Peabody Museum, Yale University, New Haven, CT 06520, and 214 Plant Sciences Building, Cornell University, Ithaca, NY 14853 - Leaves with chloranthoid characters from the Lower Cretaceous Potomac Group.

Studies of leaf remains from Zone I (Aptian?) of the Potomac Group of Virginia reinforce palynological evidence for the chloranthaceous affinities of a group

## 82 Paleobotanical Section

of Early Cretaceous angiosperms. Several species of serrate leaves possess Chloranthoid teeth with prominent glands in which the lateral veins run parallel to the margin and fuse with the gland. Similar teeth occur in some Chloranthaceae, Amborellaceae, and Tetracentraceae. One fossil species shows additional chloranthoid characters in its higher order venation, cuticular anatomy, and chemistry. Its areolation is elongate, with few freely ending veinlets, as in some species of Ascarina. Its suite of cuticular features is found only in Chloranthaceae, but individual characters occur in other families as well. The paleochemistry of the cuticular remains is most consistent with an assignment to Chloranthaceae. However, the species differs from modern Chloranthaceae in its simple craspedodromous secondary venation, its rudimentary quaternary venation, and its alternate leaf arrangement. The latter two characters suggest that this leaf group is more primitive than modern Chloranthaceae and that the family may not have originated until later in the Cretaceous.

WARD, JEROME V. Department of Botany and Microbiology, Arizona State University, Tempe, AZ 85287  
- Hexarugate pollen from the Albian of Kansas.

A study of the terrestrial palynoflora from outcrop localities (including the types) of the Cheyenne and Kiowa formations of Kansas was undertaken to assess the range of variation of early angiosperm pollen, species composition, and to compare with coeval palynofloras. One discovery is the occurrence of dicotyledonous pollen with hexarugate morphology, i.e., six non-equatorial apertures aligned in a tetrahedral fashion. These hexarugate pollen types are regarded as variants of the normally occurring tricolp(-or, -oroid)ate pollen species recognized as 21 informal morphotypes accommodated in 19 form species. This approach to classification has implications for strict typological taxa, where observance of modern pollen variation in relation to the fossil realm can lead to more natural paleotaxonomic groups. Hexarugate pollen, most common in modern Caryophyllales, complies with Van Campo's (1976) model of "successiformity" and provides a link between triaperturates and periculate grain types. Whereas the relative adaptive advantage of this morphotype may be argued (e.g., greater germination efficiency), it is probable that it is a product of selective pressures, in part operating within the diversity of mid-Cretaceous pollinating systems.

WIGHT, DAVID C.\* and CHARLES B. BECK. Division of Biological Sciences and Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109. - Aneurophytalean progymnosperms from the Millboro Shale of southwestern Virginia.

A significant portion of a large suite of permineralized axis fragments collected from the Purcell Member of the Millboro Shale (probably upper Eifelian) is assignable to the order Aneurophytales (Progymnospermopsida). Although these specimens are among the oldest structurally preserved members of this order, some show great similarity to other members of the

order which occur somewhat later in time. One such specimen consists of three orders of branching. Primary xylem of first and second order axes is protostelic and deeply three-ribbed. Order of maturation of primary xylem is mesarch with several protoxylem strands present in each rib. Traces to second order axes are produced helically. A subopposite pair of ultimate appendage traces is produced concurrently with the production of traces to second order axes. Primary xylem of the ultimate appendages is circular in outline with a single central protoxylem strand. Secondary xylem is present in both first and second order axes. This specimen shares characters with the Middle Devonian taxa Reimannia aldenense Arnold and Cairoa lamanekii Matten, and the Middle to Upper Devonian Triloboxylon ashlandicum Matten and Banks. Preservation is sufficiently good to permit the precise determination of the distribution of protoxylem strands in the primary xylem and their association with trace departure in this and other specimens. The patterns present are consistent with the view that aneurophytalean progymnosperms were derived from some trimerophyte-like form.

WINSTON, RICHARD B. Department of Geology, University of Illinois, Urbana, IL 61801.

- A Late Pennsylvania extrabasinal flora and its environment.

The Late Pennsylvanian (latest Missourian) flora of the Rock Lake Shale Member of the Stanton Limestone Formation was restudied in depositional succession as part of a broader biological and ecological study of a site at Garnett, Kansas. Twenty species of megafossils were found including five species of ovules). The megafloora is dominated by Lebachia garnettensis with Cordaites being subdominant. Morphological and comparative evidence supports the conclusion that L. garnettensis abscised its ultimate branches. Callipteris flabellifera is common but not abundant. The remaining vegetative species are rare. Nearly all the fossils collected were gymnosperms. Cordaites is most abundant in the uppermost 40 cm of the unweathered portion of the 150 cm thick deposit, especially the top 20 cm. The microflora was dominated by Potonieisporites pollen from the pollen cones of Lebachia garnettensis. The miospores which show the most distinct changes in relative abundance are Protohaploxylinus and Vesicaspora. Protohaploxylinus was common in the lower portion of the deposit but was, to a large extent, replaced by Vesicaspora near the top of the deposit. These changes, together with the increase in relative abundance and cover of Cordaites near the top of the deposit suggest that the local environment was slightly moister when the upper part of the shale was deposited, but that the conditions were generally mesic throughout the interval of deposition. The following taxonomic changes have been made: emendation of the description of Lebachia garnettensis and reduction of Dichophyllum moorei to a subspecies of Callipteris flabellifera.

WINSTON, RICHARD B. Department of Geology, University of Illinois, Urbana, IL 61801.

- Systematics of the primitive conifer Lebachia. A cladistic analysis of the genus Lebachia has been performed. The probable relations of Lebachia to other groups is reviewed. The genus Walchia sensu stricto (Ernestiodendron) is considered to be derived from Lebachia. The Cordaitales and Lebachia are considered to be sister groups and both are consider-

ed to be derived from Archaeopteris or some similar progymnosperm. These relationships are useful in determining polarities in some characters but such characters could not be polarized by reference to an outgroup. The polarized characters were used to choose the best point at which to root a Wagner network constructed with the unpolarized characters. The resulting phylogeny was used to predict the character states in certain species in which these data have not so far been obtained. Two natural groups were distinguished in Lebachia. One group had ovuliferous cones borne at the tips of its penultimate branches while the other had ovuliferous cones borne at the tips of ultimate branches. The former group contained some members with flattened short shoots in their ovuliferous cones and appears to be ancestral to Walchia sensu stricto.

ZAVADA, MICHAEL S. Department of Biology  
Indiana University, Bloomington, IN 47405  
The origin of self-incompatibility  
in angiosperms: A paleobotanical per-  
spective.

The functional significance of the pollen exine is discussed with special reference to intraspecific incompatibility in angiosperms. There is a correlation between tectate-columellate-perforate (reticulate) pollen walls and sporophytic self-incompatibility. Other pollen wall types are discussed in relation to gametophytic self-incompatibility. The evolutionary trends based on neontological data for self-incompatibility and wall structure in angiosperms are considered. The significance of these data for interpreting the earliest fossil dispersed angiosperm pollen and the role that self-incompatibility may have played in the origin and early evolution of angiosperms is discussed.

## PHYSIOLOGICAL SECTION

### Poster Session

HABERMANN\*, HELEN M. & ELSIE W. SHOEMAKER. Dept. of Biological Sci., Goucher College, Towson, MD 21204  
-Does barometric pressure affect stomatal opening?  
Stomata vary in their response to light even when the biological and environmental factors known to affect opening are controlled. Such factors include leaf position and plant age, temperature, light intensity, relative humidity, CO<sub>2</sub>, adequacy of mineral nutrients and water. A possible cause for the variability of stomatal response is fluctuation in barometric pressure (BP), an environmental factor that, according to Gale (Isr.J.Bot. 20: 334), can affect transpiration. Our studies tested for effects of ambient BP (at time of sampling and for 24 h before) on stomatal aperture & guard cell potassium level (K, % stain) in Helianthus annuus. Plants grown hydroponically in a greenhouse were sampled (4/30 to 6/3/82) after forming 17 to 25 leaves longer than 1 cm. Before testing, plants were transferred to a growth chamber (30°C & 80% RH) with the same 14/10 h day/night cycle as the greenhouse. At 9:30 EST the next morning stomatal apertures were determined by means of silicone replicas & guard cell K was estimated (using the standards of Fischer: Aust. J. Biol. Sci. 25: 1107) in epidermal strips stained with Na cobaltinitrite. For each plant 3 or 4 young, fully expanded leaves with maximally responsive stomata (generally 5th to 10th leaves) were assayed. BP was monitored with a Taylor recording barometer. With "low" ambient BP at sampling time (below 29.78 in Hg = 100.84 kPa) mean stomatal aperture was  $7.62 \pm 1.65 \mu\text{m}$  and guard cell K was  $22.83 \pm 12.25$  (N = 11 plants). At "high" BP (29.78 in Hg & above) aperture was  $3.35 \pm 2.85 \mu\text{m}$  and K was  $12.85 \pm 7.58$  (N = 17 plants). Eight of the "high" BP plants had open stomata. All 9 "high" BP plants with closed stomata (mean aperture of  $0.82 \pm 0.56 \mu\text{m}$  and K of  $8.41 \pm 1.00$ ) had been subject to increases in BP during the 4 to 12 hours prior to sampling.

MAJUMDAR\*, SHYAMAL K., and STUART A. SANDLER. Department of Biology, Lafayette College, Easton, Pennsylvania 18042.  
-Totipotency of Episcia cupreata roots grown in vitro.

Roots derived from the green callus of Episcia cupreata "pink brocade" were investigated for their totipotency potential. The roots were cultured on Murashige-Skoog medium with and without the hormones N<sup>6</sup>-benzyladenine (BA) and  $\alpha$ -naphthaleacetic acid (NAA). Callusing occurred within three to six weeks on both media. The calli clumps developed along the root's length, and it appeared light to dark brown in color. Differentiation of the callus to plantlets with leaves and roots occurred within an additional three to five weeks on the medium without the BA and NAA. Occasionally, albino plants were found to develop on this medium; however they remained small and did not produce any root system. On medium with BA and NAA the roots continued to produce calli with no noticeable redifferentiation until after ten to twelve weeks of callus formation; however the plants lacked roots. The findings are of importance in that they demonstrated totipotency of in vitro grown Episcia cupreata roots in the absence of BA and NAA hormones. The roots were able to produce callus, and the callus tissue in turn was found to differentiate into plantlets with leaves and roots.

SASAKI, KEN AND TAYLOR, IAIN E. P. Department of Botany, University of British Columbia, Vancouver, B.C., V6T 2B1, Canada.

- Myo-inositol in cell wall synthesis during germination of Phaseolus vulgaris L.

Inhibition by total submersion caused considerable seed damage as well as reduced germination and

seedling growth. Imbibition on moistened cotton in a small sample bottle eliminated the damage, allowed rapid germination and seedling growth and resulted in substantial isotope uptake for metabolic studies. *P. vulgaris* seeds were fed  $2\text{-}^3\text{H}$  myo-inositol (MI) by imbibition. The largest amount of MI was imbibed from 500mM MI (14-17  $\mu\text{moles/seed}$ ) and the highest percentage was imbibed at 1mM (30% of  $^3\text{H}$  given). During germination and growth in vermiculite, more  $^3\text{H}$  appeared in hypocotyl than in roots at all concentrations provided. Half of the label was in the 80% insoluble materials and more than 85% of it was released by hydrolysis with 2N trifluoroacetic acid. The youngest part (0-2 cm below cotyledons) of the hypocotyls in 4- and 6-day old seedlings contained larger amounts of the label than did parts 2-6 cm from the cotyledons. However, most of the label was in the oldest part of the hypocotyls (more than 6 cm from cotyledons). These results show that exogenous MI is used in polysaccharide synthesis of very young tissue and in older tissue that has completed its extension phase.  
(Supported by NSERC of Canada).

### Contributed Papers

ALLEN<sup>†</sup> RANDY D. AND HOWARD J. ARNOTT  
Department of Biology, Texas A&M University, College Station, TX 77843. Department of Biology, University of Texas at Arlington, Arlington, TX 76019. - Effects of metabolic inhibitors and growth regulators on storage protein mobilization in sunflower cotyledons.

Scanning electron microscopy was used to observe protein body digestion in cotyledon cells of *Helianthus annuus* L. Digestion occurs in three distinct stages: 1) Internal erosion of separate protein bodies. 2) Fusion of protein bodies to form larger protein vacuoles. 3) Gradual digestion and removal of storage protein from the vacuole to form a main cell vacuole. Germination of seeds in solutions of cycloheximide, a translation inhibitor, or actinomycin-D, which inhibits transcription, indicates that internal protein body erosion occurs in the absence of both RNA and protein synthesis. Protein body fusion appears to require protein synthesis but is independent of RNA synthesis. The final and most extensive phase of protein hydrolysis requires both RNA and protein synthesis for development. Digestion of protein vacuole contents is also inhibited in cells of cotyledons excised from the embryonic axis. Addition of embryonic axes or exogenously supplied cytokinin to excised cotyledons stimulates storage protein digestion. Addition of gibberellic acid or indole acetic acid to excised cotyledons does not replace the influence of the embryonic axis. High concentrations of indole acetic acid may actually inhibit protein body erosion and fusion.

ALLEN, RANDY D. and CRAIG L. NESSLER.\* Department of Biology, Texas A&M University, College Station, TX 77843 - Pectinase activity in the nonarticulated laticifers of *Nerium oleander* and its role in intrusive growth.  
Pectinase activity was localized in the nonarticulated, branched laticifers of *Nerium oleander* at the

ultrastructural level using a newly developed cytochemical localization technique. The procedure involves the use of Benedict's reagent to form an electron opaque reaction product when exposed to the reducing sugars liberated from exogenously supplied pectin. Electron opaque crystalline deposits, indicating the presence of pectolytic enzymes, were identified in the large central vacuole of oleander laticifers. Smaller amounts of reaction product were observed scattered along the middle lamella between laticifers and adjacent parenchyma cells. In control tissues, boiled prior to pectinase incubation or which were not incubated in pectin, deposits were found only in the middle lamella and not in the vacuole. Growth of the nonarticulated laticifer system in oleander is accomplished through intrusive growth between adjacent nonlaticiferous cells. The present report on the distribution of pectinase activity in oleander laticifers suggest that this enzyme is responsible for dissolving the middle lamella ahead of the growing laticifer tip.

AMIRO\*, BRIAN D., TERRY J. GILLESPIE, AND GEORGE W. THURTELL. Dept. of Land Resource Science, University of Guelph, Guelph, Ontario. N1G 2W1. - Injury response to ozone flux density in *Phaseolus vulgaris* L.

A quantitative relationship between ozone mean flux density and the length of exposure needed for the occurrence of visual foliar injury to *Phaseolus vulgaris* L. is described. Similar relationships were found for 14 day old and 6 week old plants using a whole leaf gas exchange cuvette system. Cultivars Seafarer (ozone sensitive) and Gold Crop (ozone resistant) exhibited similar responses at flux densities  $> 3 \text{ mg m}^{-2}\text{h}^{-1}$  but only Seafarer was injured below this threshold. Ambient ozone concentration and length of exposure period alone do not contain sufficient information to predict the onset of visual injury.

AMIRO\*, BRIAN D., GEORGE W. THURTELL, and TERRY J. GILLESPIE. Dept. of Land Resource Science, University of Guelph, Guelph, Ontario. N1G 2W1. - A small infrared thermometer for measuring leaf temperature in leaf chambers.

A small, inexpensive infrared thermometer is described. This instrument is easily used and is more accurate than thermocouples for leaf temperature measurements. This thermometer can be used to make leaf temperature measurements with estimated errors of less than 0.2 C when used in a typical leaf chamber.

BAJAJ, Y.P.S. and S.S.GOSAL. Tissue Culture Laboratory, Punjab Agricultural University, Ludhiana, India.

Somatic hybridization and embryo culture studies on *Arachis hypogaea* x *Arachis villosa*. Protoplast fusion and embryo culture studies have been conducted on an incompatible cross involving a cultivated tetraploid peanut (*Arachis hypogaea*, 4x=40) and a wild diploid species *Arachis villosa* (which has higher oil contents and is drought and disease resistant). The hybrid embryos which generally abort in nature, were rescued 30-35 days after pollination and successfully cultured on

synthetic media. The hybrid plants showed triploid chromosome number ( $3x=30$ ).

For somatic hybridization, a comparison of various segments of the in vitro-grown seedlings of *A. hypogaea* was made, and the optimal yield of protoplasts ( $1.5 \times 10^5/g$ ) was obtained from the excised hypocotyl segments of 10-14 day-old seedlings, treated with an enzyme mixture of cellulase (1.5%), macerozyme (1%),  $CaCl_2$  (0.3%) in mannitol at pH 5.6 incubated for 12-15 hrs. Of the two species, *A. hypogaea* was more amenable to various treatments. The mesophyll protoplasts from *A. hypogaea* were fused with callus-derived protoplasts of *A. villosa*. Treatment with 20-25% polyethylene glycol resulted in 11-13% fusion products. The genetic variables obtained as a result of various in vitro manipulations will be incorporated into peanut improvement programs.

BIESBOER, DAVID D. Department of Botany, University of Minnesota, St. Paul, MN 55108.

-Nitrogen fixation associated with natural and cultivated stands of *Typha latifolia*.

Acetylene reduction by bacteria associated with *Typha latifolia* L. roots and rhizomes was studied in the laboratory and in the field. *In situ* studies indicated that the rate of acetylene reduction in a natural cattail population was 3-fold higher than in a cultivated stand. Scanning electron microscopy and 2, 3, 5 triphenyltetrazolium chloride reduction showed that the bacterial rhizocoenosis was limited to the rhizoplane of roots and rhizomes. Seasonal changes in dinitrogen fixation, numbers of associated dinitrogen fixing organisms, and rhizome/root carbohydrates were also studied. Anaerobic dinitrogen fixing bacteria predominate in this association and show a close correlation between total acetylene reduction and population numbers during the growing season. Maximum nitrogen fixation coincides with reproductive development in *Typha* with peak acetylene reduction occurring at the time of fruit and seed development. Root sugar concentrations reach a maximum approximately two weeks prior to peak acetylene reduction suggesting that increased production of root exudates precedes an increase in total dinitrogen fixation by the associated microflora.

CHEN, CHEN-HO\*, WENDY L. JONES, and DAVID D. SONGSTAD. Department of Biology, South Dakota State University, Brookings, SD 57007 - Cloning *Lilium formosanum* through leaf and bulb scale cultures.

Young leaves stripped from floral stalks and sections of scales, 2-3 mm thick, removed from cool-treated bulbs (10°C for 4 weeks), were explanted on Murashige and Skoog's (MS) medium supplemented with 0, 0.03, 0.3, or 3 mg kinetin in combination with 0, 0.1, or 1 mg naphthaleneacetic acid (NAA) per liter. All of the cultures were incubated in the dark at 25°C. In both experiments adventitious buds, and roots in some treatments, initiated directly from explants in 4 to 5 weeks after explanting. Kinetin tended to promote bud formation but retard root initiation. NAA did the reverse. Unlike those of *L. longiflorum*, which transformed to bulblets and became dormant, the buds in *L. formosanum* cultures continued to grow and develop into independent plantlets after transferred onto MS medium devoid of hormones and incubated at 25 - 30°C under 16-hr photoperiodic cycles (cool-white fluorescent light at 2 klx). The plants flowered two years after transplanted in the soil.

ELLIS, D. E.\* and D. E. BILDERBACK. Department of Botany, University of Montana, Missoula, MT 59812. - Multiple bud formation of *Larix occidentalis* in sterile tissue culture.

The timber industry of the Pacific Northwest has been interested in discovering new methods of propagating *Larix* vegetatively. Multiple buds have been induced on 7-10 day old seedlings in sterile tissue culture but, like stem cuttings, roots are still an obstacle to reliable plantlet formation. Following hydration, seeds require a minimum of 15 days of cold stratification before germination is achieved and before buds can be induced in tissue culture. Seedlings are surface sterilized in 4% Clorox and placed on the medium of Reilly and Washer (1977), supplemented with various concentrations of benzyladenine (BA). Buds form from the epicotyl region after 6-8 weeks in culture. Elongation is achieved by excising and transferring the buds to the medium of Reilly and Washer without the addition of any hormones. Buds grow relatively slowly in tissue culture, and problems with sterility hindered progress with embryonic tissue due to bacterial contamination on the embryo in the seed.

ELLIS, D. E.\* and D. E. BILDERBACK, Department of Botany, University of Montana, Missoula, MT 59812. - The use of sterile tissue culture to induce multiple buds on *Pinus ponderosa*.

In order to meet the expanding need for genetically superior trees, researchers have begun to use sterile tissue culture as a means of vegetatively propagating conifers. Excised embryos of *Pinus ponderosa* form multiple buds on several nutrient media with varying hormone concentrations. Embryos placed on the medium of Reilly and Washer (1977) were subjected to different concentrations of benzyladenine (BA) ranging from 1 mg/l to 10 mg/l. While all concentrations yielded some multiple buds, concentrations below 2.5 mg/l and above 7.5 mg/l yielded substantially fewer buds. Embryos placed on the medium of Cheng (1975) containing 1.02 mg/l 6( $\gamma,\gamma$ -Dimethylallyl-amino)-purine(2iP), 0.88 mg/l indole acetic acid (IAA), 1.02 mg/l indole butyric acid (IBA), and 1.13 mg/l BA produced a limited number of buds. By reducing the nutrient, vitamin and hormone concentrations of both media by one half, embryos formed more buds and formed them earlier than on the full strength media.

GALEWSKY, SAMUEL\*, and CRAIG L. NESSLER. Department of Biology, Texas A&M University, College Station, TX 77843. - In vitro synthesis of phenanthrene alkaloids by somatic embryos of the opium poppy, *Papaver somniferum*.

Extracts of somatic embryos of the opium poppy, *Papaver somniferum* were examined by high performance liquid chromatography for the presence of phenanthrene alkaloids. The analysis was done by reverse phase using a C18 column with a gradient system. The solvents were: A - 10 mM perchlorate buffer, pH 4.0, with 5 mM N-butylamine; B - acetonitrile. The gradient was run from 90% to 27% A over 5 minutes and isocratic at 27% A, 73% B for an additional 2 minutes. Phenanthrene alkaloids were positively identified in suspension cultures of somatic embryos, but were not detected in callus or nonembryonic suspensions. The presence of well developed laticifers in somatic embryos may account for their ability to synthesize phenanthrene alkaloids in vitro.

GALLAGHER, JOHN L.\* , DONNA GRANT AND MICHAEL SIEGEL. College of Marine Studies, University of Delaware, Lewes, DE 19958

- Effect of perturbations on the underground reserves of *Carex lyngbyei*, *Spartina alterniflora* and *Distichlis spicata*

Various methods of assessing underground reserves have been used to evaluate the condition of perennial forage crops, such as alfalfa, when they are in the dormant stages. Cultural practices, disease or insect pests can cause the plant stands to be weakened in subsequent years by having a detrimental effect on the reserves the plants store for initial growth in the spring. Measurement of such reserves following summer growth may be a technique which could be exploited in assessing the ecological impact of perturbations to the system. The studies reported here examine the effects of defoliation, nitrogen fertilization and treatment with the herbicide amitrol. One defoliation of *Spartina alterniflora* in Georgia reduced the reserves recoverable in the fall to zero. Repeated defoliation of the Delaware stand did not have as drastic an effect nor did similar treatment on *Carex lyngbyei* in Oregon. The herbicide treatment reduced recoverable reserves quantity and duration of release to aboveground productions. In Oregon *Carex lyngbyei* stand the regrowth material from all perturbations was higher in N, P, K than in the control. Defoliation and herbicide treatments applied to Delaware *Spartina alterniflora* reduced the quantity of reserves, but did not alter the N content but P content was reduced.

GOVIL, SUDHA R., DC AGRAWAL, KP RAI AND SN THAKUR. Department of Farm Engg., Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India.

- Effect of radiation in UV region on green-gram (*Phaseolus aureus* L.) - An experiment with Laser.

The effect of laser radiation on growth, chlorophyll, nucleic acids and protein contents in green-gram has been investigated. Dry seeds irradiated with pulsed nitrogen laser\* at 337.1 nm were germinated in Petri plates (12 h illumination daily) for a week. The variations in the above parameters with exposure time are as follows:

Parameters	Irradiation time (Min.)			
	0	5	20	40
Shoot length (cm)	16.8	19.4	21.2	18.8
Root length (cm)	6.6	7.0	8.1	6.6
Fresh weight (mg/plant)	238.9	292.9	364.0	295.1
Dry weight (mg/plant)	19.5	23.0	25.8	21.8
Chlorophyll (µg/plant)	37.0	31.0	39.0	36.9
RNA (µg/mg)	11.5	27.1	15.5	8.1
DNA (µg/mg)	0.5	1.4	0.8	0.4
Protein (µg/mg)	66.4	90.5	185.6	151.4

**\*Characteristics of pulsed nitrogen laser**

Output pulse energy	..	10 <sup>-3</sup> Joule
Output peak power	..	200 KW
Output energy available	..	0.053 J/min/seed.

HAWKINS, JANICE L.\* AND JANET R. DUGLE.

Environmental Research, Whiteshell Nuclear Research Establishment, Pinawa, MB, ROE 1L0

-Growth in black ash: influence of gamma radiation

Various aspects of growth in black ash (*Fraxinus nigra* Marsh.) are being studied in the Field Irradiator - Gamma area of eastern Manitoba. Measurements of height, circumference, and diameter have been taken twice a year beginning in 1970 and continuing to the present. Long-term irradiation at dose rates ranging from 62.5 mGy/h to background began in March 1973. No ash were surviving at a dose rate greater than 15.6 mGy/h at the end of the 1982 growing season. The largest increase in girth was observed at dose rates of 0.88 mGy/h to 1.27 mGy/h. At some dose rates radiation increases leaf size. Leaves on saplings exposed to 14.9 mGy/h ranged in length from 91-353 mm (mean 182 mm). Cell size of these leaves, measured with collodion casts, was significantly larger than the controls (F=16.5; n=64). Exposure to dose rates greater than 0.25 mGy/h reduces the length of the growing season by causing later flushing and earlier abscission. At some of these dose rates, therefore, growth per unit time is considerably higher than that of unirradiated ash.

JENSEN, KEITH F. Forestry Sciences Laboratory, 359 Main Road, Delaware, Ohio 43015.

-Impact of ozone on yellow poplar seedlings stressed with air pollutants.

One-year-old yellow poplar (*Liriodendron tulipifera* L.) seedlings were stressed with air pollutants by fumigating them with either 0.05 ppm ozone, 0.1 ppm SO<sub>2</sub>, or both 0.05 ppm ozone and 0.1 ppm SO<sub>2</sub> for 12 hours per day 7 days a week. The seedlings were then fumigated for 6 hours 1 day a week with 0.2 ppm ozone. The treatments lasted for 20 weeks. Eight seedlings were harvested from each treatment at 4 week intervals throughout the study. Growth response curves for height, leaf area, leaf weight, and total weight were developed and analyses of variance were performed on the data. Significant differences were found in total weight after 20 weeks of treatment. Seedlings predisposed with SO<sub>2</sub> or SO<sub>2</sub> plus ozone had significantly less dry weight than the controls. The 0.2 ppm ozone fumigation had no effect on either the unstressed or pollutant stressed plants.

KARIMI, S. H. and I. A. UNGAR. Department of Botany, Ohio University, Athens, Ohio 45701 - Effect of aeration, shading and salinity on oxalate accumulation of *Atriplex triangularis* Willd.

To investigate the accumulation of oxalate in response to conditions present in natural habitats of *Atriplex triangularis*, plants were grown in hydroponic solutions at low and high light intensities, plus or minus aeration and in salt solutions ranging from 0 to 3% NaCl. The highest total oxalate concentration, about 12% of dry weight, was found in the leaves of plants grown under high light intensity, in well aerated and non-saline media. Shading and lack of aeration produced low total oxalate content in leaves. As media salinity increased leaf total oxalate was found to decrease. Other organs, including stems, fruits and roots, had lower concentrations of oxalate than the leaves. Shedding

leaves contained high quantities of oxalate compared to other plant organs. Addition of salt to the nutrient media resulted in an increase in the water soluble form of oxalate and a decrease in the acid soluble form. The significance of these findings in relation to the osmotic adjustment of plants and the balancing effect of oxalate in the presence of excess cations will be discussed.

KAUSCH, A.P. Department of Botany, Iowa State University, Ames, IA 50011.

- Media modifications affecting oxalate production and calcium oxalate crystal cell differentiation in *Psychotria callus* and *Yucca* isolated root cultures.

Callus cultures of *Psychotria punctata* are initiated and maintained on a modified Linsmaier and Skoog medium; isolated root cultures are made from primary roots of *Yucca torreyi* seedlings and grown in White's medium. Affects of various media additions or alterations on culture oxalate production are determined as total oxalate content. Oxalate is assayed as the butylated ester derivative with gas chromatography from freeze-dried samples. Growth regulator variations in Latin square analysis for callus cultures show no effect on oxalate content for NAA/K, IAA/BA, or 2,4-D/BA regimes despite positive growth responses to these compounds. Each of the growth regulator combinations possess different capacities to support crystal cell differentiation. Decreasing  $\text{NH}_4\text{NO}_3:\text{KNO}_3$  ratio and increasing ascorbic acid concentrations result in elevated oxalate content in callus cultures. Ascorbic acid addition to *Yucca* root cultures results in increased oxalate content and numbers of crystal idioblasts formed in the root cortex. Affects of media addition of  $\alpha$ -HPMS, lycorine and allopurinol treatments (oxalate biosynthesis inhibitors), and pH alterations are compared between *Psychotria callus* and *Yucca* root cultures.

KAUSCH, A.P.\* and H.T. HORNER. Department of Botany, Iowa State University, Ames, IA 50011.  
- Oxalic acid synthesis and calcium oxalate crystal production in roots of *Yucca torreyi* L. Cytochemical and autoradiographic analyses.

Glycolate oxidase was localized in peroxisomes of root cells by using the cerium chloride technique. Reactive peroxisomes were identified by the heavy-metal precipitate and by x-ray elemental analysis for cerium. Reactive peroxisomes were found in all parenchymatous cells except in those forming files of calcium oxalate crystal idioblasts. There was no apparent concentration of reactive peroxisomes in parenchymatous cells around the idioblasts. Incorporation of  $^{14}\text{C}$ -ascorbic acid into primary roots for periods of 3, 6, 13, 18, and 24 hours showed that the label reaches the developing idioblasts within 3 hours and is incorporated into the raphide crystals. By 12 hours, almost all of the label is found in the idioblasts and crystals. Concentration of label in the cytoplasm of idioblasts is over the crystalloplastids. The label is eventually added to the ends of already partially formed crystals indicating that their growth is bidirectional. Use of lycorine, an inhibitor of ascorbic acid synthesis, and  $^{14}\text{C}$ -glycolic acid, another major precursor of oxalic acid in other plants, supports the results presented here.

KHAN, M. A. and I. A. UNGAR. Department of Botany, Ohio University, Athens, Ohio 45701 - Seed polymorphism and germination responses to salinity stress in *Atriplex triangularis*.

The seeds of *Atriplex triangularis* exhibited a very pronounced morphological and physiological seed polymorphism. Seed size which varied from 1.0 to 2.8mm was found to be a predictor of the likelihood of successful establishment through its effect upon germination and seedling vigor. Large seed had a mean dry weight of  $2.44 \pm 0.16\text{mg}$  and a mean length of  $2.45 \pm 0.24\text{mm}$ , medium seeds had a mean dry weight of  $1.21 \pm 0.10\text{mg}$  and mean length of  $1.78 \pm 0.19\text{mm}$  and small seeds had a mean dry weight of  $0.64 \pm 0.04\text{mg}$  and a mean length of  $1.27 \pm 0.10\text{mm}$ . The degree of salt tolerance increased progressively with increasing seed size. Seeds from all size classes that were initially treated with 2 to 5% NaCl had from 85 to 100% germination after being immersed in distilled water for 6 days, indicating a transitory adverse effect of salt stress on germination. Seedling dry weight was found to be related to initial seed size. Salt stress inhibited seedling growth.  $\text{GA}_3$  was found to alleviate some of the dormancy in seeds induced by high salt concentrations. The relationship between germination and seedling growth under salt stress to the establishment of plants in native populations will be discussed.

KONING, ROSS E. Department of Biological Sciences-Botany, Rutgers University, Piscataway, NJ 08854 - The roles of plant hormones in style and stigma growth in *Gaillardia grandiflora*.

Style and stigma elongation and stigma unfolding, and the roles of plant hormones in these processes in *Gaillardia grandiflora* Van Houtte were investigated. Style and stigma elongation in vivo began just after anthesis, and style elongation was accompanied by epidermal cell elongation (greatest near the stigma) and a fresh weight increase, but not by cell division or a dry weight increase. The stigma unfolded after the style and stigma elongated. Style-stigma units excised from young disc flowers of this composite were measured as they responded to plant growth regulators applied singly, and in sequential and simultaneous combinations, in vitro. Style and stigma elongation were promoted by auxin, were inhibited by gibberellin and ethylene, and were unaffected by other growth regulators. Endogenous auxin levels and ethylene production showed parallel variation and endogenous gibberellin levels showed inverse variation with style and stigma elongation. Stigma unfolding was more sensitive to auxin applications and was promoted by applied ethylene. Ethylene production showed parallel variation and endogenous auxin levels showed inverse variation with stigma unfolding. AVG and  $\text{Co}^{2+}$  application decreased auxin-induced style elongation, and fusicoccin promoted all of the growth responses of style-stigma units in vitro. A gibberellin-auxin-ethylene-acid growth interaction mode of control is proposed for these three growth processes.

KONING, ROSS E. AND MANDY M. RAAB. Department of Biological Sciences-Botany, Rutgers University, Piscataway, NJ 08854

- The effects of applied plant growth substances on growth of *Ipomoea nil* corolla and filaments.  
It is widely known that gibberellins promote corolla growth in various plant species, and in 1973 Murakami found that gibberellins caused rapid filament elongation.

tion. The present results confirm and extend these findings. Corolla width and length and filament length were measured as the isolated parts responded to applications of the growth substances *in vitro*. Applied gibberellins greatly promoted both corolla and filament elongation with maximum effect at 10<sup>-5</sup> M. The gibberellin synthesis inhibitors, AMO-1618 and CCC, had no effect on growth. Thus gibberellin synthesis is probably not as important a part of the growth mechanism as gibberellin transport into the flower from outside, or conversion from bound or inactive forms. Applied auxins and cytokinins inhibited growth slightly, but only at herbicidal concentrations (10<sup>-4</sup> M). ACC, an ethylene biosynthesis precursor, greatly inhibited while AVG, an ethylene biosynthesis inhibitor, enhanced gibberellin-induced growth. Applied abscisic acid had no effect upon either corolla or filament growth. Fusicoccin, a proton pump stimulator, promoted early growth while vanadate ion, a purported proton pump inhibitor, greatly reduced growth. Thus it is conceivable that the natural growth mechanisms for filaments and corollas of morning glories involve both gibberellin as a positive modulator and ethylene as a negative modulator. Furthermore, the mode of action of gibberellin in these flower parts may partially include acid growth stimulation. The proposed mechanism must be tested for parallel variation of gibberellin and inverse variation of ethylene production with respect to corolla and filament growth.

LAMOTTE, CLIFFORD E. Department of Botany, Iowa State University, Ames, IA 50011.

- Exogenous abscisic acid causes reorientation of branch shoots of *Solanum andigena*. Test of the Snow hypothesis of apical dominance.

Four-leaf cuttings are fed through their cut stem bases with a solution consisting of modified Hoagland's minerals, N<sup>6</sup>-benzyladenine (BA), and abscisic acid (ABA). Two kinds of experiments are to be described. The first involves the transformation of leafy shoots to stolons, which is promoted by apical dominance in whole plants and by apically applied IAA or basally applied ABA in decapitated cuttings. These results are consistent with the Snow hypothesis. Similar effects of ABA were reported earlier by E. Pfirsich and T. Makosso (Can. J. Bot. 58:466-70, 1980) in *Stachys silvatica*. The second involves the transformation of stolons to leafy shoots, which is evoked by a release from apical dominance in rooted plants or by basally applied BA in cuttings. ABA inhibits the branch reorientation characteristic of this transformation without affecting other morphological attributes of the branch.

MAKSYMOWYCH, ANDREW B.\* JOSEPH A.J. ORKWISZEWSKI. Department of Biology, Villanova University, Villanova, PA 19085.

- Specificity of fluorophenylalanine induced *Avena coleoptile* elongation.

Studies with para-, ortho-, and meta-fluorophenylalanine demonstrate that isomeric specificity exists in the effects of these analogues on *Avena coleoptile* elongation, *in vivo* chlorogenic acid levels and extractable L-phenylalanine ammonia-lyase activity. The effects of other halogenated phenylala-

nine analogues are now under investigation. To date we have demonstrated that only fluorophenylalanine promotes coleoptile extension growth. Chloro-, bromo-, and iodo-phenylalanine inhibit coleoptile elongation. Similarly, only fluorophenylalanine treatment results in decreased chlorogenic acid levels. Incubation of coleoptile segments with the other halogenated phenylalanines protects against chlorogenic acid loss. These data are consistent with the hypothesis that fluorophenylalanine promotes coleoptile elongation by lowering the levels of potentially phytotoxic low molecular weight phenols.

Moffler, Mark D. and Michael J. Durako. Florida Dept. of Natural Resources, Bureau of Marine Research, 100 Eighth Ave. S.E., St. Petersburg, FL 33701. - Axenic culture of *Thalassia testudinum* Banks ex König (Hydrocharitaceae).

Axenic culture of seagrasses has not previously been achieved. *Thalassia testudinum* cultures were established and grown in the absence of other detectable organisms. Cultures were initiated using surface sterilized seeds (70% v/v ethanol in seawater for 30 sec) which were aseptically dissected from surface sterilized fruits (5% v/v clorox in seawater at pH 8.0 for 10 min followed by two sterile seawater rinses). Seeds were rinsed three times in sterile seawater and placed in a holding dish containing sterile seawater and penicillin-streptomycin (200 units/ml) for five minutes. Seeds were placed in 80 ml culture tubes containing 35 ml marine agar as a rooting substrate and 40 ml of defined seawater media (32<sup>0</sup>/oo, pH 8.0). Seedlings and culture media were analyzed for microbial infection after six weeks of culture utilizing standard marine bacterial/fungal isolating procedures and SEM. Mean seedling (n=24) leaf area and root length after three months of culture were 331.5 mm<sup>2</sup> ± 195.6 mm<sup>2</sup> and 21.8 mm ± 18.7 mm respectively. Axenic seagrass cultures will be important for physiological studies such as nutrient assimilation kinetics, rhizosphere and phyllosphere microbial interactions thru mono- and polyxenic culture and seagrass-epiphyte interactions. This procedure will also provide an aseptic tissue source for tissue culture studies.

PATERSON, KAROL E. Stauffer Chemical Company, Richmond, CA 94804 - Shoot multiplication in *Helianthus annuus*.

Shoot multiplication from cultured *Helianthus annuus* shoot apices can be induced by two of the cytokinins - benzyl adenine and kinetin. Zeatin and isopentenyl adenine are ineffective as promoters of shoot multiplication. The largest number of shoots is obtained by cutting a shoot apex in half longitudinally and culturing both halves on BA-medium. High BA concentrations promote tiny abnormal rosette shoots with poor survival. Gibberellic acid also promotes shoot multiplication. The multiple shoots tend to flower while still in culture. Flower heads have been observed after as little as three weeks in culture. Both the cytokinins and GA affect flowering. There is also a possible interaction between cytokinin and ethylene in this system.

RANSOM, J. STEVEN\* and RANDY MOORE. Biology Department, Baylor University, Waco, TX 76798.  
- Curvature of primary and lateral roots of Phaseolus vulgaris in response to removal of the root tip.

Root tips of primary and lateral roots of *Phaseolus vulgaris* were cut longitudinally and half of each of the root tips excised. These half tipped roots were then oriented in different directions with respect to gravity in order to quantify the resulting graviresponses (i.e., curvatures). Primary roots bend toward the uncut side of the root, regardless of how the roots are oriented. The strongest response ( $91.9^\circ$ ) occurs when the roots are oriented horizontally with the uncut side down. The weakest response ( $30.8^\circ$ ) is encountered when the roots are oriented horizontally with the uncut side up. Lateral roots respond similarly, except that the magnitudes of the curvatures in lateral roots are substantially less than in primary roots. Untreated primary roots (controls) curve  $70.1^\circ$  downward when oriented horizontally. The corresponding value for lateral roots is  $3.9^\circ$ . If the entire root tip is excised there is little or no curvature in either type of root. Therefore, columellas of both primary and lateral roots of *Phaseolus vulgaris* produce sufficient inhibitor to induce root curvature. The failure of intact lateral roots to respond to gravistimulation is due not to the absence of inhibitor production by the root cap, but rather to the failure of these roots to sufficiently redistribute the inhibitor in response to a gravitational stimulus. This is probably due, in large part, to the small size of the columella tissue in lateral roots.

SIMON, JEAN-PIERRE\* and CATHERINE POTVIN. Département de Sciences Biologiques, Université de Montréal, Québec H3C 3J7 and Botany Department, Duke University, Durham, North Carolina 27706.  
Effect of CO<sub>2</sub> enrichment and temperature on kinetic and thermal properties of Phospho-enol pyruvate carboxylase in 2 genotypes of Echinochloa crusgalli (L.) Beauv., a C<sub>4</sub> grass weed.

Two populations of *Echinochloa crusgalli* (Québec, Mississippi) were grown at the Duke Phytotron under 2 thermoperiods ( $28^\circ/22^\circ\text{C}$ ,  $21^\circ/15^\circ\text{C}$  day/night) and 2 CO<sub>2</sub> regimes (350 and 675 ppm). Thermostability, energy of activation ( $E_a$ ),  $K_m$  (PEP) and specific activity of Phospho-enol-pyruvate carboxylase (PEP<sub>c</sub>) were analyzed in partially purified enzyme preparations of plants grown for 5 weeks. Thermostability of PEP<sub>c</sub> was significantly higher in Mississippi plants and was not modified by temperature acclimation or CO<sub>2</sub> enrichment.  $E_a$  ( $Q_{10}$   $30^\circ/20^\circ\text{C}$ ) for PEP<sub>c</sub> was significantly lower in Québec plants (11 Kcal/mol) as compared to Mississippi (15 Kcal/mol) and no acclimatory shifts were observed. Significantly higher  $k_m$ s (1-1.2 mM PEP) at  $20^\circ\text{C}$  assays were obtained for Mississippi as compared to Québec plants (0.4-0.5 mM PEP) but were similar at  $30^\circ\text{C}$  and  $40^\circ\text{C}$  assays, ranging from 0.3 to 0.6 mM PEP. PEP<sub>c</sub> activity was significantly higher for Québec plants when measured on a leaf fresh weight, leaf area or protein basis but not on a chlorophyll basis.

Significantly higher PEP<sub>c</sub> activity for both genotypes was observed for plants acclimated at  $21^\circ/15^\circ\text{C}$  or grown at 675 ppm CO<sub>2</sub>.

WEBB, DAVID T.\* Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6 and OLGA DIAZ SANTIAGO, Department of Biology, University of Puerto Rico, Rio Piedras, P.R. 00931.

- Cytokinin induced bud and shoot formation by Pinus caribaea embryos in vitro.

Embryos of *Pinus caribaea* were cultured on Shenk and Hildebrandt (SH) medium with and without Benzyladenine (BA). BA was tested at 0.5, 1.0 and 5.0 mg  $\cdot$  l<sup>-1</sup>. Whole embryos were excised and placed horizontally on agar (0.9% w/v) medium and incubated at 29 C light; 25 C dark with 12 h photoperiods of 2 klux fluorescent light. Embryos taken from dry seeds developed a few buds after 9-10 weeks on medium with 5.0 mg  $\cdot$  l<sup>-1</sup> BA. Little to no bud formation occurred at the other BA concentrations. Embryos taken from seeds pretreated by dark incubation at 27 C on half-strength SH medium formed buds at all BA concentrations. Buds were evident after 4-6 weeks in the latter case, and at 5.0 mg  $\cdot$  l<sup>-1</sup> a callus composed of many buds developed. When embryos and callus with buds were transferred to hormone-free SH medium, stem elongation occurred after the second subculture. Control embryos germinated normally and did not produce buds in both experimental procedures.

WILSON, KATHRYN J. Department of Biology, Indiana University-Purdue University at Indianapolis, Indianapolis, Indiana 46223

- Callus growth and embryogenesis in tissue cultures of Asclepias tuberosa L. (Asclepiadaceae).

Tissue cultures of *Asclepias* species provide an experimental system suitable for specifically defining the biochemical and physical parameters of differentiation and growth of the cell type, the laticifer. Since laticifers typically present in *Asclepias* members differentiate in zygotic heart stage embryos, experiments were undertaken to determine culture media supporting rapid callus growth and ultimately promoting the most prolific asexual embryogenesis. Stem explants callused most rapidly when derived from seedlings no older than 25-30 days. To derive callus, explants were maintained on several combinations of 2,4-D (0-4.0 mg/l) and benzyladenine (BA) (0-2.5 mg/l) incorporated into a basic Murashige-Skoog (MS) medium. After 33 days greatest callus growth was obtained on media supplemented with 0.5 mg/l 2,4-D and 0.5 mg/l BA. Significantly greater numbers of embryoids were obtained on media supplemented with 0.5 mg/l 2,4-D combined with 1.0, 2.0, or 2.5 mg/l BA and their numbers were increased by transferring one month old callus to MS medium supplemented with .5 mg/l BA and either no or a relatively high concentration of (6.0 mg/l) of 2,4-D. Embryoids differentiate within proembryogenic cell clusters. High concentrations of auxin promote embryoid development most similar to normal embryogeny. The effect on laticifer differentiation in embryoids proliferated on high auxin concentrations currently is being investigated.

## PHYTOCHEMICAL SECTION

## Contributed Papers

CRAWFORD, Daniel J.\*, and EDWIN B. SMITH. Department of Botany, The Ohio State University, Columbus, OH 43210, and Department of Botany and Microbiology, University of Arkansas, Fayetteville, AR 72701.- Allozyme variation in *Coreopsis grandiflora* (Compositae): divergence among the three diploid varieties and origin of the hexaploid variety. *Coreopsis grandiflora* is an outcrossing, herbaceous perennial occurring primarily in the southeastern United States. The species is variable morphologically, and this variation is now accommodated taxonomically in four varieties: var. *grandiflora*; var. *harveyana* (A. Gray) Sherff; var. *saxicola* (Alex.) E.B. Smith and var. *longipes* (Hook.) T.&G. Three of the varieties are diploid ( $n=13$ ) whereas var. *longipes* is hexaploid. Populations of the diploid varieties are usually highly interfertile. An electrophoretic study of nine soluble enzymes coded by 19 genes revealed no differentiation between the diploid varieties. Comparable levels of genetic variation were found in populations of each diploid variety and within each variety as a whole. The hexaploid var. *longipes* contains the same alleles as the diploid varieties, suggesting its origin exclusively within *C. grandiflora*. This hypothesis is concordant with data from flavonoid chemistry and morphology.

EMERSON, JEAN\* Biology Department, Saint Mary College, Leavenworth, Kansas and Botany Department, University of Kansas, Lawrence, Kansas 66045 and BRUCE A. BOHM. Botany Department, University of British Columbia, Vancouver, B.C. V6T 1W5.

- Flavonoid Variation between Chromosomal Races of *Calycadenia ciliosa* (Compositae).

*Calycadenia* is a genus in Madiinae comprising about 12 annual, self-incompatible species that are found principally in California. Chromosome numbers of  $n = 4, 5, 6, 7$  and 9 are known. The genus displays contrasting modes of evolution with species such as *C. ciliosa* that consist of morphologically similar and chromosomally distinct races, and other species, similar to *C. multiglandulosa*, that consist of races that are morphologically distinct but lack chromosomal differentiation. *Calycadenia ciliosa* ( $n = 6$ ) consists of at least five chromosomally distinct races. High levels of structural heterozygosity within some populations make racial assignment difficult. The present report describes preliminary studies of the flavonoid chemistry of certain populations of *C. ciliosa*. Two dimensional thin layer chromatography has shown a rich and complex array of pigments that differ between populations. Structural studies to date have identified glycosides of luteolin, kaempferol, and quercetin. O-Methylated derivatives of the flavonols have also been detected including the novel 5,3',4'-trihydroxy-3,6,7,2'-tetramethoxyflavone. Nuclear magnetic resonance, mass spectral, and ultraviolet data will be presented in support of this assignment.

KNOX, MICHAEL J.\*, STEVEN O. LINK, and W.DENNIS CLARK. Department of Botany & Microbiology, Arizona State University, Tempe, AZ 85287.  
- Geographical variation of the alkaloids in *Mammillaria microcarpa* (Cactaceae).

Cortical tissue extracts of *M. microcarpa* from several sites in Southern Arizona were analyzed for variation in beta-phenethylamine composition by high performance liquid chromatography. Three phenolic compounds, tyramine, N-methyltyramine, and hordenine, were found to occur throughout the natural range of the species. A fourth constituent, 3,4-dimethoxy-beta-phenethylamine was generally less distributed and present in trace amounts. Plants located at lower elevations and in hotter soils (hyperthermic arid) contained higher levels of tyramine and N-methyltyramine than did plants at higher elevations in cooler soils (thermic semiarid). While tyramine and N-methyltyramine showed significant differences among sites, there was no evidence of significance for hordenine or 3,4-dimethoxy-beta-phenethylamine. It is suggested that the simpler beta-phenethylamines are more responsive to differences in their environment than are the more biochemical complex structures. We conclude that the concentration of these compounds is probably a result of an adaptive response to ecogeographic gradients.

LEVY, MORRIS. Department of Biological Sciences, Purdue University, West Lafayette, IN 47907.

- Allozyme variation among populations: an index of the significance of gene flow in plant species.

Observations of limited gene dispersal potential and of genetic subdivision within populations have been offered as evidence that gene flow is not a significant force maintaining cohesion in a species gene pool. However, long-distance seed dispersal, of essentially immeasurable magnitude and frequency, must occur during colonization episodes to account for population dispersion patterns and the size of a species range. Does such gene migration, supplemented by interpopulational pollen movement, recur sufficiently to prevent stochastic divergence among established populations? The best available data on the issue are standardized allelic variance ( $F_{ST}$ ) estimates based on allozyme variation among populations; such estimates can be related to island-model expectations for neutral alleles under migration-based panmixia. Relative to the  $F_{ST}$  expected with a homogenizing migration rate of one per generation, observed  $F_{ST}$  values for ca. 30 species are distributed dichotomously according to breeding system. Uniparental breeders exhibit heterogeneity among populations which belies cohesive gene flow but biparental breeders do not. Indeed, though the values in the latter group are 2-10 times greater than in some highly vagile animals, e.g. *Drosophila*, they are generally on the order of those for blood group loci among human populations where significant gene flow is presumed to occur. The dichotomy between breeding systems probably reflects differences in colonization dynamics as well as in the probability of incorporation of migrant genes. Thus, though gene flow is unquestionably restricted in plant species, it can not be dismissed as a potentially homogenizing influence in species where outcrossing is at a premium.

LIU, MEEI Y\*, SUMANA BANERJEE, JOHN RUFFIN, Department of Biology, North Carolina Central University, Durham, N.C., 27707.

- A preliminary study of the effects of some common environmentally occurring gaseous pollutants on free amino acid content of certain airborne pollen grains.

The purpose of this study is to compare the free amino acid content of both contaminated and uncontaminated pollen grains. The uncontaminated pollen grains of *Quercus rubra*, *Ulmus pumila*, and *Festuca elatior* are exposed to common atmospheric pollutants such as SO<sub>2</sub>, NO<sub>2</sub>, and CO. The above pollen grains are collected aseptically and contaminated at Environmental Protection Agency, Research Triangle Park, N.C. After contamination, the free amino acids are analyzed using thin-layer chromatography. Preliminary analysis indicates that there is a great variation in the number of amino acids after the pollen grains are contaminated.

NASCIMENTO, JOSÉ C. and LANGENHEIM, JEAN H.\* Centro Nacional de Pesquisas da Seringueira e Dendê, Manaus 69,000, Amazonas, Brazil and Division of Natural Sciences, University of California, Santa Cruz, CA 95064.

- Leaf sesquiterpenes and phenolics in *Copaifera multijuga* (Leguminosae) on contrasting soil types in Amazonian rainforest.

*Copaifera multijuga*, a resin-producing legume which also contains abundant phenolic compounds, is a relatively common emergent component of central Amazonian rainforests. Differences in amount of leaf sesquiterpenes and phenolics (including tannins) were not significant in 22 *C. multijuga* trees occurring on contrasting soils (i.e. sandy, nutrient-poor vs. clayey, nutrient-rich). These results differ from those considering phenolics and alkaloids among numerous species in African rainforests on similar contrasting soils, which generally support a current hypothesis that plants on nutrient-poor soils probably invest more heavily in secondary compounds (particularly phenolics) as an herbivore defense than those on nutrient-rich ones. Results with *C. multijuga* also differed in that: a) two secondary compounds occurred in the mature leaves, and b) although soil nutrients in the contrasting types differed significantly, most leaf nutrients did not.

RICHARDSON, P. MICK. New York Botanical Garden, Bronx, New York 10458. - C-glycosylxanthones in the angiosperms.

The occurrence of C-glycosylxanthones in the angiosperms is reviewed. The compounds occur in 96 species in 28 genera in 19 families and are divided between the dicots and monocots 60:18:13 and 30:10:6 respectively. Contrary to earlier claims, the compounds appear to be of little taxonomic value at any level. There is no correlation between the occurrence of C-glycosylxanthones and morphological advancement. The main value of the compounds lies in their pharmacological properties.

SCHILLING, EDWARD E. Department of Botany, University of Tennessee, Knoxville, TN 37996-1100. - Flavonoids and the systematics of *Solanum* section *Solanum*.

Leaf flavonoids of the eleven North American species of *Solanum* section *Solanum* were characterized. Eleven

flavonols, primarily glycosides of quercetin and kaempferol, were isolated. Most species have a relatively simple flavonoid pattern with one or a few glycosides. The most distinctive pattern occurs in *S. sarrachoides* which is unique in having free flavonoid aglycones as well as 3-methoxylated compounds. Although not all species have unique flavonoid complements, flavonoid distribution is consistent with current taxonomy of the section. Flavonoid data are of little help in determining ancestries of polyploid species, but do appear to rule out *S. sarrachoides* as being a progenitor of *S. villosum* and *S. nigrum*.

SPENCER, KEVIN C.\* and DAVID S. SEIGLER.

Department of Botany, University of Illinois, Urbana, IL 61801. - Coevolutionary Significance of Cyanogen Diversification in Passiflora.

The Coevolution of *Passiflora* and *Heliconius* has been the subject of much research. It has been clearly demonstrated that the system is complex and that morphological, ecological and behavioral factors play major roles in the interrelationships of these organisms. However, we feel that the host plant chemistry is central in this system. Cyanogenic glycosides and cyanohydrins were isolated from over 30 species of *Passiflora*, including most of the major subgenera. Analysis of their structures reveals a tremendous diversity in the types of cyanogens produced. The distribution of these cyanogens reflects taxonomic relationships within the genus. We have found that a strong correlation exists between host-plant preference of *Heliconius* larvae and the type of cyanogen produced by the plant species, and that these compounds are biologically active. We propose that the diverse array of cyanogens produced by *Passiflora* has arisen in direct response to herbivory by *Heliconius* larvae, and forms the proximal basis for the coevolutionary interactions between the two. The actual mechanism of adaptive response by *Heliconius* to production by its host of a novel chemical defense may involve a change in the B-glucosidases present in its digestive system.

\*STAR, AURA and ALBERTO MANCINELLI. Department of Biological Sciences, Columbia University, New York, NY 10027. \*Trenton State College, Trenton, NJ 08625.

- Effects of inductive and long term irradiation on the flavonoid complement of *Avena sativa* L. seedlings.

Light control of flavonoid synthesis has been demonstrated in a select number of plant species. Phytochrome involvement seems to be universal, and in some species a blue-light photoreceptor has been shown to be operative. Additionally, responses to light treatments seem to be dependent on the physiological state of the organism. In this study etiolated four and six day old seedlings were treated with inductive red and far red irradiation as well as long term irradiation under UV, blue, red, far red, and white light. Total flavonoid complements under each of these regimes were measured. Also, the detailed kinetics of changes in the accumulation of vitexin and isovitexin derivatives was determined. *Avena* seedlings accumulate vitexin and isovitexin derivatives differentially under specific light regimes. Flavonoid synthesis is under the control of the phytochrome system as well as that of a blue-light photoreceptor. Blue light is more effective in flavonoid synthesis in six day old etiolated seedlings than in four day old etiolated seedlings.

URBATSCH\*, LOWELL E., NIKOLAUS H. FISCHER AND GUSTAVO OBER. Department of Botany and Department of Chemistry, Louisiana State University, Baton Rouge, LA 70803 - The sesquiterpene lactones of *Calea* (Asteraceae) - a preliminary report.

The genus *Calea* L. contains approximately 100 species of mostly shrubs that grow in the montane regions of the Neotropics. Mexico, Central America, the northern Andes, and Brazil contain the greatest number of species. In an attempt to assess the interrelationships among the species of this genus, comparative sesquiterpene lactone studies are being carried out to complement our morphological and cytological investigations. Lactone studies have been completed for a number of species from diverse geographical regions. The basic skeletal types of compounds found in *Calea* include germacrolides, eudesmanolides and heliangolides. *Calea ternifolia* HBK and *C. urticifolia* (Mill.) DC. from Mexico exhibit virtually identical complements of compounds. *Calea trichotoma* Dn. Smith from southern Mexico contains only eudesmonolides similar to those reported for the Brazilian *C. rotundifolia* (Less.) Baker by Bohlmann et al. in 1981. *Calea berteriana* DC. and *C. subcordata* Blake from northern South America are similar in their lactone substituents, but different from the other species of *Calea*.

WALLACE, J. W., CHAPMAN, M., SULLIVAN, J.E. and BHARDWAJA\*, T.N. Western Carolina University and \*Government College, Ajmer, India.--Polyphenolics of the Marsileaceae and their phylogenetic significance.

Species of the Marsileaceae represent a unique group of pteridophytes of questionable origin. The polyphenolic profiles of representative species, which include flavonol-3-O-mono- and di-glycosides, C-glycosylflavones and C-glycosylxanthones, were demonstrated to have chemical features in common with the primitive leptosporangiate ferns, especially the Hymenophyllaceae. Intergeneric relationships in the

family based on morphology, cytology, fossil evidence and the polyphenolic profiles indicate that *Regnellidium* is probably not a phylogenetic intermediate in a complex or reduction series between *Marsilea* and *Pilularia*. The current evidence indicates that *Regnellidium* was probably derived from *Marsilea*.

WHITE, ROSEANN S. and HARVEY A. MILLER\* Department of Biological Sciences, University of Central Florida, Orlando, FL 32816. - Flavonoids of developmental stages in *Spathiphyllum* inflorescences.

Samples of *Spathiphyllum* "Maunaloa" inflorescences at progressive developmental stages and vegetative leaves were harvested simultaneously from a large, sheltered, monoclonal planting on the University of Central Florida campus. Six stages were defined by spathe color matched to a Munsell Color Cascade and by morphologic condition. Spathe, spadix and peduncle were separated for each inflorescence before drying at 45°C. Each structure from each stage, represented by several inflorescences, was extracted in absolute methanol. Extract was spotted on Whatman 3MM paper for two dimensional chromatography. Developed chromatograms were examined initially by long wave UV light with and without ammonia fumes. Flavonoid composition of leaf blades differed markedly from that of either the spathe or spadix. For the spadix, flavonoids were uniform through post-anthesis stages but a probable flavone was lacking in pre-anthesis. Spathe flavonoid diversity increased after anthesis with at least three compounds found only after total dehiscence of anthers. These studies demonstrate phytochemical diversity among plant organs of *Spathiphyllum* and confirm the necessity for consideration of developmental stages in chemical characterization of the inflorescence.

## PTERIDOLOGICAL SECTION

### Contributed Papers

BILDERBACK, D. E.\* and J. H. SLONE. Department of Botany, University of Montana, Missoula, MT 59812. - The apical organization of *Selaginella kraussiana*.

*Selaginella kraussiana* has a prostrate dorsiventral stem with small leaves on the dorsal surface and large leaves laterally inserted. When viewed with the SEM, the distal portion of the apex consists of large rectangular cells with their long axes oriented perpendicular to the dorsiventral plane of symmetry. When the apex is sectioned in a plane perpendicular to the dorsiventral plane of symmetry, large hemispherical and rectangular cells are observed distally. When the apex is sectioned in a plane parallel to the dorsiventral plane, one triangular and several rectangular cells are found at the most distal portion of the apex. The apical cells have large nuclei and cytoplasm filled with numerous small vacuoles. Ultrastructurally, the walls between the apical cells are thin and traversed by numerous plasmodesmata. Usually, a large undifferentiated plastid is associated

with the nucleus of each cell. Some spherosomes are present, but mitochondria, endoplasmic reticulum and dictyosomes are poorly represented.

HAUFLER, CHRISTOPHER H. Department of Botany, University of Kansas, Lawrence, KS 66045. - Predicted mechanism and natural operation of outcrossing in a homosporous fern.

Since they have potentially bisexual gametophytes, it has generally been assumed that homosporous ferns are highly inbred and genetically homozygous. Work with agar-cultured gametophytes of the xeromorphic species *Bommeria hispida*, however, demonstrated a mechanism for obligate outcrossing through antheridiogen (hormone) control of gametangial initiation and self-incompatibility of individual gametophytes. Electrophoretic analysis of natural sporophyte populations showed that based on analysis of 10 enzyme systems and 13 loci, *B. hispida* has an average of 2.67 alleles per locus, a percent polymorphic loci value of 69.2 and an average individual heterozygosity of 0.193. These values are comparable to other out-

crossing plant species. Further, the cytosolic locus of phosphoglucosyltransferase was heterozygous in all populations, proving that each of the plants sampled resulted from outcrossing between two, genetically different gametophytes. Data from natural populations, therefore, correlate precisely with the outcrossing mechanism predicted through laboratory analysis. The coordination of evidence from gametophytic and sporophytic generations in determining breeding systems in homosporous pteridophytes provides a powerful tool for exploring their reproductive biology and levels of genetic variability. Expansion of this technique in analyses of other taxa may have a significant impact on our concepts of evolutionary mechanisms in the ferns.

HAUFLER, CHRISTOPHER H.\* and DOUGLAS E. SOLTIS. Department of Botany, University of Kansas, Lawrence, KS 66045 and Department of Biology, University of North Carolina, Greensboro, NC 27412. - Diploidy in ferns: a general phenomenon?

Klekowski has calculated that the average haploid number for ferns is 57.05 (while that for angiosperms is 15.99) and has estimated that up to 96% of fern species could be considered polyploid. As discussed by Wagner and Wagner, there are two categories of polyploidy in ferns; paleopolyploidy, representing the extant, basic, generic chromosome complements, and neopolyploidy, involving multiplication of these basic sets. Klekowski has argued that paleopolyploidy combined with homoeologous chromosome pairing represents an evolutionary mechanism for storing and releasing variability. The actual operation of this mechanism requires that the homoeologous genomes differ genetically and that this variability be expressed. Another possibility is that paleopolyploids are genetically diploidized and do not evidence polyploid effects. One assay for polyploid expression involves electrophoretic analysis. If polyploids contain transcriptionally active homoeologous genomes, they should have more isozymes per enzyme system than would diploids. A preliminary survey of a diversity of fern taxa has shown that paleopolyploids have typical diploid banding patterns while neopolyploids demonstrate the multiplication of bands that would be expected through allopolyploidy. These data suggest that paleopolyploids are diploidized and do not show expression of homoeologous sets. Together with accumulating evidence that high outcrossing rates are maintaining genetic variability in natural fern populations, these new data on functional diploidy of paleopolyploids may force a re-evaluation of the significance of high chromosome numbers in ferns.

JERNSTEDT, J. A.\* and M. A. MANSFIELD. Botany Department, University of Georgia, Athens, GA 30602. - Polyacrylamide gel electrophoretic studies of proteins in *Selaginella kraussiana* stems, leaves, roots and "rhizophores."

Fresh stems, ventral leaves, aerial roots (rhizophores) and subterranean roots of greenhouse-grown *Selaginella kraussiana* A. Br. were homogenized separately, centrifuged and filtered to remove debris. Following addition of cold acetone, samples were stored overnight at -20°C to precipitate proteins, centrifuged and the resulting pellets dried. Portions of each sample were resuspended in appropriate

buffers for one-dimensional and two-dimensional polyacrylamide gel electrophoresis. Following electrophoresis, gels were stained in 0.1% Coomassie brilliant blue for a minimum of 4 hr and destained overnight. Analysis of 1-D gels showed 15-30 proteins separated on the basis of molecular weight, while two-dimensional separation and staining resulted in visualization of some 50 protein spots. The majority of proteins were common to stems, ventral leaves, and aerial and subterranean roots. However, qualitative and quantitative differences in banding and spot patterns existed between organs. The results obtained with these techniques complement information from anatomical, developmental and physiological studies of *Selaginella* rhizophores and provide an additional source of evidence for considering organ homologies within the genus.

KARRFALT, ERIC Department of Biological Sciences Fordham University, Bronx, NY 10458. - The sequence of root initiation in *Isoetes andicola* var. *gemmifera* (W. Rauh) L. D. Gomez.

The sequence of root initiation in this plant (originally described as *Stylites gemmifera*) is a novel modification of the sequence seen in other species of *Isoetes*. In typical species, which bear their roots on the lower surface of the corm, roots are initiated repeatedly at definite sites along the length of the linear, root-producing meristem. A sequence of initiation begins at or near the center of the length of the root-producing meristem and proceeds bidirectionally to each of the sites of initiation along the meristem. Each such sequence of initiation gives rise to a series of roots roughly parallel to the meristem. New series are begun before previous series are completed and the repeated initiation of roots at the same locations along the root-producing meristem results in the alignment of the members of successive series into orthostichies which intercept the root-producing meristem at relatively high angles. The arrangement of the roots on the external surface of adult plants of *I. andicola* var. *gemmifera* superficially resembles that in other species, but the sequence of root initiation differs in four essential respects. In *I. andicola* var. *gemmifera* new series never begin at the same site of initiation as a previous series but always at one which is higher in the plant than that at which the previous series began. Roots are added to each series unidirectionally (upward). Individual series are very short, usually containing only two or three roots. Most sites of root initiation function but once, a few produce two root primordia, and none were seen to have produced more than two.

MESLER, MICHAEL R. Department of Biological Sciences, Humboldt State University, Arcata, CA 95521. - Sexuality of a wild population of *Equisetum* gametophytes in northern California.

One thousand three hundred and ninety four *Equisetum* gametophytes (subgenus *Hippochaete*) were collected from a one meter quad in September, 1982. Of these, 59% were female, 32% were male, and 9% were bisexual. At the time of collection, only 6% of female and bisexual gametophytes bore young sporophytes. Gametophyte size was

correlated with sex; bisexual gametophytes were the largest (average area=36 mm<sup>2</sup>), followed by females (17.5 mm<sup>2</sup>) and males (5 mm<sup>2</sup>). The distribution of male, female, and bisexual gametophytes was studied on a finer scale by dividing the quad into 10 cm subquads. Male and female gametophytes occurred together in 98 of the 100 subquads. There was considerable variation in the proportion of each sex in the subquads, but the overall distribution did not depart significantly from a random one. Although male gametophytes often predominate in crowded cultures, I found no correlation between density and percentage of males per subquad. The presence of male and female gametophytes in close proximity suggests ample opportunity for cross-fertilization. Further, it appears that the environmental factors that influence whether a spore develops into a male or a female gametophyte must operate on a very fine scale.

MOY TAVERA, CARMEN\* and CHARLES J. HILLSON, Dept. of Botany. The Pennsylvania State University, University Park, PA 16802. -- Light and electron microscope studies of spore structure in selected tropical ferns.

-The spores of five species each of *Bolbitis*, *Tectaria*, *Polybotria*, *Elaphoglossum*, *Ctenitis*, *Arthropteris*, *Lomariopsis*, *Davallia*, *Nephrolepis*, *Leucostegia*, *Oleandra* and *Humata*, all genera of tropical ferns, were studied by light and scanning electron microscopy. Thin sections of the sporoderm of certain species were also examined with the transmission electron microscope. Spore features were then compared and used to determine natural relationships. An exospore layer and a perispore layer were observed in spores of every species including some that had previously been described as lacking a perispore. The exospore is stratified into two layers in the area of the aperture. The perispore may be unilayered, bilayered or multilayered. In some cases the inner layer of the perispore exhibits a columellate structure similar to that observed in the exine of angiosperm pollen. This study indicates that spore characteristics can be used to show relationships among species and genera of ferns and, in certain cases, to delimit taxonomic groups.

NESTER, JOAN E.\* AND RONALD C. COOLBAUGH. Department of Botany, Iowa State University, Ames, IA 50011. -Comparison of GA<sub>3</sub>-induced spore germination in *Anemia mexicana* and *Anemia phyllitidis*.

Gibberellic acid-induced spore germination in *Anemia phyllitidis* has been previously demonstrated to be pH dependent. The present investigation compared pH dependence and GA<sub>3</sub> sensitivity in spore germination of *A. mexicana* and *A. phyllitidis*. Spores were germinated in the dark in culture media containing 50 mM MES buffer (pH 3.5-7.5) and GA<sub>3</sub> (0 to 5 x 10<sup>-4</sup> g/ml). Seven days after sowing, the number and percent of germinated spores were determined. The optimum pH for GA<sub>3</sub>-induced spore germination in both species was 5.0-6.5 with 2-3 celled protonemal development. Less than 10% germination was observed in media at pH 4.0. Although the spore coat cracked open under these conditions, no protonemal development was observed. In *A. mexicana* spores cultured at pH 6.0, the maximum germination (75%) occurred

with 5 x 10<sup>-4</sup> g/ml GA<sub>3</sub>, while only 6% of the spores germinated in 5 x 10<sup>-6</sup> g/ml. *Anemia phyllitidis*, on the other hand, yielded 70% germination at 5 x 10<sup>-7</sup> g/ml GA<sub>3</sub> and only 7% at 5 x 10<sup>-9</sup> g/ml GA<sub>3</sub>. The pH optima for GA<sub>3</sub>-induced spore germination in *A. mexicana* and *A. phyllitidis* are quite similar. However, spores of *A. phyllitidis* are much more sensitive to GA<sub>3</sub> than spores of *A. mexicana*. In a separate set of experiments, acidic ethyl acetate extracts (antheridiogen) of media of *A. mexicana* gametophyte cultures were partially purified by TLC and tested for their effect on spore germination in the dark in *A. mexicana*. Two bands of germination inducing activity were clearly separated.

PHARTALE, DATTA L. Department of Botany, K.T.H.M.College, Gangapur Road, Nasik-422002, M.S., India- In Vitro studies in *Ceratopteris thalictroides* - I.

Leaves of *Ceratopteris thalictroides* (Brogne) containing a single leaf bud meristem (lbm) were cultured on Murashige and Skoogs medium (MS). Lbm when cultured on MS containing IAA (0.5mg/l), kinetin (1.5mg/l), sucrose (3%) solidified with agar (0.8%), developed healthy friable callus. Subcultures were made after every 21 days on MS supplemented with IAA (0.5mg/l), kinetin (0.5mg/l), sucrose (2%) to maintain callus without differentiation. MS containing IAA (0.5mg/l), kinetin (1.5mg/l), sucrose (3%); showed callus differentiation into 200-500 or more plantlets per culture. From above plantlets juvenile leaves and young roots were detached aseptically. These leaves when cultured on MS with IAA (0.5mg/l), kinetin (0.5mg/l), sucrose (1.5%); callus developed from apical growing points. The roots developed callus on MS containing IAA (0.5mg/l), kinetin (1mg/l) and sucrose (2%). Lbm callus developed only leaves when cultured on MS with kinetin (1-2mg/l), sucrose (3-5%) and only roots when MS was supplemented with IAA (1-2mg/l) and sucrose (2-3%). Differentiations of all types of calli into gametophytes were possible at low concentration of sucrose (0.1-1%) and into sporophytes at high concentration (sucrose, 3-5%). Regeneration of gametophytes from regenerated sporophytes was also possible (sucrose, 0.0 - 0.2%).

PHARTALE, DATTA L. Department of Botany K.T.H.M.College, Gangapur Road, Nasik-422002, M.S., India. - In Vitro studies in *Ceratopteris thalictroides* - II

Leaf bud meristems (lbm) of *Ceratopteris thalictroides* (Brogne) were cultured on Murashige and Skoogs medium (MS) solidified with agar (0.8%). Lbm developed friable healthy callus when MS was supplemented with IAA (0.5mg/l), kinetin (1.5mg/l), sucrose (3-5%). After 30-40 days, callus developed numerous bud initials protected by triangular scales with 3 glandular hairs at their corners. Scales were detached and cultured on MS containing sucrose (0.2-0.8%), they regenerated male gametophytes within

20-30 days. Scales cultured on MS containing sucrose (3-5%), regenerated sporophytic leaves in 35-50 days. Leaves originated as a direct extension of scales. Leaves were slightly broad in subapical region with blunt apex and entire margins. Vascular strands and stomata were present. Sporophytic callus was implanted near 6 months old lbm subculture callus regenerating sporophytes; implanted callus regenerated numerous gametophytes with sex organs. Aposporic gametophytes were induced on MS containing sucrose (0.2%). These gametophytes when transferred to a fresh medium (MS) supplemented with kinetin (1mg/l) and sucrose (4%), apogamous sporophytes originated directly from 5-6 large marginal cells of the gametophytes. Two slender rows of xylem tracheids with annular thickening and distinct stomata were present on apogamously produced leaves.

REYNOLDS, THOMAS L. Department of Biology, University of North Carolina, Charlotte, NC 28223. - Cyanide-resistant respiration during spore germination of the fern *Sphaeropteris cooperi*.

During the first 96 h of culture, germinating spores of the fern *Sphaeropteris cooperi* showed a gradual rise in respiratory activity to a maximum of 6.5  $\mu\text{l O}_2 \text{ h}^{-1} \text{ mg}^{-1}$  dry wt. This was followed by a transitory decline in rate, concluded by a second respiratory rise preceding the emergence of the rhizoid after 192 h of culture. Oxygen uptake during the first 120 h of germination was insensitive to 1 mM KCN but was inhibited by 1mM salicylhydroxamic acid (SHAM); however, beyond this time cyanide showed increasing inhibitory effectiveness whereas SHAM became less effective. Regardless of time of application, KCN had no effect on germination. Maximum inhibition of germination by SHAM was achieved if applied up to 120 h after culture initiation, after which spores became insensitive to SHAM. Heat treatment (50 C for 90 min) during the cyanide-resistant phase of respiration (0 h -120 h) induced cyanide-sensitive respiration and completely inhibited spore germination. Elevated temperatures had little effect if applied during the cyanide-sensitive phase (beyond 120 h). Temperature inhibited spores regained their ability to germinate if maintained in culture until the cyanide-resistant pathway was restored and then subjected to a second photoinductive light treatment. These results suggest the presence and possible involvement of the cyanide-resistant alternative respiratory pathway during germination of *Sphaeropteris cooperi* spores.

RICHARDSON, P. MICK. New York Botanical Garden, Bronx, New York 10458. - C-glycosylxanthones in the ferns.

The occurrence of C-glycosylxanthones in ferns is reviewed. The compounds have a restricted distribution within four families: Hymenophyllaceae, Aspleniaceae sensu lato, Davalliaceae and Marsileaceae. They are known to occur in 52 species in 16 genera. Reports of their occurrence have increased exponentially since the first report in 1962 and the compounds undoubtedly remain undiscovered in many ferns. The compounds appear to be of little taxonomic value at higher levels because they have evolved independently on several occasions. Their major value is probably in the confirmation of allopolyploidy.

TAYLOR, W. CARL\*, NEIL T. LUEBKE, and MARY B. SMITH. Botany Section, Milwaukee Public Museum, Milwaukee, WI 53233. - Hybridization as a source of taxonomic confusion in *Isoetes*.

The taxonomy of *Isoetes* in northeastern North America is confused because hybridization obscures differences between the described taxa. Evidence for hybridization is found by studying spore germination, gametophyte development, and sporophyte formation in laboratory cultures. Spores of twelve taxa from eighteen populations, collected in early fall, were vernalized in sterile, demineralized water at 3°C for 100 days and then incubated at 20°C with a 12L:12D photoperiod. Within 50 days most cultures approached 100% germination of megaspores. Taxa producing polymorphic megaspores either failed to germinate (*I. X eatonii*) or germinated at less than 1% (*I. X gravesii* and *I. X heterospora*). Gametophytes developing from polymorphic spores bore either abnormal archegonia or no archegonia. There was no evidence of apogamy in these cultures. Occasionally gametophytes with normal archegonia were observed among the polymorphic megaspores. These gametophytes produced sporophytes in the presence of functional spermatozooids. In nature, plants producing polymorphic spores usually are found in association with one or more taxa, suggesting the possibility of hybridization e.g., *I. X foveolata* with *I. dodgei* and *I. tuckermanii*. Morphologically definable species do exist in *Isoetes* and these are still best separated by megaspore size and ornamentation coupled with leaf characters. Chromosome counts reveal different ploidy levels supporting species distinctions and hybridization. Nearly all of the northeastern North American species of *Isoetes* can be crossed in the laboratory but it appears that hybrid sterility isolates species in nature.

WAGNER, FLORENCE S. Department of Botany, University of Michigan, Ann Arbor, MI 48109. - The *Botrychium lanceolatum* group in western North America.

Outside of western North America there are known only six species of moonworts plus two hybrids. In western North America, we estimate that there are 13 species plus five hybrids; 9 of the species are endemic. The *B. lanceolatum* group includes those moonworts with the pinnae oblong, lanceolate or linear, with central veins or costae. *Botrychium hesperium* is a distinct species, formerly treated as a variety of *B. matricarifolium*. It was confused with *B. echo*, which commonly grows with it, but differs from that species in approximately a dozen character states. *Botrychium echo* is known only from the southern Rockies, especially Colorado and Arizona, but *B. hesperium* ranges as far north as Alberta, Canada. A new species in this group is described that so far is known only in the north, ranging from Oregon to British Columbia and Saskatchewan. It differs from all of the other members of this group in a particular combination of characters, including a unique pigmentation of the sporophore stalk, a relatively long sterile segment stalk, and distinctive structure of the sterile lamina, including the form of the margins and the pinnae, as well as the cuticle. Among the hybrids observed are combinations of *B. hesperium* X *paradoxum*, *B. echo* X *minganense*, and possibly the polyploid, *B. pinnatum*. No true *B. matricarifolium* has been found in western North America, nor true *B. boreale*. Except for these, all known members of *Botrychium* subg. *Botrychium* are recorded there. Two of the endemics belong to the Lunaria Group, two to the Simplex Group, but four of them belong to the Lanceolatum Group. The fourth group, containing only one species, *B. paradoxum*, is also endemic to western North America.

## 96 Systematic Section

WHITTIER, DEAN P. Department of General Biology, Vanderbilt University, Nashville, Tennessee 37235. - Gametophytes of *Lycopodium lucidulum* in axenic culture.

Spores of *Lycopodium lucidulum* Michx. were sown on a nutrient medium containing minerals, 0.5% sucrose, and 0.6% agar. Gametophytes develop only in the cultures maintained in the dark. The white gametophytes are narrow, thickened, strap-shaped structures with dorsal and ventral surfaces. Externally, the meristem in the apical region appears as a groove under a dorsal lip of gametophyte tissue. This meristem extends along the margin of the

gametophyte. Although the lateral extension of the meristem appears to be active only close to the apical region, lateral grooves, which separate the dorsal and ventral surfaces, are present along the length of the gametophyte. The ventral derivatives of the meristem form the rhizoid bearing surface of the gametophyte. The rhizoids often have mucilaginous sheaths. The dorsal lip of tissue above the meristem contains the developing sex organs. The dorsal surface of the gametophyte is invested with uniseriate, multicellular hairs which obscure the antheridia and archegonia.

## SYSTEMATIC SECTION

### Symposium: Biological Basis for Adaptations in Grasses

WILSON, RICHARD L. Department of Biology, Syracuse University, Syracuse, NY 13210. - Grainoid avoidance, tolerance, and requirements for grain-evolutionary responses of grainoids to large herbivores?

Semi-arid habitats, grasslands and grazers appeared almost simultaneously in the fossil record. Tillering, carbohydrate reserves, reduced investment in sexual reproduction, basal meristems, and higher photosynthetic rate of younger leaf tissue are aspects of perennality, mechanisms to withstand a non-growing season, and to establish leaf area in response to early rains. Small shoots and high tiller density are advantageous in semi-arid environments where light competition is reduced. Basal meristems are also advantageous in non-light competitive environments. Flexibility of root-shoot allocation is adaptive to fertile, competitive environments where the relative abundance of light and soil resources varies. These traits can also be adaptive to herbivory. Ecological and coevolutionary relationships between grainoid and grazer species can range from predation, to commensalism, to protocoeperation. At the community or ecosystem level, grass-grazer systems can be mutualistic. A given grass may respond negatively or positively to grazing depending on grazing regime. Experimentation with Serengeti short, mid, and tall grainoids, and with a simulation model, mechanistically demonstrate those relationships.

DAVIDSE, GERRIT. Missouri Botanical Garden, P. O. B. 229, St. Louis, MO 63139.

- Morphological bases of adaptations in grasses.

The grass family is the most cosmopolitan and one of the largest of all plant families, inhabiting an incredible array of habitats, despite a rather general facies. The generalized grass morphological features of grasses that help account for this astounding

ing success will be discussed and contrasted with a selected group of variations on the basic theme for each of the major organ systems. Special emphasis will be placed on adaptations in culm and reproductive structures. Adaptations in culm morphology have been important in allowing grasses to exploit forest and aquatic habitats. Selection for efficient wind pollination, seed dispersal and seedling establishment has been especially important in modifying the morphology of inflorescences and spikelets and in changing patterns of flower development. Distinct patterns of adaptive radiation in these reproductive features are evident in each of the major groups of grasses.

REDMANN, ROBERT E. Department of Crop Science and Plant Ecology, University of Saskatchewan, Saskatoon, Sask. S7N 0W0. Structural and physiological adaptations in the leaves of xeric grasses.

The adaptation of grasses to arid and semiarid habitats involves many physiological and morphological characteristics. Grass leaf structure is intimately related to major physiological processes such as carbon dioxide exchange, energy exchange and water balance. A general overview of physiological and structural adaptations in grass leaves is presented in this paper, followed by a more detailed analysis of the effects of leaf rolling on energy exchange and water balance. Leaf rolling influences all aspects of leaf energy balance. The heat transfer coefficient can increase up to three times as leaves roll. Direct solar radiation intercepted by rolled leaves is about half that received by flat leaves. Rolling reduces transpiration by lowering leaf temperature and thus decreasing the water vapour density gradient between leaf and air. Rolling has a small relative effect on resistance to water vapour transfer because stomata close before leaves roll, and the increase in boundary layer resistance due to rolling is small compared to total leaf resistance. Rolling can increase the survival time of leaves exposed to prolonged desiccating conditions.

STEBBINS, G.L. Department of Genetics, University of California, Davis, CA 95616

- Cytogenetics and phylogeny in the Family Poaceae. The cytogenetic pattern in the family is dominated by polyploidy. From an original basic number of  $x=7$  or

6, tetraploid levels have become widespread, and in Bambusoideae, Arundinoideae and Oryzeae  $x=12$  has been the basis for higher multiples of this number. From  $x=6$ , aneuploid reduction has given  $x=5$ , and from  $x=12$ , came  $x=10$ , 9 and 8. Highest levels are 14-ploid (in *Calamagrostis*) and 18-ploid (in *Alopecurus*, *Bothriochloa* and *Saccharum*). Percentage of polyploid species is between 65% and 75%, depending upon method of estimation. Neither the geographic nor climatic distribution differs significantly from that of diploids, except in isolated examples. Genera having medium sized to large chromosomes are as likely to evolve high polyploidy as those having smaller chromosomes. Annual diploids are less likely to evolve polyploids than perennials. A spectrum of cytogenetic conditions exists from autopolyploidy to allopolyploidy: most species are intermediate between the extremes. Most autopolyploids are genetically heterozygous as a result of hybridization between differently adapted parental races. The results of an experiment lasting 40 years show that autopolyploids, artificially produced, of *Ehrharta erecta* can persist under semi-natural conditions but are much less able to colonize new areas than their diploid progenitor.

THOMASSON, JOSEPH R. Department of Biological Sciences, Fort Hays State University, Hays, KS 67601-4099

- Miocene grasses from central North America.

Species of *Berriochloa*, *Paleoeriocoma*, *Nassella*, *Archaeoleersia*, *Panicum* and *Graminophyllum* (Gramineae) collected from Miocene strata in central North America were examined and compared with modern taxa. With the exception of *Graminophyllum*, an organ genus of grass leaves, the fossil genera are preserved as the remains of the reproductive bracts (husks) which enclosed the grain.

*Berriochloa*, the oldest known genus, first appears in early Miocene strata where it has a rigid cylindrical husk and an elongated, pointed callus. These features probably evolved primarily as adaptations to grazing animals and insects. Rigid husks found on other fossil genera were a similar adaptive mechanism.

From the early Miocene forms of *Berriochloa* evolved two mid-late Miocene lineages. In one lineage the husk remained cylindrical while in the other lineage the husk became prominently inflated. Within both lineages the surfaces of the husks were variously smooth to densely covered with hooks and/or hairs. Both lineages retained the elongated, pointed callus. The lineage of inflated forms probably evolved in response to ingestion by grazing herbivores. Related living taxa such as *Stipa* and *Piptochaetium* show adaptive mechanisms similar to those of the fossils, although evolutionary changes such as the loss of the elongated callus has occurred in some forms.

Fossils of *Graminophyllum* collected in association with the fossil grass husks appear deeply ribbed and furrowed. This is caused by rows of well developed bulliform cells alternating with raised costal areas. Many of the fossil leaves collected show involution which indicates that this adaptive mechanism in the grasses dates at least to the Miocene.

## Symposium: Cleistogamy: Its Ecology and Evolution

### INTRODUCTION

Cleistogamy is widespread in its occurrence and diverse in its biological significance among angio-

sperms. It is known in primarily herbaceous taxa from 29 families. Its expression may produce marked morphological and developmental differences from the evolutionarily primitive chasmogamous condition. It may be important in reducing animal predation of seeds and in altering their size, presentation, susceptibility to fire, dispersibility and germinability.

The primary objective of this symposium is the examination of the origins and types of cleistogamy through an integration of ecological and systematic data via a bridge of evolutionary theory.

Organized by J.A. Quinn, Rutgers University, Piscataway, NJ and C.S. Campbell, University of Maine, Orono, ME.

CAMPBELL, CHRISTOPHER S.\* and JAMES A. QUINN\*. Department of Botany and Plant Pathology, University of Maine, Orono, ME 04469 and Department of Biological Sciences, Rutgers University, Piscataway, NJ 08854. - Relationships between the types of cleistogamy in grasses and variation in reproductive structures, habitats, and life-history strategies.

Cleistogamy has been reported from 321 species and 82 genera of grasses and is therefore far more common than in any other angiosperm family. It is also probably expressed in a greater diversity of ways in the Gramineae. We recognize 4 types of cleistogamy (CL) in grasses based on the source of confinement of the flowers: spikelets, upper stem sheaths, lowermost stem sheaths (cleistogenes), and the soil for subterranean flowers (rhizanthogenes). With respect to the chasmogamous counterparts of the same individual or species, these types are associated with different degrees of dimorphism of the floral and spikelet parts and of the size, dispersibility, and germinability of the seeds. Species showing CL are predominantly (79%) tufted or caespitose, and twice as many perennials as annuals have been reported to show at least one type of CL. Although about 60% of the species with CL are colonizers of disturbed, successional habitats, there are other habitats and/or selective pressures that can be linked to the development of the various CL types. Almost 2/3 of the non-ruderal CL perennials are "stress-tolerators", occurring in shallow or sandy soils of low moisture-holding capacity and/or in environments of low and unpredictable rainfall. These species commonly show the upper stem sheath type of CL. Selective advantages for cleistogenes and rhizanthogenes may include protection from herbivory, environmental extremes, or fire, and the placement of seeds in the microhabitat occupied by the mother plant.

CLAY, KEITH. Department of Botany, University of Texas, Austin, TX 78712. - Genetic and demographic aspects of cleistogamy.

Cleistogamy results in obligate self-fertilization. Genetic differences between progeny from chasmogamous (CH) and cleistogamous (CL) flowers depend on the rate of outcrossing of CH flowers and the amount of genetic variance present in the population. At the family level CL progeny should be less variable than their CH sibs, but more variable at the population level. Genetic variance is maximum when the population consists of pure inbred lines. Experiments con-

ducted with the grass Danthonia spicata showed CL progeny were significantly less variable for 14 quantitative traits compared to CH progeny from the same plant. The relationship between plant fitness and its reproductive origin (CH or CL flowers) may be influenced by non-genetic factors such as seed size, germination requirements, and dispersal differences precluding broad generalizations about this relationship. A survey of the literature provides cases of CL progeny being superior, inferior, or the same as CH progeny from a variety of species. When non-genetic differences between CH and CL progeny were experimentally controlled in D. spicata the CH progeny had slightly higher survival and reproductive rates (but non-significant) compared to CL progeny. The variance in fitness, as opposed to mean fitness, was significantly higher for CH progeny. Thus, in D. spicata, the major genetic consequences of cleistogamy and chasmogamy are on the variance rather than the mean.

LORD, ELIZABETH. Department of Botany and Plant Sciences, University of California, Riverside, CA 92521. - Comparative study of cleistogamous and chasmogamous flowers.

In cleistogamous species, two types of hermaphroditic, self-compatible flowers are borne by an individual. The closed or cleistogamous (CL) flowers set seed by self-fertilization, while the open or chasmogamous flowers achieve anthesis and may outcross. At least 58 families contain such species for which real structural differences in the two floral forms have been documented. The common denominators are reduction in, at least, the CL androecium and corolla as well as a lack of anthesis. Shape modifications may occur in all the CL organs. Pollen number is always reduced in the CL flower and often pollen size. Differences in pollen ultrastructure exist in the species studied though little work has been done on pollen-stigma interaction. Germination of CL pollen occurs in the anther with the tubes emerging from an open stomium or penetrating the wall of an unopened anther. Stigmatic receptivity is precocious in the CL flower and close proximity to the anthers ensures pollination in the closed bud. Ontogenetic study has demonstrated that divergence in form occurs early in development, always prior to anther differentiation. Precocious anther differentiation is followed by modifications in corolla form. Dissociations of parts of organs result in new shapes being produced. Ontogenetic shifts in floral form occur during inflorescence development in the annuals studied. Intermediate forms exist primarily in the CL population. Precocious development and function characterize the CL flower. Utilizing data on form and size changes over time, we have devised models to describe the ontogeny and phylogeny of the CL from the CH form.

SCHOEN\*, DANIEL J. and LLOYD, DAVID G. Department University of Canterbury, Christchurch, New Zealand - Models for the evolution of cleistogamy and heteromorphic fruits.

Models for the evolution of cleistogamy are described. The "basic" model takes into account the economy and certainty of cleistogamous fertilization, and the inability of cleistogamous flowers to contribute pollen to the outcrossed pollen pool. Com-

plete cleistogamous self-pollination is favored when allocation to maternal function, fertilization rate, and viability of progeny are sufficiently greater for the cleistogamous compared with the chasmogamous component, and when resources spent on ancillary structures in cleistogamous flowers, the cleistogamous seed costs, and inbreeding depression are low. The "complex habitat" model extends the basic model to situations in which success of reproduction by cleistogamy or chasmogamy varies according to the environment of the parent plant. In this situation, reproduction by both cleistogamy and chasmogamy may be favored. A "near and far" dispersal model addresses the question of dual modes of dispersal which often occur in cleistogamous plants. Dual modes of dispersal may be favored if a narrowly dispersed seed type is more successful at establishing in the sites located within its dispersal range, compared with a second, more widely dispersed seed type produced by the same plant. Predictions of the models are discussed with respect to relevant data, and suggestions are made for the apparent rarity of cleistogamy as a mode of self-pollination.

\*PRESENT ADDRESS: Department of Botany, University of Georgia, Athens, GA 30602.

WALLER, DONALD M. Department of Botany.

University of Wisconsin, Madison, WI 53706.

- Plant size, flower development time, and their implications for the expression of cleistogamy.

Many cleistogamous (CL) plants adjust their level of investment in CL flowers in response to variable environmental conditions. A review of these patterns reveals that when CL is facultative, larger plants or those in better physiological condition outcross the most. For selection to favor such responsiveness, either the cost of chasmogamy (CH) or its benefit should change consistently with plant size. Studies on inbreeding depression usually demonstrate a benefit to outcrossing, but this benefit is not reliably density dependent. Turning to costs, CL seeds are known to be significantly cheaper than CH seeds, both in terms of energy and the time they take to develop. If small plants or those under physiological stress take longer to produce a seed, they would have less effective time to reproduce. This would result in strong selection for efficient prior self-fertilization (i.e. CL) in small or stressed plants (or independent parts of plants). This relative time hypothesis could therefore account simultaneously for time-, size-, and energy-dependent patterns of chasmogamy.

## Symposium: Generic Concepts in the Compositae

### INTRODUCTION

Recent treatments of the Compositae, especially in the large genera Eupatorium and Senecio, have brought forward the issue of "large natural genera" vs. "small natural genera." The symposium will attempt to evaluate the whys and wherefores, wisdom, need, pragmatics and otherwise of such varying treatments. While no consensus will be sought, an effort will be made to look into the philosophical concepts and methodological approaches which occasion such varying treatments so as to ascertain if there might not be, after all, some meaningful guidelines for generic recognitions. Organized by Billie L. Turner, University of Texas, Austin, TX.

Barkley, T. M. Herbarium, Division of Biology,  
Kansas State University, Manhattan, Kansas 66506.

- Generic concept in the Senecioneae.

Since the time of Geo. Bentham the traditional view of the Senecioneae has been that of one huge genus (Senecio) plus numerous segregate genera of varying degrees of distinctiveness, plus a few entities of uncertain affinities. Data have accumulated to support the exclusion of some genera from the tribe (e.g. Arnica, Liabum, Munnozia, Schistocarpha, etc.) and to tease botanists about the circumscriptions and affinities of others. Senecio, s.l., incorporates several semi-distinctive natural assemblages which have been treated usually as sections or subgenera. The naturalness of these assemblages is generally acknowledged, as is the fact that the boundaries separating them are imprecise by whatever suites of characters are used to measure them. In several recent studies many segregate genera have been recognized, often with the circumscriptions derived from selected representative species. It is yet unclear that the recognition of numerous segregate genera provides a better taxonomy than treating the variation patterns as infrageneric taxa. A respectable case can be made for maintaining Senecio as a broad concept, at least until revisionary studies at the species level are carried out and the results subjected to critical analyses.

BOLICK, MARGARET R. Division of Botany,  
University of Nebraska State Museum, Lincoln, NE  
68588-0514. - Hennigian cladistics and the generic concept in Iva (Ambrosiinae, Heliantheae).

In 1960, Jackson divided Iva into three sections: Iva, Linearbractea, and Cyclachaena. A reanalysis of Iva using the precepts of Hennigian cladistics reveals 1) that there are no synapomorphies connecting sections Iva and Linearbractea to section Cyclachaena; 2) that there are no synapomorphies connecting the species within Cyclachaena; and 3) that the species of Iva and Linearbractea are unified by three synapomorphies. The analysis also suggests that the five species of Cyclachaena are more closely related to other genera in the subtribe than they are to Iva and Linearbractea. The resulting classification recognizes Iva and Linearbractea as Iva (sensu stricto) and the five species of Cyclachaena as separate monotypic genera.

CARR, GERALD D. Department of Botany, University  
of Hawaii, 3190 Maile Way, Honolulu, HI 96822.  
- Habitat variation in the Hawaiian Madiinae (Heliantheae) and its relevance to generic concepts in the Compositae.

The Hawaiian Madiinae comprises monocarpic rosette shrubs, mat-forming subshrubs, cushion plants, small shrubs, large shrubs, trees, and even a liana. Habitats occupied by members of the alliance range from dry scrub receiving about 40 cm of precipitation annually to summit bogs with an annual precipitation exceeding 1250 cm. In spite of enormous habitat and habitat differences and even chromosomal differentiation between the various forms, a myriad of natural and artificial hybrids demonstrates the genetic cohesiveness of the group. Thus, the Hawaiian Madiinae constitutes what is probably the most spectacular example of adaptive radiation in plants. Traditionally, four genera (Argyroxiphium, Dubautia, Railliardia, and Wilkesia) have been recognized in this group. The biosystematic

evidence and the overall pattern of variation support the merger of Dubautia and Railliardia. However, even in the narrow sense Dubautia includes a cushion plant, shrubs, trees, and a liana. Thus, in this instance habitat variation is considered to be of little or no value in the circumscription of genera.

FUNK, VICKI A. Department of Botany, Smithsonian  
Institution, Washington, D. C. 20560. - Cladistics and generic concepts in the Compositae.

Taxonomy classes are often taught that classification involves grouping and ranking. In reality we are actually concerned with grouping on two levels: the grouping of individuals (into species), and the grouping of 'groups of individuals.' There are, therefore, only two categories, species and groups of species. The importance of this concept lies in a logical extension of it, that the various levels at which the 'groups of species' are recognized are not of major concern to cladists. In discussing generic concepts we begin with a cladogram that has species for terminal taxa and ask - How do we convert this into genera, sub-tribes, etc.? To cladists, the cladogram is the classification, and the guideline for turning it into a hierarchy is as follows: while maximizing information, strive to minimize novelty and redundancy. Or, develop a classification that will retain monophyletic groups but will disrupt the present classification as little as possible and create the fewest monotypic taxa. Some Examples - Although redundancy and disruption are minimized, information is not maximized by the use of 'core genera' (e.g., Vernonia Schreb.) over smaller monophyletic groups. However, the segregates must be defined by synapomorphies and the parent group cannot be left paraphyletic as has happened in Stevia Cav. and Senecio L. Placing the genus Montanoa Cerv. in a subtribe by itself is redundant, but placing it in any other subtribe destroys the naturalness of the latter. Maintaining artificial genera (e.g., Culcittium H. & B.) is indefensible because they imply false information. Classifications giving consistent information cannot be achieved by whim. The cladistic approach gives us well-reasoned guidelines for evaluating and comparing classifications and can help in deciding on when to retain the existing genera and when to describe new ones.

GAGE, DOUGLAS A. Department of Botany,  
University of Texas, Austin, TX 78712. - Chemical features as generic criteria in the Eupatorieae.

To date over 250 species in the Eupatorieae have been chemically studied. The majority of this work has focused on terpenoid constituents. The results thus far depict the tribe as chemically heterogeneous, producing a large number of diverse sesquiterpenes, diterpenes, as well as thymol and benzofuran derivatives. When this chemical diversity is examined in relation to the traditional large genera recognized in the Eupatorieae (e.g., Eupatorium, Stevia, Mikania) no clear chemical boundaries are found. In comparison, mixed results are obtained in relating terpenoid chemistry to the limits of the more narrowly defined genera of a recent reorganization of the tribe's classification. While some of the smaller genera appear chemically distinct, others are chemically diverse, and still others are chemically indistinguishable from affiliated genera. The larger genera recognized in this treatment (e.g., Ageratina, Chromolaena) tend to be heterogeneous in their terpenoid chemistry.

JONES, ALMUT G. Department of Botany, University of Illinois, Urbana, IL 61801-3793.-- Chromosomal features as generic criteria in the Asteraceae.

In their tribal characteristics the Astereae are well defined, but determination of generic limits within the tribe has been subject of much dispute. Several examples in Astereae may serve to address three basic questions concerning usefulness of chromosome features in delimiting genera: (1) What do chromosome numbers per se tell us? (2) Can genera with more than one mode of basic chromosome number be regarded as monophyletic? (3) Are chromosomal features correlated with gross morphological characteristics that will allow construction of useful classifications? The first question immediately leads to another: can we assume that the condition of, e.g.,  $x = 9$  is homologous for all taxa sharing this character state? Many, if not most, genera in the tribe are represented by polyploid series. While some taxa may have primitively " $x = 9$ ", there is indication that others may have secondarily acquired that number, via allopolyploidy from  $n = 4+5$  or via aneutetraploidy from  $n = 10-1$ . The second question has been raised repeatedly for such genera as *Aster*, *Astranthium*, *Brachycome*, *Haplopappus*, *Heterotheca*, and *Machaeranthera* (all sens. lat.). Persuasive arguments can be presented for answers on both sides of the question. The true situation may be that some genera are monobasic, while others have more than one basic chromosome number. The decision for one or the other will (or should) be linked to an answer for the third question. Chromosomal characteristics undeniably are of fundamental importance to an understanding of interspecific relationships, but unless these microscopic features are correlated with distinct gross morphological characteristics, they probably are not useful in the determination of generic limits. On the other hand, such correlations usually do exist at the subgeneric or sectional levels.

LANE, MEREDITH A. Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, CO 80309.--Ultrastructural features as generic criteria.

The advantages of greater resolution and depth of field provided by the scanning electron versus the light microscope have led to both a re-evaluation of traditional microcharacters and discovery of "new" characters, particularly of surfaces, not easily observed by other means. Comparative studies of these characters in taxa of Compositae have shown that they are taxonomically useful, but that they are neither more nor less valuable as a means of generic delimitation than are gross or micromorphological ones. As is true of taxonomic data from any source, it is the consistent occurrence of one or more ultrastructural feature(s) as a part of a suite of correlated characters that provides sufficient information on which to base systematic decisions. Within this context, it is the "new" characters that prove most useful: the chances of finding correlated character suites rises with the number of characters observed. Among members of the subtribe Solidaginae (Astereae), corolla epidermal cell features may be consistent with other characters that differentiate related groups of taxa. However, because studies of infraspecific variation in ultrastructures are rare (due to the relative expense of SEM), these characters should be employed with caution and in conjunction with numerous others in making taxonomic decisions at the generic (or any other) rank.

POWELL, A. MICHAEL. Department of Biology, Sul Ross State University, Alpine, TX 79830. Crossing data as generic criteria in the Asteraceae.

Crossing data have long been used to help determine the position of species whose generic status is questionable, to help define subgeneric taxa, to merge genera, and, in a limited number of studies, to help establish generic boundaries. Previous studies in the subtribes Peritylinae and Flaveriinae (Helenieae) have demonstrated that crossing data can be employed as a major approach in delimiting generic entities and in establishing relationships between genera. In fact, in the above taxa crossing data proved to be more useful at the genus level than at the species level. Such crossing tests can be employed at optimum only if it is possible to produce hybrids between most of the species in the putative genera concerned. It does appear that it is often possible to obtain comprehensive data from artificial interspecific hybridizations, especially when allopatric perennial taxa are involved. The interpretation of crossing data may present problems because variable inter-fertility values in different taxa are to be expected, and independent taxonomic judgements must be made in context with information from other approaches. In the tribe Eupatorieae, where extensive generic reorganization has been proposed in recent years, hybridization tests may be possible in some groups (*Carterothamnus* X *Hofmeisteria*; *Koanophyllon* X *Pseudokyrsteniopsis*) but not in others (*Brickellia*).

ROBINSON, HAROLD\* and KING, R. M.,\*Department of Botany, Smithsonian Institution, Washington, D.C., 20560. - Generic concept in the tribe Eupatorieae. Traditional genera of the tribe, based heavily on pappus and anther appendage, prove totally indefensible, having been subjected to piecemeal alterations by all significant workers since Linnaeus, and being useless for comparison with any new evidence. The total tribal revision of the present authors, based on structure, cytology, geography and chemistry, has 180 genera in 18 subtribes. What was *Eupatorium* has been distributed among 11 of the subtribes, and is intermixed with elements of other traditional genera. *Eupatorium* (44 sp.,  $X=10$ ) remains a distinct Arcto-Tertiary genus. *Mikania* (410 sp.,  $X=18-20$ ), *Stevia* (229 sp.,  $X=11,12$ ), *Liatris* (42 sp.,  $X=10$ ), and *Brickellia* (96 sp.,  $X=9$ ) have minor changes. *Ageratum* (40 sp.,  $X=10$ ) is broadened to include epappose species. *Ageratina* (230 sp.,  $X=17$ ), the epiphytic *Neomirandea* (25 sp.,  $X=17,20$ ), *Chromolaena* (165 sp.), *Fleischmannia* (79 sp.), *Koanophyllon* (115 sp.) (all  $X=10$ ) are named or restructured to include much that was in *Eupatorium*. The subtribe Gyptidinae, mostly of eastern Brazil, is one of two most complex, but has many particularly distinct genera such as *Campuloclinium* (14 sp.), *Trichogonia* (30 sp.), *Lasiolaena* (5 sp.) and *Agrianthus* (6 sp.) (all  $X=10$ ). Most problems of numerous small genera and hybridization involve the largest subtribe Critoniinae of the moist Neotropics, but tests of many individual genera has reinforced their distinct status, i.e., *Critonia* (38 sp.), *Ophryosporus* (37 sp.), *Fleischmanniopsis* (5 sp.) and *Neocabreria* (5 sp.) (all  $X=10$ ). The reclassification reflects the fact that the tribe is neither simple nor comparatively derived in the family.

SCOTT, RANDALL W. and SCOTT D. SUNDBERG. Department of Botany, University of Texas at Austin, Austin, TX. 78712

-Microcharacters as Generic Criteria.

A study of microcharacters (as viewed under the compound microscope) in the Eupatorieae and Astereae (Compositae) was undertaken in order to evaluate their reliability as taxonomic markers. Character states of various microcharacters are widely distributed within the tribes Astereae and Eupatorieae. Correlations between microcharacters and yet other characters were used in order to evaluate their applicability in delimiting genera. A high degree of microcharacter correlation with yet other characters was found in some species groups suggesting that they are useful and consistent markers among such taxa, whereas in other groups they may be of little value.

## Symposium: Phylogenetic Systematics and Speciation

### INTRODUCTION

Usually workers in the study of speciation operate by creating (or adopting existing) historical explanations for their observations. Distributions are divided, barriers erected and various degrees of reproductive isolation are invoked. Observations from other organisms that can be explained by the same scenarios are gathered together and a 'mode' is born. This symposium is an attempt to treat the study of speciation in a more empirical manner. Various 'modes of speciation' and species definitions are tested against the patterns of relationship and distribution of taxa in birds, fish, cacti, composites and mosses. Using this method for examining speciation may allow us to differentiate between refuted and corroborated 'modes' and definitions in the various groups of taxa examined.

In the Compositae several groups have been studied enough to investigate speciation (i.e., cladograms are available). Close examination of the distribution of groups of sister species in ten Latin American genera in the flowering plant family Compositae (six genera in the Liabeae; one in the Senecioneae; three in the Heliantheae) indicates that a hypothesis of allopatric speciation is refuted least often. In addition, area cladograms for the genera (cladograms that indicate the distribution of the terminal taxa) indicate that speciation as a result of vicariance can be corroborated as well as speciation as a result of dispersal. Finally, the only useful definition for composite species is one of morphological uniqueness.

Organized by Vicki A. Funk, Smithsonian Institution, Washington, D.C.

BARROWCLOUGH, GEORGE F. Department of Ornithology, American Museum of Natural History, NY, NY 10024.

- Speciation in western North American birds.

In the 50 years since the development of the new synthesis, parapatric avian taxa in western N. A. have been studied intensively in a search for hybrid zones or other evidence of interbreeding. Such evidence has been used to relegate distinct evolutionary lineages to subspecies status, in accordance with the tenets of the Biological Species Concept (BSC). However, when the results of these studies are used to examine critically the reasonableness of the BSC, it is found that the concept does not make good evolutionary, phylogenetic, or population genetic

sense for birds, because such species taxa may represent more than one evolutionary unit and terminal taxon. This inconsistency has led to ambiguity in the examination and interpretation of modes and patterns of avian speciation. When the data are interpreted in terms of an evolutionary or phylogenetic species concept, several empirical generalizations emerge. First, sympatric and parapatric modes of speciation are not consistent with the geographical distributions and with what is known about the population ecology of these organisms. Second, it does not appear that the differences in plumage patterns commonly found between hybridizing sister taxa function as reproductive isolating mechanisms because the birds, themselves, do not use them for that purpose.

CHURCHILL, STEVEN P. Department of Botany, University of Kansas, Lawrence, KS 66045. - Patterns and processes in moss speciation.

The connecting link between systematics and evolution is phylogeny and the basic phylogenetic unit is the species. As such, species, the most fundamental hypothesis in systematics, must be monophyletic and exhibit some degree of apomorphy within the context of what is known about the biology of the taxon, in this case Musci. No species concept has been prevalent in moss systematics, which may be an asset, but future studies must address this subject. Previous considerations of moss speciation have approached the subject from one of two perspectives. Either known or assumed mechanisms have been reviewed or patterns based solely on extant distributions have been derived through a basically phenetic approach. Several processes have been defined: at the chromosomal level, polyploidy and aneuploidy are apparently frequent; particularly significant is the suggestion that half or more of the taxa examined at the gametophytic level are functionally diploid; finally, apogamy, apospory, and diplospory are thought to be frequent. While mechanisms can be described for any single event, we shall never know if the result is unique or general unless we can compare it to other events within and between monophyletic lineages. At present very few systematic studies have produced testable phylogenetic patterns. We may best study speciation, those genetic and epigenetic processes involved in the production of taxa, if we know the phylogeny of the species we study. The need now is to make predictions of processes based on observed patterns, and predictions of patterns based on detected processes which would provide an independent test of the value of each in elucidating evolutionary history.

CRACRAFT, JOEL. Division of Birds, Field Museum of Natural History, Chicago, IL. 60605.

-Patterns of speciation in South American birds.

A phylogenetic hypothesis for the differentiated taxa (=species) of a group also defines a biogeographic pattern. Congruence in such patterns implies a common history and permits us to identify those aspects of history which are unique to each group. Approximately 35-40 areas of endemism can be described for the neotropical avifauna. Cladistic hypotheses for more than 30 genera and species-groups demonstrate a remarkable degree of congruence in their biogeographic patterns. The following implications will be discussed: (a) avian speciation on continents is predominately by vicariance rather than by founder effects, (b) avian speciation patterns in

## 102 Systematic Section

the neotropics cannot be explained by the prevailing model of Pleistocene "refugia," (c) many areas of endemism--and their biotas--are older than the Pleistocene, and (d) the rate change in lithospheric complexity constitutes a deterministic causal explanation for spatial and temporal variation in speciation rates and patterns of species diversity.

GIBSON, ARTHUR C. Department of Biology, University of California, Los Angeles, CA 90024. -Plant disjunctions in arid and semiarid North America--a search for multi-area cladograms.

Current reconstructions of the floristic history of arid and semiarid North America are primarily based on patterns of extant plant ranges and infrageneric disjunctions. Unfortunately, because phylogenetic relationships of Mexican species are poorly understood, much of this reconstruction has been of the narrative type. In fact, to date most systematic treatments of Mexican taxa have not hypothesized the phylogenetic relationships of each species but have instead lumped taxa into series, sections, and subgenera and then discussed the interrelationships of these higher taxa. To begin an earnest attempt to uncover coincident phylogenetic and areal patterns, one can analyze the phylogenetic model of Mexican columnar cacti (tribe Pachycereeae), which occur in many interesting dry forests and desertscrubs, have noteworthy patterns of endemism and disjunction, and have a recent phylogenetic model of the species based on synapomorphies. In these cacti, the clades radiate from southern Mexico in various directions, so that the northern deserticolous taxa are derived versions of species found in the nearby dry tropical forests to the south. Genera of trees and shrubs in other families that co-occur with columnar cacti are analyzed with Pachycereeae to identify any recurrent patterns of disjunction or speciation and possible multi-area cladograms. An overview of other disjunction patterns in arid and semiarid Mexico is made to determine whether plant disjunctions can be used in a rigorous way to elucidate the climatic and vegetational history of Mexico and the arid southwestern United States.

### Poster Session

CLARK, CURTIS. Biological Sciences, California State Polytechnic University, Pomona CA 91768. - Herbarium label-writing on a "mainframe" computer.

Most of the drudgery of writing herbarium labels is in retyping information that does not change from one label to the next, and typing duplicate labels. The ability of computers to store information can alleviate much of this. Full-screen word-processing systems are designed for such use, but not all herbaria have these available. Our system uses instead a "mainframe" computer, of the type available on most college campuses. An interactive BASIC-language program takes input from a worker at a terminal and writes it on a file which is then sent to a word-processing program of the RUNOFF type for final manipulation into herbarium labels. We have found that a "user-friendly" program must have certain features: (1) a HELP command, (2) a standard order for inputting information, but the ability to deviate from

it at any time, (3) the ability to proof the information at any time, and (4) the ability to selectively erase information at any time. Our program has been used successfully in a one-quarter beginning plant taxonomy course. It prints labels in a standard format, which can be changed by altering one section of the program. Listings of the program will be available.

JOTCHAM, J.R. and D.W. SMITH. Department of Botany & Genetics, University of Guelph, Guelph, Ontario, Canada. N1G 2W1 -A numerical analysis of Ericaceae.

Numerical analyses were applied to a previously published data set of 60 characters for 52 genera of Ericaceae (Stevens, 1971). The classification methods applied included polythetic agglomerative and polythetic divisive (2-way indicator species analysis) procedures. The ordination methods included principal components analysis and detrended correspondence analysis. The resulting clusters were tested using multiple discriminant analysis. All analyses were performed with commercially available software. The results did not completely coincide, but they essentially agree with Stevens' treatment of the family, especially at the subfamily level. The Pyroloideae and Monotropoideae are usually well within the family boundaries as defined, but the Wittsteinioideae are a definite outlier with this data set. The ordination diagrams did not show clearly disjunct clusters in most cases, but the genera of any one subfamily tended to group together.

MACDONALD, S. ELLEN and C.C. CHINNAPPA. Department of Biology, University of Calgary, Calgary, Alberta Canada. T2N 1N4 - Morphological variation within an isolated population of *Stellaria longipes* Goldie (Caryophyllaceae) on the Athabasca sand dunes.

*Stellaria arenicola* Raup is considered to be a species (within the *S. longipes* complex) endemic to the Athabasca sand dunes in northern Saskatchewan. This unique area is characterized by shifting sands, unusual moisture conditions and intense insolation. These isolated populations share a combination of morphological characters which are distinct from other members of the *S. longipes* complex. This widely distributed complex is known to be plastic with respect to: number of flowers, habit, length of stem, leaf shape and pigmentation. The *arenicola* type is identified by its spreading habit and large yellow capsules with reflexed teeth. Twenty subpopulations of *S. longipes* (including the *arenicola* type) were studied in the Thomson Bay dune field. Morphological features including habit, capsule characteristics, stem length, pigmentation, number of flowers, leaf shape and size, and flower size and sex were characterized in each population. A gradation from the *longipes* form to the typical *arenicola* form is evident. There is great variability in capsule color and size. Environmental parameters including shading, sand accumulation, soil water potential and other soil characteristics (nutrients, organic matter and particle size) were determined for each site. The association of morphological features with microhabitat characteristics will be presented.

SIMONS, ELAINE P. and C.C. CHINNAPPA. Department of Biology, University of Calgary, Calgary, Alberta, Canada T2N 1N4. - Preliminary report on pollen morphology and microsporangium development in Astragalus and Oxytropis (Leguminosae - Papilionoideae).

There has been a great deal of confusion throughout the taxonomic history of Astragalus L. and Oxytropis DC. as to the validity of maintaining the two as separate genera. The distinction between Astragalus and Oxytropis was well documented by Barney (1952; 1964) on the basis of macromorphological differences. The present study deals with embryological characteristics of the two genera.

STOCKTON, TAMALYN. Department of Biology, Utah State University, Logan, Utah 84321. - The origin of Xylorhiza glabriuscula var. linearifolia (Asteraceae).

Xylorhiza glabriuscula var. linearifolia is a narrow endemic of southeastern Utah. It is intermediate in morphology and habitat to X. glabriuscula var. glabriuscula and X. tortifolia var. imberbis. Variety linearifolia may be a stabilized hybrid derivative. It is uniform in morphology and has high mean pollen stainability (ca. 90%). A low pollen stainability (33%) was found in a specimen believed to be a recent segregate of hybridization. Only one parental character is highly variable in the taxon, leaf dentation. There is no correlation between the presence of dentation on the leaves and pollen stainability. Approximately 25% of the plants in random transects have various degrees of dentation in their leaves. One diploid and six tetraploid populations of the taxon were studied. The diploid population has a high mean pollen stainability (ca. 98%). The tetraploid populations have slightly lower mean pollen stainabilities (ca. 88%). The diploid population differs from the tetraploid populations in leaf length, type of pubescence, and habitat preference.

TALLENT, RAYMOND C.\* and DANIEL E. WUJEK. Department of Biology, Central Michigan University, Mt. Pleasant, MI 48859. - Taxonomy of several Carex species using micromorphological characters.

The genus Carex (Cyperaceae) includes over 500 species in eastern North America with approximately 169 species recorded for Michigan. These sedges often bear subtle distinctions among species, indicating the utility of additional systematic research in several groups. Various types of systematic information have been applied in previous studies of the carices, in addition to conventional ("gross") morphological measures of fruiting and vegetative structures. The present study provided additional data from scanning electron microscopy of achenes and perigynia of twenty-two species of Carex from the sections Divisae, Ovales, Extensae, Carex (Hirtae), Vesicariae, and Lupulinae. Special attention was given to determining the intraspecific constancy and taxonomic resolution afforded by achene surface features: epidermal silica deposits and "satellites." The majority of specimens were obtained from the herbarium of the University of Michigan and achenes were prepared by simple acid-cleaning and air drying techniques. Achenes of Cobresia were also examined, for extra-generic control. Achenes from several specimens of

each species were examined and photographed at 500 to 1,000 X. Achene surface features were constant and unique at the level of section, in some groups (e.g., Ovales), and varied with species within other section (Extensae). Taxonomic resolution with these features then, varied between the species and the section level. Cluster analysis facilitated comparison of the taxonomic usefulness of these features with taxonomy by gross morphological features.

## Contributed Papers

AHLENSLAGER, KATHLEEN E.\* and KATHLEEN M. PETERSON. Department of Botany, University of Montana, Missoula, MT 59812. - Systematic studies of Salvia subgenus Calosphace section Erythrostachys (Lamiaceae).

Members of Salvia subg. Calosphace sect. Erythrostachys range from the area of Big Bend National Park (Chisos Mountains), Texas to the highlands of Mexico, and one species occurs as a disjunct in Colombia, South America. Three North American species, S. regla, S. pubescens, and S. sessei, exhibit morphological intergradation; thus, they have been taxonomically confused. The South American disjunct, S. libanensis, is a well-defined entity. The present study reports patterns of character variation of all species in sect. Erythrostachys, using morphological and anatomical evidence via statistical and computer analyses. With respect to morphological characters, S. pubescens is intermediate between S. regla and S. sessei. However, preliminary chromosome counts indicate that S. regla and S. sessei are both  $n=11$ , while S. pubescens may be a polyploid with  $n=ca.20$ . To date, polyploid species are the exception, rather than the rule, in Salvia subg. Calosphace.

AKE, KATHERINE. Department of Botany, University of Montana, Missoula, MT 59812. - Relationships of six species of Erigeron L.

Erigeron sect. Erigeron comprises a number of small closely knit groups which cannot be clearly delimited taxonomically from the remaining species in the section. According to Cronquist, three species, Erigeron asperugineus (D.C.Eaton) A.Gray, E. clokeyi Cronquist, and E. pygmaeus (A.Gray) Greene, form an assemblage which probably had a recent ancestor. The major objectives of my study were to assess the affinities of this core group as well as their relationship, as a group, to three additional species proposed by Cronquist as their closest relatives. Morphological, cytological, and anatomical evidence as well as paper chromatographic patterns of flavonoids were used in the study. The data affirm the close affinities of the core group. Morphologically, E. asperugineus and E. clokeyi are more closely related to each other; however, chromatographic patterns of E. clokeyi and E. pygmaeus are more similar to each other. Based upon morphological evidence, the closest relatives to the core group do not appear to be those species suggested by Cronquist.

## 104 Systematic Section

ALLEN, GERALDINE A. Department of Biology, University of Victoria, Victoria, B. C., Canada V8W 2Y2. - The hybrid origin of *Aster bernardinus* (Asteraceae).

*Aster bernardinus* is endemic to the Peninsular and southern Transverse Ranges of southern California, and has the polyploid chromosome number of  $n = 18$  throughout its range. Chromosome base numbers in *Aster* include 5, 7, 8, 9 and 13 (previous work has shown the base number 13 to be the result of combining 5 and 8). The reports of  $n = 18$  for *A. bernardinus* suggest a base number of  $x = 9$ . However, this species shows little resemblance to other species with this base number, but is apparently an amphiploid derived from backcrossing between the Great Basin species *A. ascendens* ( $x = 13$ ) and one of its parents, *A. falcatus* ( $x = 5$ ). Multivariate analyses using 28 morphological characters measured on specimens of known chromosome number showed that *A. bernardinus* closely resembles *A. ascendens*, but has some characteristics of *A. falcatus*. The karyotype of *A. bernardinus* includes two pairs of large chromosomes with almost terminal nucleolar organizer regions; it combines the features of the karyotypes of *A. ascendens* and *A. falcatus*. The two species *A. ascendens* and *A. bernardinus* form a bridge between two well-marked subgenera of the genus *Aster*.

ARMBRUSTER, W. SCOTT, Division of Life Sciences, University of Alaska, Fairbanks, AK 99701 - The Evolution and Chemistry of Pollinator Rewards in the Genus *Dalechampia* (Euphorbiaceae).

A parsimonious model of the phylogenetic relationships between species of *Dalechampia* was constructed using characters of inflorescence morphology. The polarity of character states was established using out-group comparisons with the Plukenetieae, coupled with analysis of character trends and vestigial structures. When data from pollination studies are incorporated into the phylogenetic model, they indicate that the earliest pollinator reward offered by members of the genus was probably pollen; pollination was probably effected by pollen-collecting bees. From this stock evolved species that secrete triterpenoid resins as pollinator rewards; the resins were (are) collected by female bees of the Megachilidae, Euglossini and/or Meliponini. More recently, from different ancestral groups of resin-secreting species there have arisen two independent lines of species that have switched to secretion of monoterpene volatiles as pollinator rewards; pollination in these species is effected by male euglossine bees.

ATKINS, RILEY J., MARY E. BARKWORTH\*, and DOUGLAS R. DEWEY. Department of Biology UMC 45, Utah State University, Logan, UT 84322. - A Taxonomic Study of *Leymus ambiguus* and *L. salinus* (Poaceae: Triticeae)

Morphological studies of populations in Utah, Idaho, Arizona, Wyoming, and Colorado belonging to three taxa of *Leymus* revealed that *L. salinus* is comprised of two subspecies, susp. *salinus* and subsp. *salmonis* comb. nov. *Leymus ambiguus* is distinct from these two taxa and occurs in the Front Range of Colorado and the Sangre de Cristo mountains of New Mexico. Tetraploid ( $2n=28$ ) and octoploid ( $2n=56$ ) races occur in *L. salinus* subsp. *salinus* and *L. ambiguus*, but only tetraploids are known in *L. salinus* subsp. *salmonis*. A naturally occurring hexaploid ( $2n=42$ ) was found in one population of *L. salinus* subsp. *salinus*.

BAKER, MARC A.\* and DONALD J. PINKAVA. Department of Botany and Microbiology, Arizona State University, Tempe, AZ 85287. - Megasporogenesis and megagametogenesis in *Opuntia fulgida*, *O. spinosior* and their triploid hybrids.

Our preliminary analysis of sectioned ovules of *Opuntia fulgida*, *O. spinosior*, and their triploid hybrids has provided further evidence that *O. fulgida* is an apomictic species, while *O. spinosior* is largely sexual. Although both have 8-nucleate *Polygonum* type embryo sacs, only those of *O. spinosior* appear to be functional and derived via meiosis. This is the first report of normal megagametogenesis in *Opuntia*. Although we have not yet determined the exact nature of the abnormalities in diploid *O. fulgida*, we have found the abnormalities in triploid *O. fulgida* and the triploid hybrids to exist because of uneven segregation of chromosomes among the four genes. Micronuclei are often present. From materials examined, the position of the functional megaspore was random among the four nuclei of the tetrads, and abortion always occurred before the formation of a functional 8-nucleate embryo sac.

BALLARD, JR., HARVEY E. Department of Biology, Western Michigan University, Kalamazoo, MI 49008. - Taxonomic revision of stemless blue violets (*Viola*) in the eastern United States.

Difficulties in identification of stemless blue violets have traditionally been attributed to random morphological variation, intergradation, and rampant hybridization. Paradoxically, all studies to date have been based on species concepts first espoused by Brainerd and his contemporaries at the turn of the century. None have involved a re-appraisal of the original taxa to ascertain whether the problem lay with the violets themselves or with erroneous classifications superimposed on them. Specimens from 31 herbaria have been examined and numerous field observations of Michigan populations made to document morphological and ecological patterns in the stemless blue violets of the eastern United States. Five broadly defined but well-marked species, *Viola cucullata*, *V. nephrophylla*, *V. pedatifida*, *V. sagittata*, and *V. sororia*, have been recognized. Each species occupies a specific plant community (e.g., *V. pedatifida* in mesic prairie). Connecting the species are *de novo* hybrids and derivatives found in highly disturbed sites and ecotones of adjoining plant communities; forms in regions where communities intergrade; and forms that appear ancestral to the 5 ecologically isolated species. For convenience most intermediates have been placed in two polyphyletic species complexes called *V. affinis* and *V. palmata*.

BANERJEE, UMESH C.\*, JOHN RUFFIN, SUMANA G. BANERJEE, Department of Biology, North Carolina Central University, Durham, N.C., 27707.

- Selection of high rubber yielding variety of Guayule (*Parthenium argentatum* Gray). During Cretaceous when angiosperms originated, most insect genera were already well established. These insect species were totally dependent on plants as a primary source of food supply. During the past several million years plants have util-

ized various strategies for their survival and to protect themselves from their predators. Among these, two strategies used by plants are very important. (1) Morphological Strategy: Plants have evolved various types of trichomes, spines, thorns, very tough epidermis, waxy coating on leaves, etc. for their defense mechanisms. (2) Chemical Protection: Various toxic chemicals and deterrents are produced by plants; examples of these are tannins, alkaloids, flavonoids, and milky juices (latex or rubber). Approximately 2,000 species of angiosperms are known to produce milky juice for their protection from predators, however, varieties with less latex are often eaten by the insects. Since the species of Guayule (Parthenium argentatum) also produce latex (rubber), we could easily select the high rubber yielding varieties by using natural predators as a tool for the selection of plants from the natural population since those plants having high rubber content are less damaged by insects. This screening method has saved our time and labor, and we have selected plants which produce more rubber without going through conventional hybridization methods and without growing thousands of seedlings for selection procedure in the field condition. We have made our observations on natural populations growing wild in southwestern Texas.

BARKLEY, T. M.\*, R. L. MCGREGOR, and R. E. BROOKS. Herbarium, Division of Biology, Kansas State University, Manhattan, KS 66506 and State Biological Survey of Kansas, Lawrence, KS 66045. - Completion of the Flora of the Great Plains project.

In 1973 the Great Plains Flora Association (GPFA) was formed among botanists of the region to prepare a floristic treatment for the grasslands of the central and northern U.S. The project has produced the Atlas of the Flora of the Great Plains and the soon-to-be-published Flora of the Great Plains. The GPFA involved taxonomists in six states and twelve regional institutions, plus specialists from elsewhere, and it was supported by both national and local sources. The project operated through a "Memorandum of Cooperation" which is a quasi-legal agreement among GPFA participants. The organizational and procedural aspects of the project may be of interest to botanists who are contemplating broad floristic programs.

BARKWORTH, MARY E. Department of Biology UMC 45, Utah State University, Logan, UT 84322. - Leymus Hochst. (Gramineae: Triticeae) in North America.

Generic recognition of Leymus Hochst. is supported by genomic, genetic, and morphological data. Much of the supposed overlap between it and other North American Triticeae reflects misunderstandings as to its limits. Members of Leymus are generally rhizomatous species with short, stiff, subulate glumes; acute to shortly-awned lemmas; and large anthers. A few species are generally cespitose but produce short rhizomes in some populations. The two coastal species differ from the others in having flat, evidently veined, nerves. Intrageneric hybrids are relatively common but hybrids with other genera are very rare, particularly when the frequency of sympatric populations is considered.

BARKWORTH, MARY E. Department of Biology UMC 45, Utah State University, Logan, UT 84322.

- Patterns of evolution in the Stipeae

The Stipeae are well represented in Eurasia, North America, South America and Australia, the largest number of species being in Eurasia. The species generally occupy xeric to semi-xeric habitats but some species have become adapted to more mesic environments, including subalpine bogs.

Similar suites of adaptive characteristics can be seen in all four areas. Species of the most xeric habitats have long awns with a strongly twisted column; long, sharp calluses; large but narrow florets and lemmas with strongly overlapping margins. These features enable the caryopsis to be buried deeply in the soil during the wet season. In North America these characteristics can be seen in members of Stipa sect. Hesperostipa and Piptochaetium sect. Podopogon. Species of more mesic habitats differ in having shorter awns and florets; calluses that are often blunt; evenly, and sometimes long, pubescent lemmas that are often not strongly overlapping. Most North American species of Stipeae belong in this group. Long hairs on the lemma or awn are particularly common among species occupying the drier habitats. Species of subalpine habitats tend to have very narrow, erect leaves as well as the other characteristics listed for species of mesic environments.

Each of these character suites appear to have developed independently in several different groups of Stipeae. This has resulted in considerable taxonomic confusion both in North America and elsewhere.

BAYER, RANDALL J. Department of Botany, The Ohio State University, Columbus, OH 43210. - The compilospecies Antennaria neodolca and its possible relationship to diploid species of the genus.

The dioecious composite, Antennaria neodolca sensu lato (Bayer and Stebbins 1982), is a taxonomically difficult, polyploid agamic complex found in the eastern United States and adjacent Canada. It has recently (Bayer and Stebbins 1982) been recognized to be composed of three subspecies namely, A. neodolca Greene ssp. canadensis (Greene) Bayer and Stebbins, ssp. neodolca, and ssp. petaloidea (Fern.) Bayer and Stebbins. All populations of A. neodolca are agamospermous and consist entirely of pistillate clones. It has long been thought that polyploid agamic complexes in Antennaria are the result of hybridization between and among diploid species. With this in mind, hybridizations were made among five diploid ( $2n = 28$ ) species of Antennaria in an attempt to discover the origins of the A. neodolca complex. Interspecific hybrids were obtained for most combinations of the five diploid species A. neglecta, A. plantaginifolia, A. racemosa, A. solitaria, and A. virginica. Representative specimens of A. neodolca s.l., the five diploids, and all the interspecific hybrids were then subjected to a numerical analysis consisting of a principle components, cluster (UPGMA), and a discriminant analysis. Also included in the analysis were specimens of A. Howellii Greene, which occurs in the northern Rocky Mountains. Results indicate that A. Howellii should be included as a fourth subspecies of A. neodolca s.l. and that the A. neodolca complex is probably the result of complex hybridization involving all diploid species of the genus except A. solitaria. Therefore A. neodolca s.l. can be considered a typical compilospecies.

BELL, JOHN M.\* and THOMAS R. SODERSTROM.  
Department of Botany, North Carolina State  
University, Raleigh, North Carolina 27650, and  
Department of Botany, Smithsonian Institution,  
Washington, D. C. 20560. - Anatomical approach  
to the placement of a new bamboo from Mexico.

An undescribed scandent bamboo which is abundant in the Engelhardtia cloud forests of Oaxaca, Mexico, shows closest similarities to the genera Aulonemia and Olmea. All three have a similar branch complement and a flower that contains three stamens and two stigmas. The open panicle of the new species resembles that of the former genus, but its narrow, elongate spikelets and prominent erect oral setae are like those of the latter. The fleshy fruits, which are characteristic of Olmea, clearly differentiate it from Aulonemia, which has dry caryopses. Since fruiting material of the new species was not available for study, a detailed anatomical investigation was made of its leaves, and the results compared with those of the other genera. The leaf anatomy is typical of Olmea in most respects but differs from Aulonemia in which all species exhibit the unusual presence of intercostal sclereids. While fruiting material will be necessary for precise classification, the evidence at hand suggests placement of the new bamboo in the genus Olmea.

BOHM, B.A.\*, K.W. NICHOLLS and R. ORNDUFF.  
Department of Botany, University of British  
Columbia, Vancouver, B.C. V6T 1W5 and Department  
of Botany, University of California, Berkeley, CA  
94720.

- Flavonoids and affinities of Menyanthaceae  
Dumortier.

The Menyanthaceae is a family of aquatic or semi-aquatic herbs comprising five genera: Menyanthes (1 sp.), Fauria (= Nephrophyllidium) (1 sp.), Nymphoides (ca. 20 spp.), Villarsia (ca. 14 spp.), and Liparophyllum (1 sp.). The family has most often been associated with the Gentianales, as the Menyanthaceae, or as the Menyanthoideae within the Gentianaceae, but its placement in the Solanales has been argued recently by Cronquist. We undertook a study of the flavonoid chemistry of the family with a view to examining relationships from a new perspective. A variety of kaempferol and quercetin glycosides occurred in all taxa studied (15 species representing all five genera). Several O-methylated derivatives of these flavonols were more limited in their distribution but clearcut correlations with generic lines were not observed. The flavonoids clearly distinguish Menyanthaceae from the Gentianaceae, however. Major phenolic compounds of the Gentianaceae include C-glycoflavones and xanthones neither of which type has been reported from members of Menyanthaceae.

BOLICK, MARGARET R. Division of Botany,  
University of Nebraska State Museum,  
Lincoln, NE 68588-0514. - A cladistic and  
biogeographic analysis of the  
Juglandaceae.

A cladistic analysis of the extant genera of the Juglandaceae was done using characters from the flowers, fruit, wood, and pollen. The Rhoipteleaceae was used as the outgroup. The resulting cladogram is congruent with Manning's (1978) classification of the

family. Platycarya, recognized by Manning as the subfamily Platycaryoideae, is the sister group to the remaining genera. Within the subfamily Juglandoideae each of the three tribes recognized by Manning is a monophyletic group: Juglandae (Juglans, Pterocarya); Engelhardieae (Engelhardia, Alfaroa, Oreomunnea); and Hicorieae (Carya). The modern distribution of the family shows three genera in southern Asia (Platycarya, Pterocarya, Engelhardia); two genera in Central America (Alfaroa, Oreomunnea); and two genera split between North America and Asia (Juglans, Carya). Based on the cladogram, it is more parsimonious to assume that the Juglandaceae evolved in eastern Asia (three dispersal events) than in eastern North America (five dispersal events). This contradicts the extremely well known fossil pollen record of the family which suggests that the family originated in North America-Europe.

BOWMAN, ROBERT N. Dept. of Botany and Plant Path.,  
Colorado State University, Fort Collins, CO 80523.  
- Intraspecific variability of leaf cuticle alkanes  
in Sedum lanceolatum (Crassulaceae) along an elevational  
gradient.

The utilization of leaf waxes in elucidation of bio-systematic relationships is well documented. This study investigated the influence of field conditions on alkane production in a taxonomically unambiguous species, S. lanceolatum Torr. Alkanes from individuals representing 44 populations ranging in elevation from 1598-3568 m were analyzed using gas chromatography. Relative percentages of 15 alkanes were determined for each population. Characterization of variability patterns in field-collected samples indicates no significant correlation between any alkane and elevation. Cluster analysis by cases based on total alkane variability shows no correlation with elevation even though localized biotypes may be in evidence. Near normal distribution of amalgamated distances derived from alkane proportions suggests that inherent variability is better explained by genetic constitution than by phenotypic plasticity. Results suggest that environmental factors associated with an elevational gradient are not directly responsible for alterations in expressed alkane phenotypes. Thus, at least in S. lanceolatum, field-collected alkane samples are meaningful in systematic interpretations.

BRECKON, GARY\* and VIVIAN NEGRON ORTIZ.  
Depto. de Biología, Universidad de Puerto  
Rico, Mayagüez, PR 00708. - Pollination of  
Zamia pumila by fungus-gnats.

Circumstantial evidence from Cambalache forest, Puerto Rico indicates that nocturnal visitation by a fungus-gnat (Diptera, Mycetophilidae) effects pollination in Zamia pumila L. subsp. pumila. The fungus gnat is the only consistent visitor to both male and female cones; visitation occurs between 10 p.m. and 2 a.m.; both cones produce an odor similar to that of fresh mushrooms; the odor is detectable between 8 p.m. and 2 a.m.; feeding larvae of the fungus-gnat are present in post-pollination

male cones, they only rarely are found in the female cone. Larvae reared in harvested microstrobilii develop into adults. Reasons for visiting the megastrobilii are not evident: the female cone may be a mimic of the male cone, but is unacceptable for oviposition and/or subsequent development; or the pollination drop may provide a reward for the visiting adult.

BRETTING, P. K. Natural History Division, Institute of Jamaica, 12 East Street, Kingston, Jamaica. - Breeding systems in Proboscidea (Martyniaceae).

Floral characteristics, degree of self-compatibility, P/S (pollen-seed ratios--equivalent to pollen-ovule ratios), and observation of insect visitors were used to estimate breeding systems in nine taxa of Proboscidea (Martyniaceae). Bees visit the flowers of most species, and are apparently the most important pollinators. Proboscidea sabulosa is primarily autogamous, P. altheaeifolia primarily xenogamous, and P. louisianica facultatively xenogamous. Within P. triloba, subsp. triloba is facultatively xenogamous, but subsp. diversifolia is relatively more autogamous. Within P. parviflora, subsp. parviflora is primarily autogamous, subsp. gracillima probably facultatively xenogamous, and subsp. sinaloensis primarily to facultatively xenogamous. The evolution of relatively more autogamous subspecies in P. parviflora and P. triloba has involved very similar changes in floral characteristics and degree of self-compatibility. Separate numerical 'xenogamy-autogamy' indices constructed from self-compatibility data and from floral characteristics are significantly correlated with each other and with pollen number, but are uncorrelated with P/S ratios and seed number. Seed (and ovule) number may be determined by factors related to successful dispersal rather than reproductive efficiency. Floral characteristics and degree of self-compatibility hence may be more precise measures of breeding systems in Proboscidea than are P/S ratios.

BRINK, DON\* and J. M. J. DE WET. Crop Evolution Laboratory, Department of Agronomy, University of Illinois, 1102 South Goodwin Avenue, Urbana, IL 61801-4798. - Sections in Tripsacum (Gramineae).

There are two main infrageneric groups within Tripsacum and they differ in several correlated characters. Variation is essentially continuous between the groups for any single character but two well defined modes of variation emerge when combinations of characters are considered. There are few intermediates and the vast majority of specimens studied fall unambiguously into one group or the other. These two groups are recognized as sections. They are the most distinct and well defined natural groups within the genus. Section Fasciculata differs from section Tripsacum in having one spikelet of a staminate pair at a rachis node with a long, thin pedicel rather than both spikelets subsessile or one supported by a short, thick pedicel; thinner internodes in the male section of each inflorescence branch; and a longer primary axis of the terminal inflorescence with more internodes and more branches. Section Tripsacum has a wide geographical range extending from the central and northeastern United States to central South America.

Section Fasciculata has a more restricted distribution extending from southern Arizona to El Salvador.

BROWN, BRETT P.\* & JAMES E. ECKENWALDER. Department of Botany, University of Toronto, Toronto, Ontario, Canada M5S 1A1 - The origin of the cardinal climber, Ipomoea X multifida (Raf.) Shinn.

The cardinal climber is a popular ornamental morning glory with red flowers and lacerate leaves. Unlike its diploid congeners in sect. Quamoclit, Ipomoea x multifida is an allotetraploid. The origin of this hybrid should be unproblematic since its originator at the turn of the century, L. Slotter, states that he crossed I. coccinea with I. quamoclit, producing sterile hybrids for 11 years until a single seed was produced that has given rise to all cultivated cardinal climbers. However, at the time Slotter worked, 8 other species now recognized as distinct were all called I. coccinea, and 4 of these were also cultivated with I. coccinea. We undertook a crossing program among these 5 candidates for parenthood and the unproblematic parent, I. quamoclit. Parents, F<sub>1</sub> hybrids, and I. x multifida were grown in a randomized block design and scored for various vegetative and floral characteristics. This data was analyzed using Principal Components Analysis and Canonical Variates Analysis. The results of the crossing program and of the morphometric analyses supported the parentage of I. coccinea, even though the F<sub>1</sub> hybrid I. coccinea x I. quamoclit was morphologically distinct from the cardinal climber. This parentage was confirmed when 6 seeds were produced on the F<sub>1</sub> plants at the rate of about 1 per 40,000 ovules. These seeds have produced tetraploid plants that are morphologically identical to the cardinal climber and freely intercrossable with it but not with either diploid parent species or with their own F<sub>1</sub> hybrid parents. The cytological mechanism leading to tetraploid formation appears to be the union of unreduced gametes that are produced in higher frequencies in the F<sub>1</sub> hybrid than in the diploid parent species.

BRUEDERLE, LEO P.\* and DAVID E. FAIRBROTHERS. Biological Sciences (Botany), Rutgers University, Piscataway, N.J. 08854. - Variability and taxonomic usefulness of achene and perigynium characters of the Carex crinita complex (Cyperaceae).

The Carex crinita complex comprises seven taxa variously organized into two or three species and corresponding varieties. These have been distinguished on the basis of infructescence structure; achene contortion; perigynium shape, dimensions, and ultrastructure; sheath pubescence; culm height; and leaf width. The majority of these characters exhibit continuous variability throughout the complex, while others are disjunct and not necessarily correlated with a particular taxon as previously described. A comparative study was undertaken examining perigynium, and achene morphology and ultrastructure utilizing SEM and light microscopy. Features examined were achene epidermis, achene contortion, perigynium ornamentation, and perigynium dimensions. Characters classically used to distinguish among taxa were found to be less useful for classification purposes than less frequently used features, in particular perigynium ornamentation and dimensions. SEM examination of achenes revealed less useful variability than that detected among other taxa within the genus, e.g. Montanae, Lupulinae.

BRUNER, JOE. Department of Botany, The Ohio State University, Columbus, Ohio 43210. - Systematics of the Schizachyrium scoparium group (Poaceae) in North America.

The Schizachyrium scoparium group ranges from North to South America. Species of this group are morphologically distinct from other members of the genus. The North American representatives of this group, some ten tetraploid ( $2n=40$ ) species, have not been the focus of a systematic study of any depth until the present time. Greenhouse comparisons of growth and habit, consideration of habitat and distributions, and phenetic studies have clarified the species variation and tend to support the taxonomic integrity of most of the species. The analysis of the following species pairs, however, suggests that the latter taxon is not sufficiently distinct from the former to warrant specific status: scoparium/littorale, cubense/rhizomatum, and gracile/sericatum. The cleistogamous reproductive mode of S. gracile and S. sericatum is an anomaly in this primarily outcrossing group, raising the question about how closely related they are to the other species. S. niveum, a severely restricted endemic of central Florida, is quite distinct from the other North American species and in a phenetic analysis groups more closely with Central American and South American species.

CAMPBELL, CHRISTOPHER S. Department of Botany and Plant Pathology, University of Maine, Orono, Maine 04469. - Systematic relationships of the grass genus Brachyelytrum.

Where Brachyelytrum belongs in the Gramineae is enigmatic. It has traditionally been associated with the Stipeae or Pooideae on the basis of morphological similarity. Anatomical data from embryos and leaves contradict these morphological similarities as do new data on the seedling morphology of Brachyelytrum. In the width and orientation of the first seedling leaf blade, Brachyelytrum resembles stipoids and pooids, but it differs from most of them in its short first internode (the seedling mesocotyl) and lack of adventitious roots at the coleoptilar and scutellar nodes. Actually, Brachyelytrum is closer to various members of the Bambusoideae (sensu lato -- including woody bamboos, herbaceous bambusoids and oryzoids) in embryo anatomy, some leaf epidermal features and the first internodes and lack of adventitious roots of the seedlings. On the whole, however, the genus appears to be distantly related to other grasses. The current distribution of its two taxa -- one species or variety in the Eastern United States and the other in China and Japan -- suggests considerable geologic age and the possibility that it represents an early departure from the probable birthplace of grasses in tropical forests.

CANNE, JUDITH M. Department of Botany and Genetics, University of Guelph, Guelph, ON, N1G 2W1. - Sectional limits in North American Agalinis Raf. (Scrophulariaceae).

Recent work with the North American species of Agalinis indicates that the infrageneric taxonomic interpretations accepted by F.W. Pennell in his treatment of the genus in the 1920's and 1930's require modification. The following features form the primary bases for the present circumscription of sections and subsections: corolla form; patterns of pubescence on the corollas; morphology of the calyx; capsule shape; color, size and surface patterns of

seeds; morphology and anatomy of leaves and stems; morphology of seedlings; organization of the inflorescence; chromosome number. Two of the larger groups, section Erectae with a base chromosome number of  $x=13$  and section Purpureae subsection Purpureae with a base chromosome number of  $x=14$ , are maintained essentially as accepted by Pennell except that two species from other subsections of section Purpureae are moved to section Erectae. Subsection Setaceae ( $x=14$ ) of section Purpureae is reduced to four species. The small sections Aspereae and Heterophyllae are united. Some members of section Tenuifoliae are combined with the species of section Purpureae subsection Pendunculares to form a separate section. The monotypic section Linifoliae is maintained. The small genus Tomanthera Raf. is reunited with Agalinis.

CANTINO, PHILIP D. Department of Botany, Ohio University, Athens, OH 45701. - Chromosome numbers, chromosome size, and intergeneric relationships in subtribe Melittidinae (Labiatae).

The Melittidinae (Labiatae) was established as a subtribe by Endlicher, perpetuated by Bentham and Briquet, and has generally been recognized by more recent authors. Endlicher, Bentham, and Briquet all delimited the group on the basis of gross morphology of the calyx and corolla. Few of the character states they cited are found in all genera of the Melittidinae, and none are unique to the subtribe; they occur in various combinations elsewhere in the family. Chromosome numbers have been reported for two of the six genera of the Melittidinae (Melittis,  $2n=30+2-8B$ ; Physostegia,  $2n=38,76$ ). New counts, reported here, establish a diploid number of 18 for Synandra and Macbridea and 28 for Brazoria. Chromosomes of Synandra and Macbridea are three times as large as those of Brazoria and Physostegia. Neither cytological data nor traditional floral characters support the retention of the Melittidinae as a natural grouping.

CHINNERY, LOUIS E. Department of Biology, University of the West Indies, P.O. Box 64, Bridgetown, Barbados. - Variation of ray-floret length in Bidens pilosa L., implications for taxonomy in the Asteraceae.

Largely on the basis of capitulum morphology, Sherff (1937) split Bidens pilosa into a number of varieties and forms. The ray-florets from plants of varieties radiata and minor, which he separated on the basis of ray-floret length, have been measured. The results show (a) that variation of ray-floret length is continuous within varieties and that the two varieties merge, (b) that there is a linear relationship between ray-floret length and the number of disc-florets which have opened, and (c) that this is due to an increase in length of both the ligule and

tube portions of the corolla. The results are compared with data on the variation of ray-floret length in Senecio vulgaris L.. The use of ray-floret size in identification and classification of ligulate members of the Asteraceae is questioned.

CHOLEWA, ANITA F. Department of Biological Sciences, University of Idaho, Moscow, ID 83843 - A biosystematic study of Rocky Mountain populations of Sisyrrinchium section Bermudianae.

Since the early 1900's, when Bicknell and Greene described many of the North American species of Sisyrrinchium (Iridaceae), only the Pacific Northwestern members of the genus have received a biosystematic treatment. As a result, much confusion still exists regarding the taxonomy of other populations. A biosystematic study of the Rocky Mountain populations was made to discover and define discontinuities with taxonomic value. Detailed morphological examinations were supplemented with chromosome counts, flavonoid chromatographic patterns, breeding system studies, and artificial hybridizations. Based on data gathered from these areas, five groups were defined. Three of these correspond to S. idahoense (including S. heterocarpum and S. juncellum), S. montanum (including S. alpestre and S. heterocarpum), and S. septentrionale. A fourth group, S. radicum, is tentatively being separated from the closely related S. demissum. The fifth represents a new species: S. pallidum Cholewa sp. nov. ined., which is characterized, in part, by pale blue flowers.

CHUANG, T. I.\* and L. R. HECKARD. Department of Biological Sciences, Illinois State University Normal, IL 61761 and Jepson Herbarium, Department of Botany, University of California, Berkeley, CA 94720. - Systematic significance of seed-surface features in Orthocarpus (Scrophulariaceae).

Scanning electron microscope and light microscope examination of seed-coat features of 26 species of Orthocarpus have allowed recognition of many species-level differences (summarized in a key) and of three seed-coat types that parallel taxonomic subgroups but support realignments at generic and infrageneric levels. Type 1 seeds (subg. Orthocarpus, sect. Orthocarpus) have a lateral hilum, sculptured inner tangential seed-coat walls, and a tightly fitting outer seed coat. They are very similar to seeds of Cordylanthus. Seeds of Types 2 and 3 have a terminal hilum and membranous inner tangential cell walls. Type 2 seeds (subg. Orthocarpus, sects. Castillejoidea and Cordylanthoides, with one exception) have a net-like, loosely fitting outer seed coat that shows close relationship to seeds of Castilleja. Inner tangential walls of Type 2 seeds normally rupture. Type 3 seeds (subg. Triphysaria, with two exceptions) have a tightly fitting outer seed coat and inner tangential walls are always retained. Seed features support evidence from floral morphology and chromosome numbers that Orthocarpus as currently recognized is not a monophyletic lineage.

CLARK, CURTIS. Biological Sciences, California State Polytechnic University, Pomona CA 91768. - Systematics and biogeography of the Encelia frutescens alliance (Asteraceae: Heliantheae). Encelia frutescens and three other taxa comprise a monophyletic group diagnosed by

a scant strigose leaf pubescence of short, broad multicellular hairs, and reduced or missing rays. The taxonomy of the group has been confused by inadequate collection, interspecific hybridization, and misinterpretation of the importance of raylessness. Recent treatments lump all four taxa plus one distantly related species and two hybrids in a single polymorphic species. Cladistic analysis provides an hypothesis of relationships among the taxa. Encelia resinosa, the sister taxon of the other three, has the most northern distribution, in the deserts of the Colorado Plateau. E. "Grand Canyon", sister taxon to the remaining two, occurs only in its namesake. The two remaining taxa, E. frutescens and E. "San Felipe", may represent a single evolutionary species; the former is widespread in the northern Sonoran and Mojave deserts and the latter inhabits northeastern Baja California. From vegetation records preserved in ancient woodrat nests, it is evident that as recently as 8000-yr b.p. the region was too cold to support the species in their present form. The older species have moved north into areas of new desert, and newly derived species now occupy the harsher deserts to the south.

CLARK, LYNN G. Department of Botany, Iowa State University, Ames, IA 50011.

- Bud morphology in Chusquea (Poaceae: Bambusoideae).

Chusquea, the largest genus of bamboos, with over 100 species, is distinguished by its solid culms, multiple independent buds per node and chromosome number of  $2n=40$ . The bud complement in Chusquea, consisting of one primary bud subtended by 2- numerous smaller independent subsidiary buds, apparently is unique among bamboos. The bud morphology of approximately 50 species of Chusquea was investigated using dried bulky specimens or material fixed in FAA. Two types of primary buds were found within Chusquea. One, the "triangular" type, is much more common and like those of other bamboos. The other, the "circular" type, to date has been found in only nine species of Chusquea. The arrangement of the subsidiary buds is highly variable, and appears to be species-specific. Among the species studied, 10 basic patterns of bud arrangement are recognized, with individual variation in the prophyllum, size of buds and other characters occurring according to species. These bud patterns appear to be important in determining evolutionary trends within the genus.

CLEMANTS, STEVEN E. Herbarium, New York Botanical Garden, Bronx NY 10458. - Flavonoids of Befaria.

The genus Befaria (Ericaceae: Rhododendroideae), the only member of the tribe Befarieae, was surveyed for leaf flavonoids. Quercetin glycosides are found throughout the genus. Of more limited distribution and thus more interesting taxonomically, are myricetin glycosides, 3,5-O-dimethylquercetin (Caryotin) and 5-O-methylflavonol glycosides. Flavonol aglycones are also present in some species. The Befarieae is often placed near the Cladothamneae because they are both polypetalous, however the Cladothamneae lack 5-O-methylflavonols and Caryotin. The Rhodoreae, also considered closely related to the Befarieae, have 5-O-methylflavonols and Carotin

(Rhododendron). This evidence supports the idea that the Befarieae is more closely related to the Rhodoreae than to the Cladothameae. The flavonoid data will be presented in a phylogentic context using cladistic methods.

CLEMANTS, STEVEN E. Herbarium, New York Botanical Garden, Bronx NY 10458. - Systematics of Befaria Mutis ex L.

Befaria (Ericaceae: Rhododendroideae) is a shrubby or arborescent genus found in pine woods in Florida and Cuba, and in montane forests, subparamo and paramo areas of Mexico, Central America and South America. The genus is placed within its own tribe and is related to the Rhodoreae and the Cladothameae. Past investigations of the genus have resulted in two different subgeneric classifications. Fedtschenko and Basilevskaja relied upon inflorescence morphology and pubescence to define four sections and two subsections, many of which are unnatural assemblages. Mansfeld and Sleumer relied on anatomy and inflorescence morphology to divide the genus into two sections, the racemosae (with one species) and the glaucae (with 25 species), and no further subdivisions were made. In the present study floral morphology, especially the relative spreading of the petals, is used to make a more natural subgeneric classification. At the species level, over reliance on hair types by previous workers resulted in unnecessary splitting. Field and herbarium studies suggest that hair type is often variable within populations and should not be relied upon a priori as a specific character. A preliminary phylogeny of the genus will also be presented based upon morphology, anatomy and chemistry.

CONNOLLY, VICTORIA\* & JAMES E. ECKENWALDER. Department of Botany, University of Toronto, Toronto, Ontario, Canada M5S 1A1 - Hybridization between white poplar and native aspens in southern Ontario.

Populus alba is an introduced poplar species that often hybridizes with the two native aspen species in the northeastern United States and adjacent Canada. Hybrids among the three species differ greatly in relative abundance in Ontario. P. x rouleauiana (P. alba x P. grandidentata) is far more prevalent than either P. x heimbürgeri (P. alba x P. tremuloides) or P. x smithii (P. grandidentata x P. tremuloides). We sought to determine at what stage(s) of the hybridization process this advantage of P. x rouleauiana might occur. Prepollination barriers interposed by differences in flowering phenology are not adequate to explain the discrepancies. Differences in viability of seeds of hybrid origin, when present, are inconsistent with differences in prevalence of the hybrids. A complete crossing program among several male and female genotypes of each species was undertaken to assess variations in compatibility among them. Catkins were collected at intervals in a time sequence after pollination for each pistillate parent in the crossing program. Observations of pollen germination and pollen tube growth were made on three stigmas from each catkin using fluorescence microscopy. The percentage of pollen germinated, rate of growth of pollen tubes, and rate of penetration of the ovary all differed among different crosses. There was considerable variation among different genotypes within species and reciprocal crosses did

not behave similarly. There were striking differences in the behavior of pollen tubes on the stigmas. These variations cloud the interpretation of the results, but it seems that here, too, there is no obvious basis for the predominance of P. x rouleauiana

CRINS, WILLIAM J.\* and PETER W. BALL. Department of Biology, Erindale Campus, University of Toronto, Mississauga, Ontario L5L 1C6. - Revisionary studies in Carex section Extensae: preliminary results.

The eight North American members of Carex section Extensae fall into three groups based on morphology. The first two groups are characterized by divergent or reflexed perigynia within the pistillate spikes. Carex cryptolepis, C. flava, and C. lepidocarpa possess perigynia in which a distinct angle is formed between the body and the beak. Carex demissa, C. saxilittoralis, and C. viridula lack this feature. The remaining taxa, C. extensa and C. hostiana, form a third group in which the perigynia ascend within the pistillate spikes. The majority of the species in the section occur in both North America and Europe. However, no attempt has previously been made to compare the North American and European plants. In the present study, morphological variation and discontinuities within the complex have been investigated through the use of principal components analysis and discriminant analysis. The initial phase of the investigation was conducted using 53 morphological characters. On the basis of these analyses, it appears that C. saxilittoralis is not distinct, and should probably be united with C. viridula. Morphological and cytological evidence suggest that the European C. serotina is conspecific with C. viridula. The European C. scandinavica is also allied with C. viridula, but may represent a distinct taxon at a rank below that of species. The North American plants of C. hostiana, considered to be varietally distinct by Fernald, do not differ significantly from the European plants. The remainder of the North American species are distinct from each other morphologically and cytologically.

CROAT, THOMAS B. Department of Botany, Missouri Botanical Garden, P. O. Box 299, St. Louis, MO 63110. - A discussion of the subgeneric classification of Anthurium. A discussion is presented of the sectional classification of both Schott (1860) and Engler (1905) and new findings are presented which modify these classical systems. Schott (1860) divided Anthurium into 28 sections. Engler (1905) adopted much of Schott's system intact but greatly modified it. Recent studies generally prove that the system by Schott was more natural. An illustrated review of the classification system as currently accepted is presented and a number of new subgeneric groupings are proposed. Specifically, a split is proposed for sect. Xiaiophyllum and sect. Urospathix and Porphyrochitonium as presented by Engler are greatly modified. In addition new sections are proposed for existing members of sect. Beljionchium and major modifications are proposed for sect. Schizopachium and sect. Semaephyllum.

CROW, GARRETT E. Department of Botany and Plant Pathology, University of New Hampshire, Durham NH 03824.- New England's rare, threatened, and endangered vascular plants.

New England's flora, although recent in development (post-glacial), is rich and diverse. The native vascular plant flora is estimated to number 2570 taxa and of those indigenous to our region, 479 taxa (18.6% of the flora) are viewed as rare, threatened, or endangered. Pedicularis furbishiae, Potentilla robbinsiana, and Isotria medeoloides have been officially listed as "Endangered" under the Endangered Species Act of 1973, and 24 are currently under consideration by the U. S. Fish and Wildlife Service for listing. Additionally, 74 taxa are of "national significance," including many taxa whose occurrence within the United States is extremely limited, but may, for instance, be more frequent in arctic regions of North America. Several critical species are discussed, including distribution, phytogeographical affinities, threats, and measures for protection and recovery.

DAVIS, JERROLD I. Department of Botany KB-15, University of Washington, Seattle, WA 98195.  
- Genetic assimilation of phenotypic plasticity in Puccinellia (Poaceae).

Experimental study of phenotypic plasticity in Puccinellia suggests that genetic assimilation of differences in phenotypically plastic characters has been an important process in evolutionary diversification in this group. Divided clones representing several taxa were cultured in a series of salt- and drought-stress treatments representing naturally encountered environmental conditions. For each of 41 characters, genetic variation (among clones) and environmentally induced variation (among treatments; phenotypic plasticity) were calculated by analysis of variance. These two sources of variation are positively correlated; genetic variation is greatest in the most plastic characters (e.g., width of leaf blade, length of inflorescence). While plastic characters exhibit high levels of genetic variation among taxa, they are taxonomically weak because plasticity obscures the genetic differences. The most reliable taxonomic characters are non-plastic ones with moderate rather than high levels of interspecific variation. It is possible that differences among taxa in some of these characters result from chance fixation events, rather than from natural selection.

DAVIS, JERROLD I. Department of Botany, KB-15, University of Washington, Seattle, WA 98195.  
- Revision of the Puccinellia nuttalliana complex (Poaceae).

A systematic revision of the Puccinellia nuttalliana complex is presented. Plants of this group are endemic to saline and alkaline habitats, and exhibit a strong plastic response to the drought- and salt-stress conditions under which they grow. Character plasticity obscures genetically determined relationships, thereby contributing to taxonomic difficulties in the group. Multivariate analysis based on characters determined experimentally to be relatively non-plastic clarifies the delineation of taxa. Important characters include number and angle of divergence of inflorescence branches, indument of pedicels, shape of glume apices, and length and margin of lemmas. Patterns of anatomical variation of foliar surfaces support the evolutionary relationships deduced from morphological characters.

Further support for these relationships is derived from chromosome numbers, breeding systems, and habitat preferences of the taxa.

DONOGHUE, MICHAEL. Department of Botany, San Diego State University, San Diego, CA 92182-0058.

- Pollen diversity in the Caprifoliaceae sensu lato and the evolution of the exine in Viburnum.  
Studies with the scanning electron microscope reveal two very different kinds of pollen in the Caprifoliaceae s.l. The ten genera of the Caprifoliaceae sensu stricto have large, oblate to spheroidal, usually tectate grains, while Viburnum, Sambucus, and Adoxa have smaller, usually prolate grains, with an incomplete tectum. This distribution of pollen types is congruent with many other characters. There is reason to think that Viburnum, Sambucus, and Adoxa form a monophyletic group, and hence it is appropriate to consider the evolution of pollen within this clade. Since the exine in Sambucus and Adoxa is reticulate with psilate muri, this kind of pollen (Type A) is considered ancestral within Viburnum. Pollen with a reticulate exine but with scabrate muri (Type B) is considered to be derived from the ancestral condition. In turn, retipilate or pilate pollen with scabrate pilae (Type C) is thought to be derived from Type B pollen. On cladograms of Viburnum that most parsimoniously account for a wide variety of characters a single change is required from Type A to Type B pollen, and there are changes from Type B to Type C pollen in sections Lantana, Lentago and Pseudotinus. Small but consistent differences between Type C pollen in these three sections lend support to the hypothesis that this kind of pollen has arisen by convergence and cannot be considered a synapomorphy. This study provides an example of the relationship between cladistic analysis and the analysis of particular character transformations.

DORN, PAMELA S.\* and WILLIAM L. BLOOM. Dept. of Botany, University of Kansas, Lawrence, KS 66045.  
- Anthocyanin variation in an introgressive complex in Clarkia.

Clarkia nitens and C. speciosa ssp. polyantha are distinct species which differ chromosomally, morphologically, and physiologically. The most conspicuous difference is flower color; C. nitens has yellow stigmas and petal parts while those of C. s. ssp. polyantha are lavender or purple. Geographically intermediate between C. nitens and C. s. ssp. polyantha is a third taxon, C. s. ssp. polyantha-North, which is chromosomally very similar to C. nitens, but morphologically similar to C. s. ssp. polyantha. Previous studies indicate that C. s. ssp. polyantha-North arose by the introgression of C. s. ssp. polyantha genes into C. nitens. The only significant morphological difference between C. s. ssp. polyantha and the hybrid derivative is that C. s. ssp. polyantha-North flowers are darker purple. Available evidence suggests that this occurred as a result of character displacement. In addition to its increased intensity, the purple of C. s. ssp. polyantha-North is genetically more dominant to the yellow of C. nitens than is the purple of C. s. ssp. polyantha. Analysis of anthocyanins shows that the  $\beta$ -glucosides and 3,5-diglucosides of malvidin, cyanidin, and delphinidin are present in each taxon, although variation is observed in both total anthocyanin content and relative proportions of individual compounds.

## 112 Systematic Section

The increased purple intensity of *C. s. ssp. polyantha*-North is due to greater concentrations of cyanidin and delphinidin glucosides than are present in *C. s. ssp. polyantha*. Continuing hybridization and biochemical studies should elucidate the genetic control of the increased purple intensity of *C. s. ssp. polyantha*-North and its increased genetic dominance.

DOYLE, JEFF J.\* ROGER N. BEACHY and WALTER H. LEWIS. Department of Biology, Washington University, St. Louis, MO 63130. - Ribosomal genes of *Claytonia* (Portulacaceae)--molecular cloning.

The ribosomal gene (rDNA) tandem repeating units of various cytotypes from the two eastern North American species of *Claytonia* were initially compared by restriction endonuclease mapping using isolated total nuclear DNA. The variation observed in this type of experiment appears due to gain or loss of recognition sequences (usually six base pairs in length) required for cleavage by the restriction endonucleases, and is for the most part localized in the nontranscribed spacer separating the 18S and 25S ribosomal genes. In order to study this variable region in more detail, molecular cloning of *Claytonia* rDNA was undertaken. Genomic libraries were prepared using the cloning vector pHC 79, which is capable of incorporating over 30 kilobases of foreign DNA. Libraries were screened using the rDNA repeat from soybean, and those colonies containing *Claytonia* rDNA sequences were isolated and subcloned for more efficient handling into the bacterial plasmid pUC 12. Restriction mapping of rDNA clones indicates that some restriction endonuclease sites in the genomic DNA, though present, are not accessible to enzymes (perhaps due to some modification), and suggests caution in analysis of genomic digestion patterns. Hybridization probes prepared from *Claytonia* rDNA clones appear to be of great utility in elucidating patterns of variation within the eastern North American *Claytonia* complex.

DOYLE, JEFF J.\* BETH F. LADIN and ROGER N. BEACHY. Department of Biology, Washington University, St. Louis, MO 63130. - Seed storage protein variation and evolution in Leguminosae tribe Phaseoleae.

Glycosylated seed storage proteins with similar physical and chemical properties occur throughout the Leguminosae. Because these proteins appear to evolve at a rapid rate they may be useful indicators of evolutionary relatedness at various taxonomic levels. We have screened seed protein extracts of over 60 legume genera for reactivity to antisera prepared against the glycosylated seed storage protein of *Glycine max*. Screening involved SDS-polyacrylamide gel electrophoresis of immunoprecipitated proteins, which allows the determination of the molecular weights of homologous subunits, as well as the more sensitive enzyme-linked immunosorbent assay (ELISA). Sampling emphasized the tribe Phaseoleae, from which all eight subtribes were examined. Greatest homology occurs, as expected, within the subtribe Glycinineae, where similar subunit patterns occur in many genera. A characteristic feature of this subtribe is the occurrence of high molecular weight (above 70,000 daltons) polypeptides. Other subtribes of the Phaseoleae show varying degrees of relatedness to the test antisera; of note is the strong homology shown by the taxonomically difficult *Erythrina*. Weaker homology is found beyond the Phaseoleae in the Tephrosieae, Desmodieae, Robinieae and Sesbanieae. The imperfect correlation between taxonomic position and antigenic homology is likely due to the lability of the genes encoding the

proteins; a comparison of these genes suggests that duplications of gene regions, coupled with divergent selection pressures on different domains of the proteins and their genes could produce the observed network of protein relationships.

DUGLE, JANET R., Environmental Research, Whiteshell Nuclear Research Establishment, Pinawa, MB, ROE 1L0.

-What is "key" about key characters?

Taxonomic characteristics and classification systems have been described as natural or artificial, and it is generally believed that key characters should be as natural as possible. Many factors influence the development and usefulness of key characters for identification and classification of plant material. One of these, the environmental plasticity of a character, (the phenotypic change occurring as a result of a change in environment) is very important. Some new insights into the effect of the environment on plants can be gained by a study of plants which have grown under long-term low dose rates of gamma radiation in the Field Irradiator - Gamma area of mixed boreal forest in eastern Manitoba. Among the key characters that are influenced by environmental factors (in this case, gamma radiation) are leaf margin, number of leaflets, phyllotaxy, branching, length to width ratios, color of petals, number of flowers, size of fruits, and phenology of the plant. Some species exhibit more plasticity of morphological expression than do others. A few examples of species exhibiting varying characters are *Lonicera dioica*, *Fragaria virginiana*, *Populus tremuloides*, *Fraxinus nigra*, *Betula papyrifera*, *Ulmus americana*, *Aralia nudicaulis*, *Galium septentrionale* and *Epilobium angustifolium*.

ECKENWALDER, JAMES E.\* & SPENCER C.H. BARRETT.

Department of Botany, University of Toronto, Toronto, Ont., Canada M5S 1A1 - Phylogenetic systematics of Pontederiaceae.

We sought to explain the geographical distribution of the Pontederiaceae and the distribution of such features as breeding systems and chromosome numbers in this small, aquatic monocotyledonous family, using phylogenetic reconstructions. Six different methods of cladogram construction were applied to a data set embracing all 34 extant species and subspecies of the family. Trees resulting from the various procedures were compared using several optimality criteria, including a new measure called effectiveness. When treated as phylograms, a Wagner tree using all characters and presupposing a liliaceous ancestor was most effective (32.4%), and far more effective than a UPGMA-derived tree (1.0%). When treated as phenograms, and evaluated using the cophenetic correlation coefficient ( $r_{cs}$ ), the UPGMA tree was clearly superior ( $r_{cs}=0.856$ ) to the best Wagner tree ( $r_{cs}=0.624$ ). Despite numerous differences of detail, a reasonable consensus of many trees can be constructed. The most parsimonious interpretation of breeding system distribution in Pontederiaceae treats heterostyly as a synapomorphy of only one lineage of the family. Mirroring repeated transitions to homostyly in this heterostylous lineage, more than two thirds of the character state changes of the trees are homoplasious. While chromosome numbers display little homoplasy, geographical distributions are confusing. A vicariance explanation of the biogeography of the family, based on a Gondwanan distribution, seems less parsimonious.

monious than an origin in South America, followed by repeated eastward dispersals. The cladograms raise questions about the present classification of the family, but their resolution is awkward.

ELISENS, WAYNE J. Department of Botany, Miami University, Oxford, OH 45056. - Systematic approaches to generic delimitation in *Maurandya* s. lat. (Scrophulariaceae-Antirrhineae).

A reexamination of previous taxonomic treatments of *Maurandya* s. lat. has been undertaken using new information from comparative macromorphology, chromosome number, pollen morphology, seed coat morphology and anatomy, reproductive biology, crossability/fertility relationships, and geographic distribution. Evaluation of these data in a tribal context and the finding of six new species have been particularly useful in delimiting supra-specific boundaries and assigning rank. All the species are homoploid and share the chromosome base number  $x=12$  which is unique in the tribe. The basic categories of pollen morphology (2 types), seed coat morphology (5 types), seed coat anatomy (2 types), and sexual organ timing/place-ment (2 types) correlate well with macromorphological characters. Artificial hybridization studies indicate wide interspecific cross-compatibilities with the vast majority of viable hybrids of intra-generic origin. These data and subsequent cladistic analyses suggest that the *Maurandynae* is a monophyletic, new world group of 20 species in 4 genera sufficiently distinct from other tribal genera to warrant subtribal rank. Correlation of cladistic branching pattern and geographic distribution suggest that the subtribe originated in xeric habitats of the southwestern United States and northwestern Mexico; taxa have subsequently migrated/radiated along the Sierra Madre Occidental to more mesic habitats of southern Mexico and Guatemala.

EYDE, RICHARD H. Department of Botany, Smithsonian Institution, Washington, DC 20560. -- Classifying the Cornaceae, problems and progress.

From reviewing what is known of *Cornus* and its allies true and false, I infer that *Cornus* has evolved in two main lines, one surviving as 30 or so closely linked species with blue (or white) fruits, the other as a more diverse group of 20 or so red-fruited species. Traits that go with fruit color to make the major split include bracted vs. bractless inflorescence, size and shape of pollen, serological reactions, and iridoid vs. non-iridoid glucosides. The red-fruited species fall into three subgroups: dwarf cornels, showy-bracted and disciflorous dogwoods, cornelian cherries. Fruits of the third subgroup are not always red, but all, including those of "*Afrocrania*," have distinctive cavities within the fruit-stone. Blue-fruited species with small inflorescence bracts are nearer than any red-fruited ones to the ancestors of *Cornus*. Other authors have said otherwise, but much of their evidence can be explained away. Though *Cornus* links most securely with *Nyssa* and *Davidia*, *Mastixia*, with its *Cornus*-like trichomes, may have diverged from *Cornus* later on. Evidence linking *Cornus* to *Mastixia* is not as strong as I would like, but it is stronger than that linking *Cornus* to any other genus of the Pflanzenreich Cornaceae.

FADEN, ROBERT B. Department of Botany, Smithsonian Institution, Washington, D.C. 20560. - Floral dimorphism, pollen dimorphism and floral biology in a West African Commelinaceae, *Palisota hirsuta* (Thunb.) K. Schum.

*Palisota hirsuta*, a large shrubby Commelinaceae to 4 m tall, is common in West Africa. In Ghana and in cultivation plants flower once a year, between December and June. The strongly-scented flowers, which are produced in large thyrses, are all similar superficially, but on closer inspection they are found to be either perfect or staminate. The dimorphism between the two flower types is in the degree of development of the gynoecium and in the position, size and anther sac dehiscence of one of the stamens. Within all flowers two of the three polliniferous stamens produce copious amounts of "feeding pollen." Only one stamen -- the dimorphic one -- produces pollen that is capable of effecting fertilization. The pollen grains from the two types of stamens within each flower are dimorphic. Although the plants are self-compatible, outcrossing is enhanced by the flower structure and by the spatial and temporal distribution of the different flower types on the plant.

FAIRBROTHERS, DAVID E. Department of Biological Sciences-Botany Unit, Rutgers University, Piscataway, NJ 08854. Serological Investigation of the Annoniflorae (Magnoliiflorae).

Serological data obtained from seed meal extracts used in double diffusion and line immunoelectrophoresis experiments were analyzed by mean absorption similarity coefficients. Sixteen taxa belonging to the Annonaceae, Illiciaceae, Lauraceae, Magnoliaceae, and Schisandraceae were used in the analyses. Using unweighted pair group method analysis (UPGMA) dendrograms of serological similarity were generated. Line immunoelectrophoresis allowed direct comparisons of similarities and differences among various antigen samples in a single gel by positioning the appropriate samples next to each other. The analysis showed *Illicium* and *Schisandra* to have 92% serological similarity. The members of the Lauraceae revealed three serological groups. The descending order of serological similarity is as follows: Magnoliales → Illiciales → Annonales → Laurales. Both the Annonales and Laurales have approximately equal similarity with the Magnoliales.

FROHLICH MICHAEL W. Department of Biological Sciences, Union College, Schenectady, NY 12308. -

The common-is-primitive rule: how common is common?

Character state polarity is sometimes evaluated by the common-is-primitive rule, but the reliability of this method has been debated. Donoghue and Madison (AIBS, 1982) opposed its use in outgroup analysis. They show that the most parsimonious character state assignment to the branch leading from outgroup to ingroup (or, equivalently, to the root of a tree) is extremely sensitive to exact tree topology; even a rare character state may be primitive. They recommend determining enough of the topology to evaluate the rooting character state directly. While desirable, this is often impractical or impossible. In the absence of other information, can any use be made of character frequency data? One may consider

## 114 Systematic Section

all topologically distinct trees and calculate what percent of them root in each of the possibly primitive states. I consider strictly dichotomous trees with unlabeled interior nodes and  $n = a + b$  labeled termini representing  $n$  taxa,  $a$  of the common state and  $b$  of the rare state. The percents of trees rooting in the common, rare or equivocal states are % A, % B and % AB respectively. Calculations are made by explicit formulae (for  $b = 1, 2$  and  $3$ ) or by a computer algorithm. The % A, % B, and % AB depend strongly on the ratio of  $b$  to  $n$  but only weakly on  $n$ . As  $b/n$  decreases % B declines rapidly (% B < 5% for  $b/n = .30, n \leq 30$ ), % AB declines slowly and % A increases almost linearly. Low percent outcomes may often be disregarded in subsequent cladistic analysis without seriously increasing the overall chance of error. This approach may be useful 1) in preliminary studies, 2) in dealing with unresolved multichotomies within larger trees and 3) in evaluating the effects of remote outgroups in the outgroup substitution method (Donoghue and Cantino, Ms).

FRYXELL, PAUL A. U.S.D.A., Texas A&M University, College Station, TX 77843. - Floral symmetry and zygomorphy in the Malvaceae.

Flowers of the Malvaceae are typically actinomorphic, with radial symmetry. The petals are individually more or less asymmetrical, giving the corolla a "pinwheel" appearance. The five imbricate petals may overlap in a left-handed or right-handed manner (i.e. clockwise or counterclockwise). Studies have shown that in most species, flowers of an individual plant are about 50% of each type, that is the direction of aestivation is random. In a few species, however, the direction of aestivation is evidently non-random, although the significance of this phenomenon is not clear. In typically actinomorphic malvaceous flowers, other flower parts (calyx, androecium, gynoecium) are asymmetrical--with the exception of the genus Abelmoschus in which the calyx splits laterally to an asymmetrical form; the flowers of Abelmoschus are otherwise radially symmetrical. A small number of species of Malvaceae, however, have developed a more or less zygomorphic (i.e. bilaterally symmetrical) form. This development of zygomorphy is correlated with floral presentation and is presumably also correlated with pollinating animals, although observations on pollinators are scarce. In these cases, all flower parts (sometimes with the exception of the calyx) show bilateral symmetry, i.e. the flowers as a whole are zygomorphic. Three distinct patterns of zygomorphy have been observed. Two of these have evidently occurred only once each (in Hibiscadelphus spp. and in Periptera sp. nov.), whereas the third has evidently occurred repeatedly in several different genera (e.g. Pavonia, Hibiscus, Kosteletzkya). As might be expected, zygomorphy tends to occur in species with relatively showy flowers.

FURLOW, JOHN J. Department of Botany, Ohio State University, Columbus, Ohio 43210. - Evolutionary divergence and classification of the Alnus viridis complex (Betulaceae).

Alnus viridis (s. lat.) consists of a series of geographic races of mostly circumpolar distribution. During the past century, these have been treated variously as subspecies of one or more species and as separate species (A. viridis, A. crispa, A. sinuata, A. fruticosa, and A. maximowiczii). The taxonomy of the group remains a source of disagreement today,

though there has been a trend in recent years to view the complex as consisting of a single species. To determine the degree of morphological divergence and phenetic relationships among the components of the group, univariate and multivariate statistical procedures, including analyses of variance, tests of homogeneity, cluster analyses, and discriminant analyses, were applied to 120 characters of 38 OTU's representing geographical segments of all the taxa involved. With the exception of A. maximowiczii, the races were found to possess strong affinities among themselves equivalent to those existing among segments of other species of the genus, this supporting the treatment of the group as one widespread species. Populations of the "green alder" of Alaska, British Columbia, Washington, and adjacent regions, which for many years have been treated as identical with A. viridis subsp. crispa (A. crispa) of boreal northeastern North America, are shown by the analyses to be divergent from subsp. crispa and instead closely allied with A. viridis subsp. fruticosa (A. fruticosa) of Siberia, suggesting their original introduction into the continent from Asia across the Bearing Strait. Subsp. crispa, on the other hand, shares strong similarities with A. viridis subsp. viridis of Europe, pointing to an eastern introduction of that group.

FURLOW, JOHN J. Department of Botany, Ohio State University, Columbus, Ohio 43210. - The phylogenetic relationships of the genera and infra-generic taxa of the Betulaceae.

The Betulaceae are an ancient and diverse family distributed throughout the Northern Hemisphere. Their six genera have been combined and divided in recent taxonomic treatments to form a wide variety of groupings of separate families, tribes, genera, and infra-generic taxa. Often, this work has paid only cursory attention to critical but relatively unfamiliar groups, including species of several genera in eastern and southern Asia, and few attempts have been made to reconstruct its phylogeny on the basis of comprehensive data. In this study, 21 subgroups of the family have been analyzed using morphological characters and numerical cladistic methodology to obtain an estimate of their evolutionary relationships. The family is initially divided into two major evolutionary lines (tribes Betulae and Coryleae), and each of these includes sublines corresponding to the commonly recognized genera, all of which appear as monophyletic assemblages. Betula and Alnus are each comprised of several groups recognizable as subgenera, these being mostly broadly correlated with latitudinal climatic zones. In addition, many of the genera contain ultimate groups of species correlated with geographical regions and recognizable at the sectional level. The most complex relationships occur within the genus Alnus, the most diverse group of the family and the most unsettled at the infrageneric level. Here the subgenera are perhaps more equivalent to some of the genera of the Coryleae. Within Alnus, the problematical group containing A. maritima of eastern North America and A. nepalensis and A. nitida of Asia is shown to represent a distinct phylogenetic line equivalent to the other subgenera.

GABEL, MARK L. Division of Science and Mathematics, Black Hills State College, Spearfish, SD 57783. - A biosystematic study of the genus Imperata (Gramineae: Andropogoneae).

A revision of the weedy grass genus Imperata is proposed. The present study presents the results of

field and herbarium studies, supplemented by chromosome numbers, leaf anatomy, and starch gel electrophoresis. Morphological measurements were analyzed using principal component analysis and cluster analysis. Nine species are recognized including: *I. cylindrica*, *I. condensata*, *I. minutiflora*, *I. brasiliensis*, *I. cheesemanii*, *I. tenuis*, *I. conferta*, *I. contracta*, and *I. brevifolia*.

GIANNASI, DAVID E.\*, G. T. PRANCE and L. CORADIN. Department of Botany, University of Georgia, Athens, GA 30602, The New York Botanical Garden, Bronx, NY 10458, and Secção do Botanica, Centro Nacional de Recursos Genéticos, CENARGEN-EMBRAPA, Ave. W5 Norte (Parque Rural), Caixa Postal 102372, 70000-Basiléia-DF, Brazil. - Flavonoids in Parinari (Chrysobalanaceae).

A survey of flavonoids in 31 Asian, African and Neotropical species of *Parinari* showed a predominance of flavonol glycosides based on myricetin, quercetin and kaempferol. The African taxa split into two groups based on the presence or absence of myricetin glycosides. The Neotropical taxa, a complex of closely related ecologically differentiated species are chemically very similar and with few exceptions lack myricetin as does one group of African species. The Asian taxa are similar to the Neotropical ones in their flavonoid patterns and general lack of myricetin glycosides. The presence of myricetin, considered a primitive flavonoid character, suggests that the African species producing these flavonoids represent a primitive nucleus from which a non-myricetin group may have evolved giving rise by subsequent eastward and westward expansion to two myricetin-lacking phytogeographic lines. This hypothesis is in agreement with current proposals for geographic evolution in the Chrysobalanaceae in general.

GIANNASI, DAVID E.\*, G. MORTON and R. BUTA. Department of Botany, University of Georgia, Athens, GA 30602, Department of Environmental Sciences, University of Tennessee, Chattanooga, TN 37403, and Department of Biological Sciences, Rutgers University, Newark, NJ 07102. - Chemical documentation of the hybrid origin of *Solidago X asperula*.

A flavonoid study of *Solidago X asperula* in New Jersey was undertaken to determine if the previously described hybrid origin of this taxon could also be documented chemically. The hybrid swarm studied grows in a disturbed residential area along the Toms River. Small numbers of both parents, *S. rugosa* and *S. sempervirens* are found in the area along with a larger number of putative hybrids. *Solidago rugosa* is unique in its possession of two flavonol and two apigenin-C-glycosides while *S. sempervirens* is distinct in its possession of a diosmetin-7-O-diglycoside. The hybrids show various degrees of morphological intermediacy and some backcrossing to the parents. Likewise, hybrid flavonoid profiles are mostly additive confirming their hybrid origin. In addition, many of the hybrids produce two "novel" flavonoids (luteolin 7-O-mono- and diglycoside) not found in either parent. Their occurrence in the hybrids may be due to genetic disruption resulting in the expression of previously unsequenced intermediates (normally leading to diosmetin) not observed in the parents. Isolated stands of both parents from other areas do not exhibit these hybrid compounds,

except for one population of *S. sempervirens* from nearby Sandy Hook, suggesting that it may be a relic-tual population of *S. sempervirens* which has experienced previous hybridization and introgression. The chemical data support Goodwin's earlier studies documenting the hybrid origin of *S. X asperula*.

GIANNASI, DAVID E.\* and KARL J. NIKLAS. Department of Botany, University of Georgia, Athens, GA 30605, and Section of Plant Biology, Cornell University, Ithaca, NY 14853, - Paleobiochemistry of the Juglandaceae.

Leaf compression fossils of a *Juglans* sp., from the Clarkia Flora (Idaho, 22-16 x 10<sup>6</sup> KA years) were examined chemically and provide excellent 2D-PC flavonoid and hydrocarbon profiles. The fossil *Juglans* sp. is characterized by three flavonol 3-O-glycosides, which are found collectively only in extant North American taxa (*J. nigra* and *J. major*). One of the fossil flavonoid markers occurs sporadically in one or two New World species of *Oreomunna*, *Carya*, and *Juglans*, but are absent in Asian representatives of the latter two taxa despite suggested strong floristic relationships between the eastern United States and southern and eastern China. The fossil flavonoid markers occur in two species of *Engelhardia* (endemic to southern China and southeast Asia). Based on steroid and other hydrocarbon constituents, the Juglandaceae may be separated into two groups: *Alfaroa*, *Oreomunna*; *Engelhardia*, and *Juglans* and *Carya*. Although the morphology and flavonoid chemistry of the fossils suggest a more immediate relationship to extant North American taxa, the occurrence of the three "marker" compounds in *Engelhardia* may represent only a biosynthetic parallel at the generic level.

GILMARTIN, AMY JEAN \* and KAREN SIMMONS. Department of Botany, Washington State University, Pullman, WA 99164-4230. - Phylogenetic analysis in Umbelliferae: I. putative sister groups to *Lomatium*.

*Umbelliferae* includes about 275 genera, of which *Lomatium* is the largest western North American genus. In order to polarize characters for a cladistic analysis of *Lomatium* species, we sought to identify sister taxa from among 11 genera putatively close to *Lomatium*. Using *Pastinaca* as an outgroup to the 11 genera, up to 15 characters could be polarized. Trees and networks were generated manually and with computer programs. *Prionosciadium*, *Cymopterus* and *Peucedanum* were identified as likely sister taxa. These and other combinations of genera were used to polarize characters for a study of the 73 species of *Lomatium* in part II.

GILMARTIN, AMY JEAN and KAREN SIMMONS \*. Department of Botany, Washington State University, Pullman, WA 99164-4230. - Phylogenetic analysis in Umbelliferae: II. species of *Lomatium*.

*Lomatium* includes about 73 species unique to western North America. The genus has traditionally been a difficult group because of the large number of species and the high degree of vegetative uniformity among them. Consequently, no sections or infrageneric groups have been formally recognized and no phylogeny of the entire group has been proposed.

## 116 Systematic Section

Our goal was to use Hennigian cladistic methods to determine monophyletic groups of Lomatium species, as well as the relationships among groups. Sister taxa to Lomatium identified in the generic analysis were used to polarize characters pertinent to Lomatium. Phylogenies were constructed and putatively monophyletic groups of species were identified. These support, in part, an earlier phenetic study that identified a group of 12-16 species having one oil tube in the intervals of mature fruits and two on the commissure.

GOULD, JOYCE\* and JOSEF SVOBODA. Department of Biology, Erindale College, University of Toronto, Mississauga, Ontario. L5L 1G6.

-Vegetation and Floristics of the Lake Hazen area, Northern Ellesmere Island.

The Lake Hazen area is situated on northern Ellesmere Island in the Canadian Arctic Archipelago at 81°49'N, 71°18'W. The vegetation and flora of the area is diverse compared to other areas on Ellesmere Island. Vegetation of the lowland consists of a number of plant communities distinct from those of the higher elevations due to differences, in part, of moisture and substrate. The flora is rich with approximately 115 species recorded (Savile, 1964) compared to 49 species for the western Queen Elizabeth Islands (Savile, 1961). Several additional species were recorded in 1982 including Draba glabella Pursh and Sagina intermedia Fenzl. These collections represent extensions of the northern part of the range of both species. This work was supported by N.S.E.R.C. and the Ministry of Colleges and Universities (Ontario) and the University of Toronto.

HALL, DAVID W. 209 Rolfs Hall, University of Florida, Gainesville, FL 32611.

- Florida grass habitats.

Grasses comprise a significant portion of the vegetation of Florida and make up about one-seventh of the species of flowering plants in the state. They occupy diverse habitats and predominate as the natural ground cover over large areas. Tolerance or lack of tolerance to moisture and soil type and to competition from other plant species influence the presence of certain grasses in different vegetational communities. Wet coastal marshes, inland prairies (savannas), swamps, and flood plains support grasses tolerant of high levels of moisture; on the other hand, the sandy flatwoods dominated by pine and saw palmetto, and the pine-turkey oak ridges, support the growth of drought resistant forms. Grasses introduced or favored by man--pastures, roadsides, lawns and golf course turf--must be considered in any comprehensive discussion of the habitats of Florida grasses as a whole.

HARTMAN, RONALD L. Department of Botany, University of Wyoming, Laramie, WY 82071. - Two novelties in the Umbelliferae from the central Rocky Mountains.

Recent studies on Rocky Mountain umbels have led to the recognition of two undescribed species. The first, from the Lost River and Lemhi ranges of central Idaho, was initially collected by Ray Davis in 1940 and confused with the more southern Cymopterus nivalis. The second novelty, secured first by Frank Tweedy in 1900 in a post-fruiting

stage, has been confused with Oreoxis alpina from the Southern Rockies. Only recently was it rediscovered and flowering and fruiting material obtained. It is now known to be relatively frequent in the southern half of the Big Horn Mountains of Wyoming. Both taxa are restricted to calcareous or dolomitic substrates and have a chromosome number of  $n = 11$ . They are tufted, acaulescent herbs with yellow flowers. The fruits, which are terete in cross section, have prominent dorsal and intermediate ribs whereas the lateral nerves are winged. Affinities appear to be with Cymopterus which has been characterized, in part, by well-developed wings on all the nerves. A recent survey of the fruits of Cymopterus sensu lato indicates that the surface wings have been lost in at least four separate lines. Consequently, the inclusion of these new species within Cymopterus would not modify drastically the generic circumscription.

HAUBER, DONALD P.\* and R. C. JACKSON. Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409. - Evidence for autopolyploidy in Helianthus ciliaris DC.

Helianthus ciliaris is a widespread perennial weed found throughout the Southwest and parts of Mexico. Recently, it has been revealed that H. ciliaris is a complex composed of two ploidy levels, a tetraploid ( $n = 34$ ) and a hexaploid ( $n = 51$ ). Meiotic samples were collected from both tetraploid and hexaploid populations and analyzed quantitatively as to the frequency of the different configuration types at diakinesis. In the case of the tetraploids all individuals from all populations sampled demonstrated chromosome pairing behavior as expected according to the autotetraploid model. However, the status of the hexaploid is unknown at this time. Evolutionary implications concerning the tetraploid will be discussed.

HAUSER, LARRY A. Department of Botany, University of Illinois, Urbana, IL 61801 - Phylogenetic relationships and phenetic similarities among species of Thelypodopsis and Thelypodium (Brassicaceae).

The 36 species currently classified in either Thelypodopsis or Thelypodium were studied with regard to interspecific relationships and generic delimitation. The boundary between the two genera, like many other closely related Brassicaceae genera, is indistinct and somewhat arbitrary. Thirty-five primarily morphological and anatomical characters were evaluated for each of the species examined. Phylogenetic (Wagner) trees were constructed with Stanleya, Warea, and Romanschulzia considered probable outgroups. In addition, phenetic similarities were studied using cluster analysis and PCA with a directed nearest neighbor network. Results indicate that Thelypodopsis does not represent a distinct monophyletic group and must be either subdivided or possibly combined with other genera such as Thelypodium and Caulanthus. The "Hesperidanthus" species, for example, represent a distinguishable group, but their recognition at the generic level would necessitate further subdivision of Thelypodopsis. Within Thelypodium, as currently delimited, three subgenera, as described by Al-Shehbaz, were recognized. The implications of the recent removal of Rollinsia paysonii from Thelypodium for several other species were also considered.

HELLQUIST, C. BARRE. Department of Biology, North Adams State College, North Adams, MA 01247. - Observations on Potamogeton hillii in North America.

Potamogeton hillii has been considered as either a rare or endangered species in all states and provinces where it occurs and is currently under review by the United States Fish and Wildlife Service for possible listing under the Endangered Species Act of 1973. Prior to 1960 it was collected at 22 localities. Since 1970, 57 new areas have been located. This species is almost exclusively found in regions of limestone bedrock throughout its range. Presently it is most abundant in western New England and northern Michigan. During 1982 it was relocated in Connecticut and Ohio. Potamogeton hillii appears to be spreading its range in the limestone regions where it presently occurs. It is usually found in clear, cold water of small streams, farm ponds, and beaver ponds which have muddy bottoms. Contrary to the literature, winter buds are extremely common, being formed late in the season. The abundant winter buds and fruit produced help guarantee the continued spread of this species. More localities should be looked for near existing and previous sites as long as they are within the limestone region. Potamogeton hillii should not be considered for protection nationally and should be omitted from consideration in the states where locally abundant.

HELLQUIST, C. BARRE\* and ROBERT L. HILTON  
Department of Biology, North Adams State College, North Adams, MA 01247. Environmental Science Program, University of Massachusetts/Boston, Boston, MA 02125. - The taxonomic status of Potamogeton lateralis (Potamogetonaceae) from North America.

Potamogeton lateralis, one of the rarer pondweeds in North America is a dimorphic species that bears flowers on plants with emerged leaves and fruit on separate plants that produce submersed leaves only. This pondweed is similar to P. vaseyi which produces flower and fruit on plants with floating leaves. Two populations of P. lateralis have been studied in New England. In both cases P. lateralis did not occur in the same location during two consecutive years. Instead, during the second year, typical P. vaseyi was present. Chemotaxonomic studies involving flavonoids of P. lateralis, both fertile and sterile, P. vaseyi, and fertile P. pusillus var. tenuissimus have shown that P. lateralis as previously described is actually a composite of the former two species. Most of the type specimens observed contained only sterile plants with floating leaves. Fertile material on the type sheets proved to be P. pusillus var. tenuissimus. Therefore, the taxon was described from two elements, P. vaseyi and P. pusillus var. tenuissimus. The P. vaseyi element appears to form a juvenile stage which takes on the characteristics of P. lateralis as described in the literature, but this stage is a transient stage which persists for short periods of time.

HILLS, MATTHEW H.\*, TERRY W. LUCANSKY, AND WILLIAM LOUIS STERN. Department of Botany, University of Florida, Gainesville, FL 32611. - Comparative anatomy and systematics of woody Saxifragaceae: Cuttsia viburnea F. v. Muell.

The purpose of this work is to provide vegetative anatomical and morphological data, especially wood anatomy, for the monotypic genus Cuttsia, and to use

these data to determine the taxonomic position of Cuttsia within the Saxifragaceae sensu lato. Cuttsia viburnea F. v. Muell. is a shrub or small tree endemic to southeast Queensland and northeast New South Wales, Australia. It possesses simple, ovate, serrate leaves in an alternate phyllotaxy. The nodal pattern is trilacunar, three-trace, with the three traces fusing in the petiole to form one large, medullated, concentric petiolar strand. The midvein also is a concentric bundle in the basal half of the lamina and becomes a collateral bundle toward the apex of the leaf. The adaxial epidermis is biseriate, and the abaxial epidermis is uniseriate. Stomata occur only on the abaxial epidermis, and the stomatal apparatus is anomocytic. Mesophyll consists of biseriate palisade and spongy layers. The wood lacks growth rings and possesses numerous, mostly solitary, circular to oval pores. Perforation plates are scalariform with numerous bars per plate. Intervascular pitting is opposite to alternate. Thick-walled tracheids, occasionally with spiral thickenings, are present. Diffuse apotracheal parenchyma is common but not abundant. Vascular rays are uniseriate, homocellular and multiseriate, heterocellular. Ray tissue is abundant. Cuttsia viburnea possesses most of the characteristics of the archetypal woody saxifrage, and the distinctive petiolar vasculature is similar to that in Forgesia borbonica Commers., a Mascarene Islands endemic.

HOLLOWELL, VICTORIA C.\* and THOMAS R. SODERSTROM. Department of Biology, University of South Carolina, Columbia, S.C. 29208, and Department of Botany, Smithsonian Institution, Washington, D.C. 20560. - Re-examination of the genus Eremitis (Poaceae: Bambusoideae).

The neotropical genus Eremitis was erected in 1877 by Doell to encompass the single herbaceous bambusoid species E. monothalamia. Tutin in 1936 merged Eremitis into the related, more extensive genus Pariana; but Calderón and Soderstrom in 1980 reinstated the genus with the single species E. parviflora (=monothalamia). Re-evaluation of morphological, anatomical and field data in combination with observations on numerous recent collections supports the view that Eremitis is distinct from Pariana. Three new species have been discovered in Brazilian coastal rain forests: E. glabra and E. robusta from Bahia and E. breviglumis from Espírito Santo. Cleistogamous subterranean inflorescences as well as multiple inflorescences on each aerial culm characterize this interesting assemblage. Striking dimorphism of the spikelet whorls within each inflorescence and reduction in stamen number from six or more to only two further distinguish the genus. Preliminary diploid chromosome numbers of 67 or 68 for E. breviglumis, 86 for E. robusta and 92 for E. parviflora are substantially greater than any yet reported in Pariana or other Bambusoideae. Re-definition of Eremitis to include E. parviflora and the newly recognized species is proposed.

HUCK, ROBIN B. Department of Botany, University of North Carolina, Chapel Hill, NC 27514 - Clarification of the generic limits of Dicerandra (Labiatae) by hybridization experiments.  
An understanding of the systematics of Dicerandra pivots on a resolution of the relationship between

the two most widely distributed, but morphologically distinct, species in the genus: *D. linearifolia* and *D. odoratissima*. The former species which is the type for the genus has exerted stamens and a geniculate corolla tube with the upper limb flaring to a standard; the latter, inserted stamens and a tubular corolla with the upper limb cucullate. Should *D. odoratissima* be retained within the genus? One author, as recently as 1982, has suggested that these two are reproductively isolated and that *D. odoratissima* could be raised to a generic level. Data from field and breeding studies accumulating since 1979 add new insights. Six hundred forty interspecific crosses were attempted on 110 plants collected from 16 populations throughout the species' range in the southeastern United States. Out of 2560 possible nutlets (4 per cross), 306 nutlets produced mature flowering plants. Flowers of interspecific  $F_1$  hybrids consistently showed characters intermediate to the parents. A count of 37,177 pollen grains of these  $F_1$ s indicate a viability of 84% overall. Pollen viability of  $F_1$ s of sympatric parental species rose to 92.5% as compared with 78.6% for  $F_1$ s of allopatric parentals. A count of 5029 grains of the  $F_2$  showed a viability of 75.0%. The subsequent discovery and analysis of a natural hybrid swarm coupled with the above data suggest a close genetic relationship with gene exchange occurring in sympatric areas between *D. linearifolia* and *D. odoratissima*. While a degree of reproductive isolation is acknowledged, the retention of *D. odoratissima* within *Dicerandra* is upheld.

JACKSON, R. C. Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-4149  
- Gametic selection as a possible isolating mechanism in chromosomal races of *Haplopappus gracilis*.

Controlled crosses have been made between the  $n = 2$  Dibivalens and the  $n = 3$  tribivalens races. Reciprocal  $F_1$  hybrids of the two chromosomal races have been used to produce  $F_2$  and backcross generations. Seeds from such crosses can be germinated easily, and standard methods can be employed to determine possible karyotypes with  $2n = 4, 5,$  and  $6$  chromosomes. Equal numbers of  $n = 2$  and  $n = 3$  sperms and eggs are produced from  $2n = 5$   $F_1$  hybrids because of preferential disjunction of a trivalent so that 2 small, acrocentric chromosomes always go to one pole with a nucleolar organizing chromosome, and the larger metacentric from the trivalent goes to the other pole with a N.O. chromosome. Data obtained thus far show that when equal numbers of  $n = 2$  and  $n = 3$  pollen grains are applied to  $2n = 4$  stigmas the  $n = 4$  pollen grains are more successful. Conversely, when an equal mixture of  $n = 2$  and  $n = 3$  pollen grains are brushed on a  $2n = 6$  stigma, the  $n = 3$  pollen grains are more successful. If these same mixtures are applied to  $2n = 5$  hybrid stigmas, equal numbers of the two chromosomal types of pollen are involved in fertilization. The differential gametic success of fertilizing the eggs from homokaryotypes with the same karyotype appears to be a partial isolating barrier when the two races come into contact.

JACOBS, BRIAN F., CHARLES R. WERTH, AND SHELDON I. GUTTMAN\*. Department of Botany and Department of Zoology, Miami University, Oxford, Ohio 45056.  
- Genetic relationships in *Abies* (fir) of eastern U.S.: an electrophoretic study.  
*Abies* (fir) is widely considered to consist of two species in the eastern U.S., *A. balsamea* (L.) Mill.

and *A. fraseri* (Pursh.) Poir., distinguished by relative cone bract to subtending cone scale lengths and number of leaf hypodermal cells. Intermediate individuals have been recognized as *A. balsamea* var. *phanerolepis* Fern. An understanding of the relationship between the two presumptive species over the last 18,000 years hinges on the interpretation of the intermediate. Two alternative hypotheses view the intermediate as either an interspecific hybrid or an intraspecific variant. Twenty gene loci were electrophoretically analyzed in population samples from all three taxa in an attempt to resolve the systematic relationships of *Abies* from the eastern U.S. Cluster analysis failed to group populations into the three recognized taxa. All populations and taxa shared similar complements of alleles at comparable frequencies for 13 polymorphic loci. Genetic distances among populations ranged from 0.103 to 0.0. These data support a conspecific status for all of eastern U.S. *Abies* and suggest intermediate fir is not of hybrid origin. Our results are consistent with those of recent studies which conclude that *A. fraseri* and *A. balsamea* are only recently (18,000 years) diverged taxa.

JANSEN, ROBERT K.\* and NEIL A. HARRIMAN. Department of Botany, Ohio State University, Columbus, OH 43210 and Department of Biology, University of Wisconsin-Oshkosh, Oshkosh, WI 54901. - Numerical taxonomic studies of the *Juncus biflorus*-*J. marginatus* species pair.

The *Juncus biflorus*-*J. marginatus* complex comprises a morphologically variable species pair common throughout the eastern United States and occurring as far south as Argentina. Historically these two taxa have been treated as distinct species. A number of morphological features, especially culm diameter, number of leaves per stem, number of veins per leaf and width of leaves, inflorescence height, number of glomerules per inflorescence, number of flowers per glomerule, anther persistence, and seed characteristics have been used to separate them. Overlap in these features, however, has caused difficulty in recognizing these taxa throughout their ranges. To aid in understanding the patterns of morphological variation and to resolve the taxonomic limits of these two taxa, a detailed numerical taxonomic study of *J. biflorus* and *J. marginatus* was initiated. Fourteen characters were measured for several hundred populations, and the data were subjected to clustering, principal components, and discriminant analyses. The results support the merger of the two taxa into a single variable species.

JENSEN, RICHARD J. Department of Biology, Saint Mary's College, Notre Dame, IN 46556. - Cladistics of eastern North American red oaks: testing Trelease's hypothesis.

In his classic monograph of the American oaks (Mem. Nat. Acad. Sci. 20: 1-255), William Trelease presented a scheme of phylogenetic relationships among the taxa he recognized. Although he doubted the accuracy of the entire scheme, Trelease was confident of the relationships depicted for the better studied

groups. Among the latter were the taxa of red and black oaks of eastern North America. Trelease's scheme was based on "fundamental characters," though he did not specify which, and on the assumption that his serial groups (e.g., Coccineae) reflected natural groups. I have been examining patterns of character state distribution among these oaks and have come to the conclusions that (1) some of Trelease's serial groups are not definable by the characters I have employed and (2) his scheme of phylogeny is incongruent with either a maximum parsimony or maximal clique analysis. Specifically, series Coccineae, Laurifoliae, and Marilandicae appear to be polyphyletic or paraphyletic assemblages. While much additional work needs to be done, the results presented suggest either that these taxa are not a monophyletic group or that there is a vast amount of homoplastic evolution in the characters analyzed.

JOHNSON, MILES F. Department of Biology,  
Virginia Commonwealth University, Richmond, VA  
23284 - SEM Palynology of *Ageratum* L.

*Ageratum* L. (Eupatorieae -- Asteraceae) consists of approximately 43 species which occur in Mexico, Central America and South America. *Ageratum conyzoides* is a pantropic weed. Johnson, in 1971, and King and Robinson, in 1972, have studied the taxonomy of the genus but the ultrastructure of the pollen has not been investigated. Pollen of more than half of the taxa was examined by SEM. The pollen is tricolporate, echinate and commonly spherical, but spherical and prolate grains in a single specimen of *A. corymbosum* are noted. The colpus is usually deeply incised and often outlined by the exine which may be granular, warty, rugose or bear irregular patches. The echinae are usually porous; some bear longitudinal ridges. Though the pollen is basically uniform, there are surface variations which tend to support the taxonomy of the recent investigators.

KEIL, DAVID J. Department of Biological Sciences,  
California Polytechnic State University, San Luis  
Obispo, CA 93407. - Biogeography of *Pectis* (Asteraceae) in the West Indies.

Caribbean basin biogeography of *Pectis* reflects a history of dispersal, differentiation and polyploidy. Approximately twenty species of *Pectis* occur in the West Indies and peninsular Florida. Most occupy more than one island (often several) that are separated by deep-water barriers. Five of the taxa represent wide ranging species with large mainland distributions in Mexico, Central America or South America. The remainder are endemic to the West Indies or have marginal distributions in mainland areas. All *Pectis* taxa in the West Indies appear to be self-compatible. The achenes are very small and bear a well-developed pappus. Eight of the thirteen taxa for which chromosome counts have been determined are polyploids with the  $4x$ ,  $6x$  and  $8x$  levels represented. In contrast only seven of 51 mainland taxa counted to date are polyploid, and two of these are also represented at the diploid level.

KEIL, DAVID J. Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, CA 93407 - Chance convergence and the identity of *Pectis linearifolia* (Asteraceae).

The *Pectis linearifolia* "complex" of peninsular Florida comprises two morphologically similar endemic "taxa". *Pectis linearifolia* Urban is an apparently sexual tetraploid species ( $2n = 4x = 48$ ) from mid-peninsular regions. Foliar glands in this species contain lemon-scented oils. In south peninsular Florida morphologically very similar sterile triploids ( $3n = 36$ ) occur together with *P. prostrata* Cav. ( $2n = 24$ ) and *P. leptoccephala* (Cass.) Urban ( $2n = 48$ ), both of which are apparently sexual species. Both *P. leptoccephala* and the triploids have "spicy-scented" oils; *P. prostrata* is not scented. The triploids and *P. prostrata* both form an achene complex in which the phyllaries and all the enclosed achenes fall together as a unit at maturity. This feature is lacking in *P. leptoccephala* and *P. linearifolia* (s.s.). The triploids are apparently F-1 hybrids between *P. prostrata* and *P. leptoccephala* that by chance closely resemble *P. linearifolia*. Despite their considerable morphological similarity, *P. linearifolia* and the triploids have apparently originated independently and are taxonomically distinct.

KOLTERMAN, DUANE A.\* and ROBERT R. KOWAL. Department of Botany, University of Wisconsin, Madison, WI 53706. - The origin of hexaploid *Senecio pseud aureus* var. *semicordatus* (Asteraceae, Senecioneae): the bearing of flavonoid chemistry and morphological data.

*Senecio pseud aureus* Rydb. var. *semicordatus* (Mack. & Bush) T. M. Barkley is found in the central United States and adjacent Canada, from Manitoba through the Dakotas, Minn., Wis., Iowa and Nebr. to Kan. and Mo. Chromosome counts indicate that the taxon is composed of two races, a diploid ( $n=23$ ) in the north and an approximate hexaploid ( $n=ca. 69$ ) in the south. Flavonoid data, obtained from greenhouse-grown plants, show that hexaploids from Mo. (3 populations) are chemically very similar to northern diploids (9 populations from N. and S. Dak., Minn., Wis., and Iowa) and, therefore, are probably autohexaploids. A Kansas population of hexaploids assignable to var. *semicordatus*, on the other hand, appears to represent a hybrid swarm, with much contamination from an adjacent population of *S. plattensis* Nutt., a widespread tetraploid species ( $n=46$ ) of the Great Plains with scattered occurrences eastward. The Kansas hexaploids are chemically both variable and intermediate between var. *semicordatus* (diploid and hexaploid) and *S. plattensis*. The flavonoid data are supported by both field observations and morphological data from plants grown in transplant gardens in Madison, Wis.: the Missouri hexaploids are similar to northern diploid var. *semicordatus*, while the Kansas hexaploids are intermediate between these and *S. plattensis*. Autopolyploidy and hybridization are common in the *S. aureus* complex; flavonoid chemical and morphological data clearly indicate that *S. pseud aureus* var. *semicordatus*, as well, shares both propensities with its allies.

KOWAL, ROBERT R. and DUANE A. KOLTERMAN.\*  
Department of Botany, University of Wisconsin,  
Madison, WI 53706. A measure of dissimilarity  
for multivariate binary (presence/absence) data  
with examples of its use on biochemical data  
from *Cnidoscopus* (Euphorbiaceae) and *Senecio*  
(Asteraceae).

As a measure of dissimilarity between two groups, A and B, we use the average number of compounds by which they differ,  $\bar{n}_{AB}$ , an extension of a simple count of the number of compounds by which two individuals differ to two groups of individuals. For all possible pairs of individuals, one from each group, one can count the number of compounds by which the two individuals differ. The measure is the average of all such counts and can be calculated with the equation

$$\bar{n}_{AB} = \sum_{i=1}^p (a_i + b_i - 2a_i b_i)$$

where p is the total number of compounds observed and  $a_i$  and  $b_i$  are the frequencies of compound i in groups A and B, respectively. The average number of compounds by which a group differs from itself,  $\bar{n}_{AA}$ , also provides a measure of variability within groups which can be used directly to evaluate the relative sizes of differences between groups; it equals twice the sum of the variances of the presences and absences of each compound. The measure is used on flavonoid data from *Cnidoscopus* (Euphorbiaceae) and *Senecio* (Asteraceae); metric multidimensional scaling provides a two- or three-dimensional representation of the distance matrix. Two more familiar measures of dissimilarity--squared Euclidean distance and Manhattan distance--give similar representations of relationships among groups. We prefer  $\bar{n}_{AB}$  because it is intuitively reasonable and provides a measure of error variability.

LAMMERS, THOMAS G.\*; ROGER W. SANDERS, DANIEL J. CRAWFORD, H.-D. BEHNKE, TOD F. STUESSY, and MARIO SILVA O. Department of Botany, Ohio State University, Columbus, OH 43210; Fairchild Tropical Garden, Miami, FL 33156; Zellenlehre, Universität Heidelberg, West Germany; and Departamento de Botánica, Universidad de Concepción, Chile. - Cytology, flavonoid chemistry, ultrastructure, and systematic relationships of Lactoridaceae.

The angiosperm flora of the Juan Fernandez Islands contains one endemic family, the Lactoridaceae, with a single species, *Lactoris fernandeziana*. The family is in serious danger of extinction. Only 5 individuals in 3 populations were encountered during 2 expeditions in 1980 to the largest island, Masatierra. Study material was collected from portions of these individuals. Five leaf flavonoids have been identified: three kaempferol 3-O-glycosides and two isorhamnetin 3-O-glycosides. The chromosome number is  $n=20$ . TEM observations of sieve elements reveal S-type plastids. The morphological relationships of the Lactoridaceae place it clearly within the Magnoliidae, the most primitive subclass of dicotyledons. Its restriction to Masatierra, which geologically is only 4 million years old, suggests that the family originated elsewhere and previously had a much wider distribution. Extinction has apparently eliminated all populations except those now endemic to the Juan Fernandez Islands.

LANDON, JAMES\*, MARGARET R. BOLICK and MICHAEL R. VOORHIES. Divisions of Botany and Vertebrate Paleontology, University of Nebraska State Museum, Lincoln, NE 68588-0514. - Medial Miocene paleoecology of Nebraska.

A new method of paleoecological analysis, based on Carlquist's work on the ecology of xylem structure (Carlquist, 1977), is applied to fossil wood from the medial Miocene (12 to 14 million years old) of Nebraska. The fossil wood samples are from several localities in the Valentine Formation with most of the samples coming from the Crookston Bridge Member, a unit rich in vertebrate fossils. The values for Carlquist's vulnerability index of the fossil wood are similar to those of the modern woody flora of Nebraska. The climatic indications from the fossil wood agree with MacGinitie's (1962) conclusions from the Kilgore leaf and pollen flora (also from the Crookston Bridge Member in northern Nebraska) that the climate then was warm temperate to subtropical and relatively dry, bordering on subhumid. Most fossil vertebrate assemblages from the lower Valentine Formation are dominated by grazing ungulates but also contain a larger number (16) of browsing genera than any higher stratigraphic levels. This gives an unusually detailed picture of the mid-Miocene upland pine-oak savanna and floodplain forests that preceded the grasslands in central North America.

LEE, GREGORY J. Department of Botany, University of California, Davis, California 95616. - A bio-systematic study of *Phacelia marcescens*, *Phacelia stebbinsii* and *Phacelia quickii* (Hydrophyllaceae). *Phacelia marcescens* Eastw. ex Macbr., *P. stebbinsii* Const. and Heckard, and *P. quickii* J. T. Howell form a group of three closely related species. Previous treatments have emphasized the similarity of *P. marcescens* and *P. quickii*. *P. stebbinsii* was first described in 1970, at which time it was likened to *P. quickii*. A systematic investigation of the three taxa has revealed that *P. stebbinsii* is more closely related to *P. marcescens* as judged by a number of morphologic characters: calyx size and shape, pollen color, leaf morphology, fruit shape, and method of seed dispersal. Additionally, *P. quickii* does not hybridize with either *P. marcescens* or *P. stebbinsii*, whereas *P. marcescens* and *P. stebbinsii* hybridize if *P. marcescens* is the carpellate parent. The  $F_1$  and  $F_2$  progeny are fully fertile. At present, *P. marcescens* and *P. stebbinsii* are known to differ only in flower color and in the number of seeds produced per fruit. Their distinctness is maintained by the following isolating mechanisms: (1) geographic isolation, (2) unilateral crossability, and (3) an intraspecific advantage of *P. marcescens* pollen. An examination of the taxonomic characters which distinguish these three species indicates that several are part of an adaptive complex related to seed dispersal and seedling establishment. The relationship of calyx size to fruit weight in these three species, and in related species groups, indicates that the sepals are important photosynthetic organs.

LEE, GREGORY J. Department of Botany, University of California, Davis, California 95616. - The systematic and ecological significance of calyces in the *Phacelia humilis* group (Hydrophyllaceae). The *Phacelia humilis* group (Hydrophyllaceae) is an assemblage of approximately thirty annual taxa. The

calyces of these plants provide useful taxonomic characters. Of particular significance are the size and shape of the calyces, the variation between sepals within a calyx, and the amount of accrescence. A survey of the species complexes within the P. humilis group shows that for closely related taxa a larger calyx is correlated with a larger fruit. This correlation was investigated and found to be statistically significant at the species level, at the population level within a species, for individuals within a population, and for fruits from individual plants. Experimentally, it was determined that the relationship is not due to allometry, indicating that it has functional significance. The hypothesis that the sepals are important photosynthetic organs was tested by growing plants without leaves. These plants flowered and produced viable seed solely on stem and sepal photosynthate. Sepal size variation within a calyx, pedicel length, and compactness of the inflorescence represent an adaptive syndrome which decreases the self-shading of photosynthesizing floral parts.

LEMKE, DAVID E. Department of Botany, University of Texas, Austin, Texas, 78712. - Lignified trichomes as taxonomic characters.

Trichomes have long been recognized as being of importance in comparative systematic investigations. One type which has received scant attention, however, is the lignified trichome. These can be easily identified by their staining reaction in Azure B and may prove to be of diagnostic value because of their restricted occurrence among flowering plants. A survey of the literature reveals that they are known only from the Hernandiaceae, Cistaceae, Flacourtiaceae, Turneraceae, Symplocaceae, Simaroubaceae, Lamiaceae, and Dipsacaceae. The presence of unicellular lignified hairs on the young stems, leaves, and calyces of Neopringlea (long considered to be of uncertain affinities) provides additional evidence for placing this genus in the Flacourtiaceae.

LEMKE, DAVID E. Department of Botany, University of Texas, Austin, Texas, 78712.- Tribal redefinitions in Flacourtiaceae.

The Flacourtiaceae is a large tropical family which, because of its polythetic nature, has developed a reputation as a taxon in which to place many genera of uncertain affinities. The most recent treatment of the family is that of Hutchinson, but while his classification is in many respects an improvement on those of earlier workers, it still contains a number of disparate elements. In the present study the tribes Scolopieae, Homalieae and Prockieae are redefined on the basis of morphological and anatomical data and become much more homogeneous elements. Hutchinson's tribe Banareae is here dismantled; the genera Banara and Pineda are placed in the Prockieae, Trimeria in the Homalieae, and the anomalous genus Asteropeia transferred to the Theales.

LERSTEN, NELS R. Department of Botany, Iowa State University, Ames, Iowa 50011. -Taxonomic and evolutionary significance of embryo suspensor distribution in Leguminosae.

Embryo suspensors in the Leguminosae have long been known to exhibit a range of size and shape that

approximates the variation found in angiosperms as a whole. Until now, no attempt has been made to seek any coherent patterns among legume suspensor diversity. I have collated about 200 published descriptions according to the most recent classification scheme for the family. Taxa represented include Mimosoideae (12 genera, 21 species), Caesalpinioideae (7 genera, 9 species), and Papilionoideae (about 65 genera, 150 species). The first two subfamilies are mostly suspensorless whereas suspensors usually occur in the latter. They are mostly inconspicuous in the putatively primitive and intermediately placed tribes, as well as in some advanced tribes. Other advanced tribes have conspicuous suspensors of diverse form which are of taxonomic significance, for example, in Loteae/Coronilleae, Crotalariaeae, and Genisteae. A unique 4-celled, multinucleate suspensor occurs uniformly among Viciae but nowhere else. Large and/or bizarre suspensors are clearly a derived feature in Leguminosae; suspensor variation supports the evolutionary trends in the family postulated on other evidence. Such comparative knowledge also helps to place into perspective the results of recent intensive studies on the Phaseolus suspensor.

LES, DONALD H. Department of Botany, The Ohio State University, Columbus, Ohio 43210. - Taxonomic implications of aneuploidy and polyploidy in Potamogeton (Potamogetonaceae).

A synoptic study of chromosome number reports for 73 species of Potamogeton presents evidence supporting the conclusion that the genus is characterized by two different polyploid lineages (one based upon  $x=7$  and the other upon  $x=13$ ). Analyzed comparatively, chromosome numbers also indicate that the diploid level of the genus is  $2n=14$ , and that the  $x=13$  lineage arose by aneuploidy from a  $2n=14$  progenitor. Comparisons developed by juxtaposition of chromosome numbers with morphological characters and classification ranks indicate that subsections Pusilli, Oxyphylli, and Amplifolii may not represent entirely natural assemblages. The past use of chromosome numbers to demonstrate the primitiveness of floating leaves in the genus is challenged due to lack of correlation of these features when a larger number of species is considered. Chromosome numbers were found to correlate geographically with the hypothetically proposed birthplace of the genus.

LEVIN, GEOFFREY A. Department of Biology, Ripon College, Ripon, WI 54971. - Phenetic and cladistic analysis of the foliar morphology of Phyllanthoideae (Euphorbiaceae).

Systematists frequently regard leaf morphology as being of little taxonomic use, particularly at higher taxonomic levels, despite the recent advances made by paleobotanists in the classification of fossil leaves. In order to test the value of foliar characters in an extant group, a study of the Phyllanthoideae, the most primitive subfamily of the Euphorbiaceae, was undertaken. Leaves of 275 species representing 52 of the 58 genera were described using 26 characters derived from Hickey's architectural terminology and 17 cuticular characters. Phenetic relationships between OTUs representing subgenera or undivided genera were initially analyzed using similarity graph clustering. Results using all OTUs were difficult to interpret, apparently due to extensive convergence between members of the subtribe Phyllanthineae and other OTUs. Most of the Phyllanthineae exhibit a specialized branching pattern in which

determinate lateral branches resemble compound leaves. Analysis using the 68 OTUs that lack this branching pattern produced clusters similar to those in classifications based on characters more widely recognized as being of systematic value. In a few cases, excessive convergence did cloud relationships, probably because of the use of overall similarity as the basis for classification. The results of a cladistic analysis, in which the polarity of character states was determined using other subfamilies of the Euphorbiaceae and primitive genera in the Flacourtiaceae as sister groups, even more closely resembled previous classifications. Obtaining such clear results using a group not known for having diagnostic leaves argues against the widely held idea that foliar morphology is of little systematic value.

LOWREY, TIMOTHY K., and DANIEL J. CRAWFORD.\*  
Department of Botany, University of Witwatersrand, Johannesburg, South Africa, and Department of Botany, The Ohio State University, Columbus, OH 43210.--Allozyme divergence and evolution in Tetramolopium (Compositae: Astereae) of the Hawaiian Islands.

Tetramolopium is a wholly insular genus of shrubby or suffrutescent perennial Compositae with a limited disjunct distribution in the Hawaiian Islands and New Guinea. In Hawaiian Tetramolopium there has been the evolution of distinctive morphological features. The taxa are, however, completely interfertile with fertile F<sub>1</sub>, F<sub>2</sub>, and F<sub>3</sub> hybrids being obtained, but no natural hybrids are known. Biogeographical evidence suggests that introduction of Tetramolopium into Hawaii may have resulted from a single recent introduction, indicating that morphological divergence and adaptive radiation occurred rapidly. Electrophoretic studies of allozyme variability support this hypothesis because there has been little divergence at gene loci coding for soluble enzymes. The mean genetic identity for pairwise comparisons of 19 populations from seven species is 0.95. This is comparable to values normally obtained for conspecific populations as contrasted with a mean genetic identity of 0.67 for populations of congeneric species. The situation in Tetramolopium also contrasts sharply with other instances of high genetic identity between species where the taxa are very similar morphologically, yet reproductively isolated. Only a few genes may be responsible for the morphological and ecological differences between species of Hawaiian Tetramolopium.

LUCKOW, MELISSA A. Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407. - A morphometric and cytological study of Pectis longipes (Compositae). Pectis longipes is an herbaceous perennial occurring in southern Arizona, eastern New Mexico, and northern Mexico. Chromosome counts of n=12 and n=24 have been reported for the species. Field work also revealed that plants have one of two scents, designated as either "lemon" or "spicy". Chromosome counts from thirty populations show that the tetraploids are lemon-scented while the diploids are spicy-scented. A morphometric study using ordination and discriminant analysis was undertaken to determine if the races could be distinguished morphologically. Nineteen variables including vegetative, floral, and pollen characteristics were measured for twenty

individuals from each of six populations (three diploid, three tetraploid). Discriminant analysis performed best, correctly assigning 92% of the individuals. Of the incorrectly assigned individuals, all but one was assigned to another population of the same ploidy level. Canonical vectors separate populations by ploidy level primarily on the basis of pollen size.

MAGRATH, LAWRENCE K. Discipline of Biology, Department of Math/Science, University of Science and Arts of Oklahoma, Chickasha, OK 73018. - Orchidaceae native to Oklahoma: distribution and ecology.

The family Orchidaceae is represented in Oklahoma by 17 genera and 30 specific and subspecific taxa. The taxa represented are: Aplectrum hyemale, Calopogon tuberosus var. tuberosus and var. simpsonii (?), Coralorrhiza odontorrhiza, C. wisteriana, Cypripedium calceolus var. pubescens, Epipactis gigantea, Goodyera pubescens, Habenaria repens, Hexaletris spicata, Isotria verticillata, Liparis lillifolia, Listera australis, Malaxis unifolia, Pogonia ophio-glossoides, Platanthera ciliaris, P. clavellata, P. flava var. flava, P. lacera var. lacera, P. leucophaea, Spiranthes cernua (?), S. lacera, S. magnicamporum, S. odorata, S. ovalis, S. praecox, S. tuberosa, S. vernalis, Tipularia discolor; Triphora trianthophora. The largest number of taxa are concentrated in the SE corner of the state, with secondary concentrations in the NE and S central parts of the state. McCurtain county in the extreme SE corner has the largest number with 21 taxa, followed by Choctaw with 19, LeFlore with 16, Pushmataha with 14, Bryan with 11, Cherokee with 9, Delaware and Adair with 8, Ottawa, Haskell and Caddo with 7. Orchids have been reported from 50 of the 77 counties in the state. The only part of the state in which they have not been reported at the present time is the panhandle. Orchids occur in five major types of habitat, in Oklahoma: 1) prairie and grassland (6 taxa), 2) woodland (15 taxa), 3) open sphagnum bogs (5 taxa), 4) sphagnum bogs in wooded areas (4 taxa), and 5) open stream banks over limestone in the Arbuckle Mts. (1 taxon).

MAZE, JACK. Department of Botany, University of British Columbia, Vancouver, B. C. V6T 2B1, Canada. - A study of the factors affecting morphological differentiation in a population of Pinus ponderosa.

Trees are amongst the most variable of organisms, the result, it would seem, of fusion between gametes from genetically different individuals. Genetically different individuals may result from selection, either past or present, causing population differentiation over small geographic areas or selecting for different individuals in different climatic regimes that prevail during different years. However, selection is not necessary to explain genetically different individuals. The evolutionary theory of Wiley and Brooks predicts an increase in variation as a consequence of natural laws pertaining to increasing disorder. The effect of habitat differences, age, size of trees and past climate as evidenced by tree ring site summaries on the pattern of variation was estimated by calculating the percentage of variation in principal components analysis axis scores for which each factor accounts. In all comparisons made, the greatest percentage

of variation (73-94%) was unaccounted for by any of the factors tested. While it may be argued that relevant selective factors were missed, it should be pointed out that such arguments can lead to the unacceptable stance of explaining away unpopular results by asserting that the important elements were not measured. A large percentage of variation that is apparently unaccounted for by selection is a prediction that would follow from the theory of Wiley and Brooks.

McCALL, CLAIRE\* and RICHARD B. PRIMACK, Biology Department, Boston University, Boston, MA 02215.

- Does pollination level affect fruit set in the field?

An unresolved question of plant reproductive biology is the relative importance of pollinator activity, resource limitation, and ovule abortion in regulating the final production of seeds. An experimental field study was undertaken to determine if inadequate pollination limited fruit set in 5 species of perennial forest herb. The experiments consisted of comparing the seed production of approximately 40 plants which were cross-pollinated by hand with 40 control plants. All plants were exposed to normal insect visits and grown in their natural environment. In Uvularia sessilifolia, Geranium maculatum, and Maianthemum canadensis, there was no difference in the fruit set of experimental and control plants. In Smilacina racemosa, fruit set was increased slightly (27% vs 20%). In Lysimachia quadrifolia, fruit set was increased dramatically by hand-pollinations in one population (61% vs 28%), but not in a second population (36% vs 33%). Hand-pollinations were effective at increasing fruit set on some days, but not others. In species in which fruit set is limited by pollinator activity, we still need to know if increased fruit set results in a corresponding decrease in some other fitness components such as subsequent survival or fruit production in later years.

MCCORMICK, SUSAN P.\* AND FRED GANDERS, Department of Botany, University of British Columbia, Vancouver, BC V6T 1W5. - Leaf flavonoids of Hawaiian Bidens.

Leaf flavonoids were investigated for populations of nineteen Hawaiian Bidens species. Individual plants surveyed by two-dimensional TLC contained between ten and thirty flavonoid compounds. Individual compounds have been isolated and identified using co-chromatography, UV, proton NMR and mass spectrometry. The flavonoids are primarily anthoclor pigments including 4'-O-glycosides of butein, marein and lanceolin and 6-O-glycosides of sulphuretin, marmetin and leptosidin. Butein derivatives with methylation at the 3 or 4 position were present in some populations of B. torta. Kaempferol and quercetin monosides and biosides were present also in most populations.

MCDUGAL, KAREN. Department of Biology, University of North Carolina, Chapel Hill, NC 27514.

- Geographic variability in flavonoid profiles of red oak, *Quercus rubra* L.

Red oak, *Quercus rubra* L., is widely distributed throughout eastern North America. It is rich in flavonol glycosides, especially myricetin and quercetin pentosides. Two forms of red oak in the

southern Appalachians differ in their foliar flavonoid profiles and elevational distribution. Low elevation trees synthesize primarily quercetin glycosides; those at high elevations also produce myricetin glycosides. Trees with reduced levels of myricetin occur at mid elevations. Using HPLC we have obtained quantitative data on individuals from over the species range. These indicate that red oak chemotypes and the degree of population heterogeneity are correlated with latitude, longitude and elevation. Myricetin-rich individuals occur primarily along the Appalachian range and at high latitudes. High elevation populations from the Ouchita Mountains of western Arkansas also display this pattern. These high latitude-high elevation populations exhibit a high degree of inter-population homogeneity, although there is some quantitative intra-population variability. Quercetin-rich trees are found at low elevations on the eastern and southern range extremes. These populations are also very homogeneous chemically. West of the Appalachians, populations are highly heterogeneous and contain both myricetin and quercetin producing individuals. The myricetin chemotypes in this area are somewhat reduced in overall quantity, similar to trees at mid elevations on the eastern slopes. From central Alabama and Georgia to central Ohio and Indiana, within-population variability approaches that between populations, with the frequency of myricetins positively correlated with increasing latitude.

MCNEILL, JOHN\* and STEVEN J. WOLF. Department of Biology, University of Ottawa, Ottawa, K1N 6N5, Canada. - Cytotaxonomic studies on *Polygonum* Sect. *Polygonum* in eastern Canada.

Existing treatments of *Polygonum* Sect. *Polygonum* (including the *P. aviculare* complex) are extremely divergent in the number of species that they recognize and in the criteria that they use for species delimitation. The group is particularly well represented in Atlantic Canada, where the number of species maintained ranges from 8 in a review by Mertens and Raven (1965) to 21 in an account of chromosome numbers by Löve and Löve (1956). Chromosome counts from over 120 populations of the group in eastern Canada have revealed only tetraploid and hexaploid plants. It is postulated that the *P. aviculare* complex is represented, not only by introduced weedy plants referable to *P. aviculare* in the narrow sense (= *P. monspeliense*) (2n=60) and *P. arenastrum* (2n=40), but also by native tetraploid and hexaploid populations that are distinguishable but by different character combinations. These include not only *P. buxiforme* (2n=60) and *P. boreale* (2n=40) but also a number of undescribed variants. In addition to these members of the *P. aviculare* complex, five other species of the section can be distinguished in eastern Canada. Most of these more distinct species with shining nutlets appear to be native to North America, but the coastal *P. raii* (2n=40) is almost certainly introduced. Our data suggest that chromosome doubling in members of the section has occurred independently several times.

MILLER, JOHN M\*, CHARLES E. FELLOWS and KENTON L. CHAMBERS. Department of Biology, Sul Ross State University, Alpine TX 79832 and Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331 - Cytogeographic patterns and relationships of the *Claytonia sibirica* complex. Chromosome counts in dividing pollen mother cells from one hundred and forty populations of *Claytonia*

*sibirica* (s.l.) reveal a polyploid series based upon  $x=6$ . One rosette-forming diploid has rhomboid to deltoid mature basal leaves and occurs in the mountains of northern California, Oregon, Idaho, and British Columbia. This species grows in cool, moist habitats. A second diploid, sp. nov. prov., possesses linear mature basal and cauline leaves and vigorous rhizomes. Consistently mistaken for *C. sibirica* var. *heterophylla* (= *Montia heterophylla*), this taxon occurs near Mount Shasta southward at mid-elevations in palustrine habitats of the Sierra Nevada. In the Klamath Region diploids occur which are morphologically intermediate between deltoid-leaved rosette-forming diploids and linear-leaved, rhizomatous diploids. These plants proliferate new rosettes from bulbils and stolons. Bulbiliferous tetraploids with narrow basal leaves occur in the Klamath Region. Non-bulbiliferous, deltoid-leaved tetraploids are the most widespread cytological race indigenous to woodlands of *Alnus rubra* and *Pseudotsuga menziesii* except where replaced by hexaploid cytotypes on the northern California coast. Morphological variation and polyploidy in *C. sibirica* (s.l.) is parallel to other euploid complexes in *Claytonia* section *Limmia*, where unreduced gamete fusion coupled with limited natural hybridization among ancestral diploid species has led to higher chromosome levels. Inadequate knowledge of diploid taxa and the parallel variation exhibited by polyploid races has been the source of past taxonomic confusion in *C.* section *Limmia*.

HELL, DAVID. Missouri Botanical Garden, Washington University, P.O. Box 299, St. Louis, MO 63166. - Artificial hybridizations, leaf surface characters, and systematics of *Erythrina* (Leguminosae).

*Erythrina* (Leguminosae Papilionoideae) is a pantropical genus of about 110 species of trees, shrubs, and suffrutescent herbs. All but a few species are diploid, with  $n=21$ . A series of artificial interspecific hybridizations, including "wide crosses" across the geographic and taxonomic range of the genus, were synthesized in botanical gardens in Hawaii in 1961. These hybridizations, together with the chromosomal homogeneity of *Erythrina*, suggest that the genus as a whole may be considered a homoploid complex with no internal barriers to interspecific hybridization. *Erythrina* exhibits a range of unusual leaf trichome characters. SEM and anatomical studies of leaf surfaces of species and hybrids are presented and related to the systematics of the genus.

NICHOLS, DIANE M.\* and EDWARD L. SCHNEIDER, Underground Resource Management, Inc., Austin, TX 78703, and Department of Biology, Southwest Texas State University, San Marcos, TX 78666. - The floral biology of *Argemone aurantiaca* G.B. Ownbey (Papaveraceae).

The floral biology of a white prickly poppy, *Argemone aurantiaca*, has been investigated. Anthesis occurs over three consecutive days with flowers opening each morning (ca. 8:00 a.m. CDT) and closing in the late afternoon (ca. 5:00 p.m. CDT). Early morning first-day flowers are protogynous, but by late morning the numerous stamens begin to dehisce, releasing large quantities of pollen. By the end of the second day anthers have shriveled and the stigma has become non-

receptive. During the third day the white petals as well as the yellow stamens undergo abscission. In the populations studies, Hymenoptera (e.g. *Dialictus* and *Halictus*) and Coleoptera (e.g. *Euphoria* and *Lytta*) were the most abundant and effective pollinators. Observations have revealed that Hymenoptera are effective cross-pollinators while Coleoptera facilitate self-pollination (indirect autogamy), since the beetles commonly remain for long periods of time in the same first- or second-day flower. The beetles also can be found "entrapped" in flowers at night by the closure of the flower. It is suggested that the overall floral architecture (e.g. open-dish shape, large numbers of stamens, masses of pollen, etc.) as well as the floral behavior (open and closing mechanism) are adaptations which facilitate the pollination of *Argemone* by beetles. The presence of an ultraviolet reactive corolla is viewed as an adaptation to enhance cross-pollination by Hymenoptera.

NICKRENT, DANIEL L. Department of Botany, Miami University, Oxford, Ohio 45056. - Interpretation of allozymes of 6-PGD in triploid endosperm tissue of *Arceuthobium* (dwarf mistletoe-Viscaceae).

Dwarf mistletoes are obligate, dioecious parasites of members of the Pinaceae in the New World. These plants have been a source of taxonomic confusion owing to their reduced morphology, high degree of sympatry, and host relationships. Although others have experienced difficulty in resolving enzyme systems in dwarf mistletoe using horizontal starch gel electrophoresis, seeds of *A. vaginatum* ssp. *cryptopodum* give excellent banding at the 6-phosphogluconate dehydrogenase locus. Megasporogenesis in *Arceuthobium* conforms to the *Allium* type and the resultant endosperm is triploid. The gel banding patterns derived from the endosperm tissue confirms the triploid condition since all heterozygotes for this dimeric protein are asymmetrical. The dosage effect is exerted by the triple fusion phenomenon of endosperm cell nuclei production. The paternal chromosome contribution is one and the maternal contribution two. Genetic data derived from this type of analysis is being used to examine 1) the biosystematics of 22 taxa in the genus *Arceuthobium*, 2) population dynamics (e.g. conformation to Hardy-Weinberg equilibrium, and 3) the concept that niche width (here the number of hosts colonized) may be correlated with the degree of heterozygosity for a particular taxon.

PACHECO, PATRICIA, DANIEL J. CRAWFORD, MARIO SILVA O., and TOD F. STUESSY.\* Department of Botany, Ohio State University, Columbus, Ohio 43210, and Departamento de Botánica, Universidad de Concepción, Concepción, Chile. - Flavonoid evolution in *Robinsonia* (Compositae) of the Juan Fernandez Islands.

The flora of the Juan Fernandez Islands contains many endemic genera. The endemic *Robinsonia* of the Compositae with seven species is the second largest genus in the archipelago with six species on the largest and oldest island, Masatierra, and the seventh on the smaller, more remote, and younger island Masafuera. The total flavonoid complement among all these species is 13 compounds, including the aglycone quercetin, and the glycosides based on apigenin and luteolin (flavones), isorhamnetin and quercetin (flavonols), eriodictyol and naringenin (flavanones), and taxifolin (dihydroflavonol). The distribution of these compounds among species of

Robinsonia correlates with the previously established subgenera and sections. The most likely hypothesis for the evolution of flavonoids within the genus is that the ancestor had only flavonols. In sect. *Eleutherolepis* a gain of flavanones, dihydroflavonols, and flavones occurred. Within this section *R. masafuerae*, the only species of the genus on the geologically younger island, Masafuera, has apparently lost apigenin during its evolution within the last 1 million years.

PALMER, PATRICIA G. Department of Biology, Louisburg College, Louisburg, North Carolina 27549. - An SEM analysis of epidermal features of African grasses and its paleoecological applications.

Approximately 200 genera of tropical East and West African grasses are being analyzed with scanning electron microscopy to describe the epidermal features of the abaxial and adaxial leaf surfaces. A comparison of the major diagnostic features as viewed with light microscopy and SEM will be made to show advantages of SEM in many cases. SEM is particularly useful in identifying fossil grass leaves in African lake sediments. An analysis of the fossil grass cuticles in sediments from Lake Bosumtwi, Ghana, West Africa, shows an abundance of grass cuticles of the Poideae subfamily in the late Pleistocene layers. This indicates a paleotemperature several degrees cooler than the present day.

PARKER, WILLIAM H.\* and JACK MAZE. School of Forestry, Lakehead University, Thunder Bay, Ont. P7B 5E1 and Department of Botany, University of British Columbia, Vancouver, B.C. V6T 2B1 - Intraspecific variation in *Abies lasiocarpa* from British Columbia and Washington.

Sixteen natural stands of *Abies lasiocarpa* (Hook.) Nutt. were sampled from British Columbia and Washington to investigate patterns of intraspecific variation in this species. Principal components analysis and canonical variates analysis were performed separately on seed-cone data, needle morphology data, and needle flavonoid data. Although significant differences were detected between populations based on each of the three data sets, only variation in needle morphology followed a geographic pattern. With the exception of the Vancouver Island population, three geographic groups were discerned based on their needle morphology: 1) populations from the coastal mountains of British Columbia, 2) those from the eastern interior of British Columbia, and 3) those from the Cascade Mountains of Washington. Although the Vancouver Island population was grouped with the interior British Columbia populations based on needle morphology, it was similar to the other coastal populations based on flavonoid data. These inconsistent results among the three different types of taxonomic evidence suggest that the evolution of each of the three classes of characters has been partly independent from the other two and underscore the need to consider a variety of traits when drawing taxonomic conclusions in *Abies*. Our data offer little support for the recognition of infraspecific taxa within the study area, and are in contrast to Hunt and von Rudloff's results (Taxon 28:297-305) which led them to conclude, based primarily on terpenoid data, that coastal and interior populations of subalpine fir were two separate species.

PAVLICK, LEON E. Botany Division, British Columbia Provincial Museum, Victoria, B.C., Canada, V8V 1X4. - Studies on the *Festuca ovina* complex in the Canadian Cordillera. The *Festuca ovina* complex in the Canadian Cordillera was studied. Based on morphology and anatomy seven taxa are characterized and their taxonomy discussed. The proliferous material of the *ovina* complex in the Cordillera is different from *F. vivipara* (L.) Sm. and a new name, *F. krajinae*, is proposed. A new variety from western British Columbia, *F. saximontana* Rydb. var. *robertsiana*, is described. The other taxa treated are: *Festuca saximontana* Rydb. var. *saximontana*; *F. saximontana* var. *purpusiana* (St.-Yves) Frederiksen & Pavlick; *F. brachyphylla* Schult. & Schult.; *F. baffinensis* Polun.; and *F. minutiflora* Rydb., a species rarely collected in Canada. Distributions are given.

PERINO, CHARLES H.\* Illinois Department of Transportation, 2300 S. Dirksen Parkway, Springfield, IL 62764 and JAMES R. ESTES Department of Botany, University of Oklahoma, Norman, OK 73069. - Systematics of *Chaetopappa* series *Effusae* (Compositae).

A morphological examination of the *Chaetopappa* series *Effusae* (*C. effusa*, *C. keerlioides*, and *C. parryi*) was done. *Chaetopappa effusa* is recognized as a distinct genus on the basis of seven morphological characters: disk style branches, phyllaries, pappus, corolla trichomes, anther appendages, leaf structure, and chromosome number. The new genus, *Loshinnsia*, gen. n., has one species, *L. effusa* (Gray) Perino & Estes comb. nov., and it is restricted to the eastern edge of the Edwards Plateau of central Texas.

PHILLIPS, MARC N. and ROBERT R. KOWAL.\* Department of Botany, University of Wisconsin, Madison, WI 53706. - Systematics of *Saxifraga pensylvanica* and a putative segregate species, *S. forbesii* (Saxifragaceae).

George W. Burns in 1942 recognized the tetraploid (n=28) species, *Saxifraga forbesii* Vasey, occurring in the Midwest mostly on sandstone cliffs in unglaciated areas. It was split from *S. pensylvanica* L. of northeastern North America, within which Burns recognized three subspecies: tetraploid, hexaploid, and octoploid (n=28, 42, 56). To re-evaluate Burns' work, samples from seven populations from Missouri (1) and Wisconsin (6), possibly representing *S. forbesii* (based on habitat, range, and Burns' annotations of specimens), and twelve populations from Wisconsin, representing ordinary *S. pensylvanica*, were grown in a transplant garden. The resultant data on 30 morphological characters, petal color, flowering time, stomates and pollen were analyzed with appropriate statistical techniques including canonical analysis. Although abundant differences occurred among local populations, none existed

between *S. pensylvanica* and populations supposedly representing *S. forbesii*. Hybridizations showed no genetic isolation between the two. Chromosome counts from the garden were uniformly  $2n=ca. 8x$ , even though mostly tetraploids were expected based on Burns' annotations. A count from the type population of *S. forbesii* gave  $2n=ca. 10x$ , and one from *S. pensylvanica* from North Carolina, where Burns predicted tetraploids, gave  $2n=ca. 11-14x$ . Thus, no morphological or cytological evidence exists for recognizing *S. forbesii*, and the polyploid complex within *S. pensylvanica* is both more diverse and more morphologically cryptic than Burns had supposed.

PILATOWSKI, RONALD E. Department of Botany, The Ohio State University, Columbus, OH. 43210.  
- A phenetic analysis of Liatris Series Graminifoliae (Compositae; Eupatorieae).

*Liatris* Schreber is a large genus of perennial herbs of eastern North America. Series Graminifoliae consists of five species distributed along the Coastal Plain, Piedmont, and Mountain provinces of the American Southeast. A phenetic study using the NT-SYS package was done on this group, using a total of 46 characters on a total of 126 OTU's representing the five recognized species in the Series: *L. gracilis*, *L. graminifolia*, *L. helleri*, *L. regimontis*, and *L. turgida*. Results of this phenetic study indicate the following: (1) *L. helleri*, an Appalachian endemic which has been suggested to be an ecotype of *L. graminifolia*, was found to comprise a distinct group in the analysis; (2) The somewhat morphologically similar *L. turgida*, also an Appalachian endemic, was found to be distinctive; (3) Overlap between two species found on the Coastal Plain of North and South Carolina, *L. graminifolia* and *L. regimontis*, suggests hybridization, an observation made by other investigators of the genus; (4) Plants collected from the unique steephead habitats in the vicinity of the Apalachicola River in Liberty County, FL., which have traditionally been regarded as *L. gracilis*, segregate from the main body of this species in factor analysis; and (5) Two major groups can be distinguished in the analysis which correspond to flavonoid differences found in the Series.

POHL, RICHARD W. Department of Botany, Iowa State University, Ames, Iowa 50011. -Current blooming status of the bamboo flora of Costa Rica.

I have observed native and cultivated bamboo stands for 17 years. Species currently blooming are (native): *Chusquea longifolia*, *C. meyeriana*, *C. "talamancae"*, *Otatea acuminata*, *Rhipidoeladum bartlettii*, and *Swallenochloa subtessellata*; (cultivated): *Bambusa vulgaris*, *B. longispiculata*, *Phyllostachys aurea*: The following have been seen in bloom since 1965, but are currently only vegetative: *Aulonemia patriae*, *Arthrostylidium venezuelae*, *Bambusa paniculata*, *Chusquea "cariblanco"*, *C. coronalis*, *C. scabra*, *C. tonduzii*, *C. virgata*, *Elytostachys clavigera*, *Rhipidoeladum maxonii*, *R. pittieri*, *R. racemiflorum*, *Swallenochloa longiligulata*, *S. vulcanalis*. *Bambusa arundinacea*, a cultivated Asiatic species, was in widespread bloom in the 1970's, but is now vegetative. The following native species have never been observed in bloom: *Arthrostylidium harmonicum*, *A. pubescens*, *Chusquea "hispidissima"*, *Chusquea "tarrazu"*. Massive gregarious blooms of *Chusquea longifolia* occurred on Volcán Irazú and of *Rhipidoeladum bartlettii* near the Rio Pacuare.

POLLARD, A. JOSEPH. Department of Botany and Microbiology, Oklahoma State University, Stillwater, OK 74078.

- Biosystematic studies of gene flow and natural selection in *Urtica dioica* (stinging nettle).

An extreme variant of *Urtica dioica*, characterized by paucity of stinging hairs, tall unbranched growth form, long narrow leaves, and late flowering, occurs in large numbers at Wicken Fen, Cambridgeshire, England. Experimental cultivation of plants collected along a transect crossing the boundaries of the variant population has revealed that:

- (1) Significant gene flow into the population occurs by both seed and pollen transport.
- (2) Pollen flow also has significant effects within populations, acting to smooth out variation expressed in the adult generation.
- (3) Patterns of variability do not indicate that natural selection is acting to limit the range of variability contained in the seed population.
- (4) It would be erroneous to conclude from (3) that selection is not occurring, since, for a long-lived perennial like *U. dioica*, patterns of variability may be more related to historical factors than to current selectional regimes.

PRIDGEON, ALEC M.\* and WILLIAM LOUIS STERN. Department of Botany, University of Florida, Gainesville, FL 32611. - Osmophores in selected Orchidaceae: location and ultrastructure.

Osmophores are floral tissues specialized for synthesis and secretion of fragrances serving as pollinator attractants. Location of osmophores on flowers of Orchidaceae may or may not have an assignable role in the pollination process. In members of the fly-pollinated subtribes Pleurothallidinae and Bulbophyllinae, osmophores are positioned at sepal apices, petal apices, or both, and probably function only in attraction of pollinators over long distances. Osmophores of many euglossine-pollinated orchids, however, are usually situated on the adaxial surface of the labellum over or under the column, so that male bees come into contact with pollinia or the stigmatic surface. At the ultrastructural level in osmophores of the myophilous genus *Restrepia*, a strongly osmiophilic and lipidic exudate is synthesized in papillose epidermal cells of the dorsal sepal and petals. As the exudate is amassed, the cuticle ruptures to form numerous pores that extend from the cell wall. Mitochondria and amyloplasts are especially abundant at anthesis. Lipid droplets, perhaps counterparts of the terpenoid fragrances produced, also appear in the cytoplasm and vacuole of epidermal cells at anthesis. Data drawn from these and other lines of inquiry should assist in indicating relationships below the subtribal level in Orchidaceae because the evolutionary history of this family is, by and large, the history of adaptive change and refinement in floral morphology and fragrances.

RABELER, RICHARD K. Beal-Darlington Herbarium & Lyman Briggs School, Michigan State University, East Lansing, MI 48824-1312. - Petrorrhagia (Caryophyllaceae) of North America.

As an outgrowth of the discovery of *Petrorrhagia prolifera* (L.) P. Ball & Heyw. in Michigan, the genus *Petrorrhagia* (Ser. in DC.) Link, revised by Ball & Heywood in 1964, is applied to North American material. Four species, all introduced from Europe, are considered based on field study and an extensive herbarium survey. The history of introduction (where known), distribution, and current status of

each species will be presented. Petal vein color is described as an additional character that can be used in distinguishing the three species of the P. prolifera complex occurring in North America.

REYNOLDS, HOWARD C. Dept. of Biology,  
Ft. Hays State University, Hays, KS 67601  
- Botanizing Papua New Guinea

The author had the opportunity to study and photograph the flora and fauna of PNG as a member of the Pre-Congress Botanical Tour to that country in connection with the XIIth International Botanical Congress held in Sydney, Australia. The natural history highlights were observed between Aug. 8-19, 1981. The author had previously observed the natural history of PNG as a member of the Medical Dept. of the U.S. Army during WW II about 38 years prior to his second visit. Since part of the tour was made by motor vehicle, a good opportunity was afforded to observe the Nothofagus forest in the area around Mt. Hagen and the Castanopsis forest in the vicinity of Goroka, both in the highlands. Good examples of lowland rain forest were observed in the vicinity of Madang and Lae along the east coast. "Manmade" grasslands were especially extensive as observed in the Ramu and Markham river valleys with members of the Andropogoneae (Bluestem tribe) as dominants. Port Moresby with its pronounced dry season and Savannah type vegetation was in marked contrast to the tropical rain forest which makes up about 75% of the vegetation of PNG.

REZNICEK, ANTON A.\*, and PAUL M. CATLING, University of Michigan Herbarium, North University Bldg., Ann Arbor, Michigan 48109 and Biosystematics Research Institute, Agriculture Canada, Wm. Saunders Bldg., C.E.F., Ottawa, Ontario K1A 0C6.  
- The Identity of Carex caesariensis and C. subimpressa.

Carex caesariensis, known only from southern New Jersey and C. subimpressa occurring more widely in the middle west, are two puzzling species of Carex sect. Paludosae. Both have been suspected of being hybrids. Carex caesariensis has usually not been considered a good species. A hybrid parentage of C. trichocarpa and C. walteriana has been proposed. Because of a unique combination of characters, including elongate sterile culms, reddened sheath apices and long beak teeth, there is little doubt that C. trichocarpa is one parent. Although we were unable to rediscover C. caesariensis in the field, we propose that the other parent is actually C. lanuginosa. Statistical analysis using a number of characters supports this, as well as the ecological characteristics of the type locality. Carex subimpressa was originally described as a hybrid of C. hyalinolepis and C. lanuginosa. Subsequent authors often have been inclined to recognize it as a good species, presumably because of its wide range. Also, specimens referable to C. subimpressa have been collected beyond the range of C. hyalinolepis. However, morphological and anatomical characteristics support its hybrid origin, as do field studies of natural populations. Collections from beyond the range of C. hyalinolepis are shown to be referable to hybrids of different parentage or abnormal forms of other species.

RICHARDSON, P. MICK. New York Botanical Garden, Bronx, New York 10458. - Problems of congruence of chemical and morphological data.

The current taxonomic treatment of Lasthenia recognizes 16 species in 6 sections (Ornduff, 1966). A thorough analysis of the flavonoids in the genus has been interpreted as confirming the current sectional boundaries (Bohm, Saleh and Ornduff, 1974). Character compatibility analysis of the flavonoid data appeared to also support the prevailing taxonomy of the genus (Estabrook, 1980). However, when the character state polarities of Bohm et al. (1974) were used in a cladistic analysis the results disagreed with the earlier interpretations. The protein electrophoresis data of Altosaar, Bohm and Ornduff (1974) also disagreed with the current taxonomy of the genus. If there has been correct interpretation of all the data then congruence among them would be expected. Reinterpretation of all the available data is necessary in order to understand this case of incongruence.

ROBBINS, LAURIE R. Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409.  
- Systematics of the fleshy-fruited Yuccas in the Chihuahuan Desert.

Relationships among eight species of fleshy-fruited Yuccas in the Chihuahuan Desert were investigated. Morphometric, flavonoid, and electrophoretic techniques were employed in an effort to elucidate relationships within several species complexes. Historically, because of large plant size and the inaccessibility of several of the species, sample sizes have been small. The true degree of intra- and interpopulational variation, therefore, has never been established. In this study, the analysis of large samples revealed considerably more morphological variability than previously reported. This variability blurs taxonomic boundaries within several of the species complexes. Additionally, flavonoid and electrophoretic data further indicate a more conservative treatment of the group than produced by previous workers.

ROBERTS, MARVIN L. and ROBERT R. HAYNES\*. Department of Biology, University of Alabama, University, AL 35486. - Chemosystematics of the genus Najas (Najadaceae).

The infrageneric classification of Najas has been based on leaf sheath morphology and the occurrence of a floral envelope. Recent evidence from seed coat morphology suggest other divisions within the genus. An examination of flavonoid pigments in North American taxa indicates considerable diversity in flavonoid composition. Najas marina, in subgenus Najas, produces flavone-7-O-glycosides. Certain taxa of subgenus Caulinia produce the same compounds and also 5-O-substituted flavones and 3-O- and 7-O-substituted flavonols. Najas flexilis and N. guadalupensis stand apart from these taxa in lacking 7-glycosylated flavones but producing 5-deoxy flavones and flavonols. Geographic and/or seasonal variation in flavonoid profiles are apparent in several species. The flavonoid data largely support an infrageneric classification based on seed coat morphology.

ROBERTSON, KENNETH R. Illinois Natural History Survey, Champaign, IL 63120. - How to identify members of the genus *Amaranthus*.

Species of the genus *Amaranthus* (including subgenus *Acnida*) are difficult to identify for someone not familiar with the group, and many specimens in herbaria are misidentified, often grossly so. In this paper, the important morphological characteristics used to distinguish species of *Amaranthus* will be discussed and illustrated with photographs. Within a given geographical area, species are rarely distinguishable vegetatively. Flowers are essential, and mature fruits are also frequently necessary; both flowers and fruits are usually found on plants collected from late summer until the end of the growing season. The flowers of *Amaranthus* are imperfect, and each species is consistently either monoecious or dioecious. This is the first character to determine when identifying an *Amaranthus*. Other characters used to distinguish species are: inflorescence type and position (terminal panicles or axillary clusters); size and shape of inflorescence bracts; number, size, and shape of tepals of carpellate flowers; number of tepals and stamens of staminate flowers; size, texture, shape, and dehiscence of utricles; and color, size, and surface texture of seeds.

SCHLESSMAN, MARK A. Department of Biology, Vassar College, Poughkeepsie, NY 12601 - Floral biology of American ginseng in southeastern New York.

American ginseng, *Panax quinquefolium*, is threatened by commercial collecting. Because the floral biology of *P. quinquefolium* is of interest to ginseng growers, conservationists and botanists; I initiated a study of floral morphology, pollination and mating systems of a population in southeastern New York.

In 1982 I observed 3 types of flowers: perfect with 2 styles and 2 developed ovules; perfect with one style and 1 developed ovule; and functionally staminate with 1 style and no developed ovules. Perfect flowers were homogamous, with styles recurved and stigmas receptive at anthesis. Emasculation and bagging experiments and hand-pollinations in the field showed that: 1) pollination is required for seed set; 2) *P. quinquefolium* is self-compatible; and 3) selfing may occur via autogamy. The predominant floral visitors were syrphid flies (*Mesograpta bosci*, *Melanstoma mellinum*), halictid bees (*Dialictus* sp.) and ants (*Prenolepis imparis*, *Myrmica brevinodis*). The mean percentage of flowers bearing fruits in a sample of 64 naturally pollinated individuals was 29 + 23.

Reproductive status was correlated with the morphological class, and hence age, of individuals. All 1-pronged plants were vegetative, and only 46% of the 2-pronged plants flowered. In contrast 96% of 3-pronged plants and all of the 4-pronged plants bore flowers. The mean percentages of 1-styled flowers were 93 for 2-pronged, 60 for 3-pronged, and 11 for 4-pronged plants. The low level of fruit production and abundance of 1-styled flowers in this population suggest that reproduction is resource-limited.

SCHLICHTING, CARL D. Department of Botany, University of Texas, Austin, TX 78712. - Evolution of phenotypic plasticity in *Phlox Drummondii*. Phenotypic plasticity is the ability of an

individual plant to respond to differing environmental conditions. The evolution of the plasticity of a variety of characters (e.g. dry weight, flower size, reproductive effort) was examined within *Phlox Drummondii*. A number of cultivated varieties have been derived from wild *P. Drummondii*, and in some areas of Texas these cultivars have 'escaped' back into the wild. Comparison of the plasticity of wild, cultivated and feral populations shows varying amounts of evolution of plasticity for different characters. For example, the pattern and amount of plasticity of flowering time are quite similar for wild *P. Drummondii* and the cultivar Chamois Rose, whereas an escaped cultivated population from Jewett, Texas has much less plasticity and a different pattern of response to environments. The relative amounts of evolution of the plasticity of various characters may be related to the effects of drift or natural/artificial selection, depending on the adaptive nature of the plasticity of that particular character.

SCHNEIDER, EDWARD L. Department of Biology, Southwest Texas State University, San Marcos, TX 78666. - Floral Biology of *Ondinea purpurea* den Hartog.

The floral biology of *Ondinea purpurea*, consisting of an apetalous subspecies and a newly discovered petaloid subspecies, has been investigated. Anthesis occurs over a 3-day period. First-day flowers are protogynous and characterized by colorful reflexed perianth and staminal parts. The pollen-receptive stigmas of first-day flowers secrete a fluid that fills the small stigmatic cup. As potential pollinators are attracted and attempt to land on the distally exposed gynoecium, they contact the stigmatic fluid which loosens pollen from the insect's body and pollination is achieved. Second- and third-day flowers are functionally staminate. On the basis of comparative reproductive anatomy and pollination syndromes the placement of *Ondinea* in the Nymphaeaceae *sensu stricto* is supported.

SCHWARZ, A.G.\* AND R.E. REDMANN. Department of Crop Science and Plant Ecology, University of Saskatchewan, Saskatoon, Sask. S7N 0W0. - Phenology of northern halophytic C<sub>3</sub> and C<sub>4</sub> grasses.

In Saskatchewan, C<sub>3</sub> and C<sub>4</sub> species coexist in saline habitats. The phenology of *Agropyron trachycaulum* (C<sub>3</sub>), *Spartina gracilis* (C<sub>4</sub>), *Puccinellia nuttalliana* (C<sub>3</sub>), and *Distichlis stricta* (C<sub>4</sub>) was studied from May to September. Observations of growth stage, height, number of leaves, and number of tillers were made on twenty individuals of each population. Environmental measurements included air and soil temperatures, rainfall, soil water content, and salinity. Spring regrowth began earlier in C<sub>3</sub> plants than in C<sub>4</sub> plants. Species from the strongly saline vegetation zone (*P. nuttalliana* and *D. stricta*) began flowering earlier than species from the moderately saline vegetation zone (*A. trachycaulum* and *S. gracilis*). Within both zones, flowering of C<sub>3</sub> and C<sub>4</sub> species was essentially simultaneous. New growth occurred in autumn among the C<sub>3</sub> plants. Distinct temporal separation of the C<sub>3</sub> and C<sub>4</sub> grasses probably is impossible, because of the relatively short growing season.

SEAMAN, FRED C. Harding Laboratories, New York Botanical Garden, Bronx, NY 10458. - Terpenoid characters and the systematics of *Montanoa* (Asteraceae).

Sesquiterpene lactone and diterpene chemistries of the genus *Montanoa* (Heliantheae) are being surveyed. Seventeen of the 30 taxa have been investigated, and novel compounds have been identified from each taxon. These novel compounds provide the basis for deriving skeletal and substitutional characters which are important in the study of *Montanoa* systematics. Examples of important characters are novel germacrane-12,6 $\beta$ -olides (skeletal) and C-5 hydroxylation (substitutional). The distribution of chemical characters is being compared to a morphologically based cladistic analysis and taxonomic revision by V.A. Funk. Preliminary results indicate that there are areas of conflict between the distribution of novel chemical characters and the subgeneric and sectional boundaries proposed by Funk. However, the chemical characters support her treatment of the *M. tomentosa* and *M. leucantha* complexes. A hypothetical biosynthetic (biogenetic) rationale for these novel characters is presented.

SEAVEY, STEVEN R. Department of Biology, Lewis and Clark College, Portland, OR 97219. - A novel self-incompatibility in *Epilobium obcordatum* (Onagraceae).

Seed set in greenhouse-grown individuals of *Epilobium obcordatum* is 3 to 13 times greater in outcrossed flowers than it is in selfed flowers. Self pollen germinates and grows normally through the style to the ovary, self fertilization occurs and early embryonic development is apparently normal. Sometime between day 3 and day 9 following pollination, selfed embryos frequently cease developing and remain in an undifferentiated, globular state; the endosperm of these embryo sacs is not as abundant as in normally developing embryo sacs. Seed set following delayed and mixed pollinations demonstrates that self pollen removes ovules from the pool of potential seeds, even though all fruits contain a large proportion of unfertilized ovules.

SHULTZ, LEILA M. Intermountain Herbarium, Department of Biology, Utah State University, Logan, UT 84322. - Origin and distribution of *Artemisia rothrockii* (Asteraceae, Anthemideae). *Artemisia rothrockii* was described by Asa Gray in 1876 from populations near Olanca Peak in the southern Sierra Nevada mountains of California. The name has since been misapplied to more widespread populations of putative hybrid origin. Similarities between the central Sierran and Rocky Mountain populations of *Artemisia* have given rise to reports of *A. rothrockii* throughout the Rocky Mountain Region. Flavonoid profiles of the taxa involved are discussed with an estimation of their utility in determining interspecific relationships. Morphological and chromosomal evidence, as well as unique features of leaf anatomy, are used to support the recognition of *A. rothrockii* as a California endemic. Populations normally referred to as *A. rothrockii* appear to be hybrids of various subspecies of *A. tridentata* and *A. cana*.

SIMMONS, KAREN S. Department of Botany, Washington State University, Pullman, WA 99164-4230. - Androdioecism and sex ratios in *Lomatium* Raf. (Umbelliferae).

Species of *Lomatium* exhibit unique and interesting breeding systems. This primarily entomophilous genus of 73 western North American species ranges from andromonoecism to androdioecism. This results in very skewed male-biased individual and population sex ratios. Eight field sites of *Lomatium* species have been monitored for sex ratios for up to three years. Shifts in population sex ratios and individual gender expression have both been documented in *L. triternatum* and *L. nudicaule*. Shifts have been observed in both directions, towards increased maleness and decreased maleness, but sex ratios were always more than 50% male and ranged as high as 76% male. A high percent of aborted ovules was also observed in most populations, resulting in even more male-biased functional sex ratios: Sexual selection for increased male competition may be an important selective force in the evolution of this system.

SMITH, EDWIN B. Department of Botany and Microbiology, University of Arkansas, Fayetteville, AR 72701. - Biosystematic studies of the Californian *Coreopsis* (sections *Tuckermannia*, *Pugiopappus*, and *Euleptosyne*).

Biosystematic studies of the eight species of Californian *Coreopsis* were attempted. The group is refractory to the biosystematic approach. Artificial interspecific hybridizations were attempted in all combinations but produced only one successful combination (*C. maritima* X *C. gigantea*). All eight species are  $n = 12$ . The meiotic chromosomes of the perennials (section *Tuckermannia*) are much larger and easily distinguishable from those of the annuals (sections *Pugiopappus* and *Euleptosyne*), but the chromosomes of each subgroup (annuals or perennials) are not easily distinguishable *inter se*. The three sections are well-differentiated morphologically and deserve sectional status. On the basis of several trends in morphology presumably indicative of phylogeny, section *Tuckermannia* is most primitive, *Pugiopappus* intermediate, and *Euleptosyne* the most advanced. Probable phyletic lines within the sections appear rather clearcut in sections *Tuckermannia* (from *C. gigantea* to *C. maritima*) and *Pugiopappus* (from *C. calliopsidea* to *C. bigelovii* to *C. hamiltonii*), but less obvious in section *Euleptosyne*. The most likely phylogeny in the latter section appears to be *C. stillmanii* to *C. douglasii* to *C. californica*, even though this involves a reversal in achene characters within the section. This entire group in California was probably derived from the primitive Mexican/South American section *Pseudoagarista*.

SODERSTROM, THOMAS R. and FERNANDO O. ZULOAGA \* Department of Botany, Smithsonian Institution, Washington, D.C. 20560 and Instituto de Botanica Darwinion, San Isidro, Republica Argentina. - Systematic value of the sculpturing and epidermal patterns of the antheridium of *Olyra* (Poaceae: Bambusoideae).

The bambusoid genus, *Olyra*, comprises some twenty species in tropical America, distributed from

southern Mexico to northern Argentina. The species of this monoecious grass have been distinguished on the basis of the type of female and male spikelets, their arrangement within the inflorescence, and disposition of the inflorescence within the plant. As in other members of the Olyreae, the antheria of *Olyra* are hard at maturity and resemble those characteristically found in the unrelated tribe, Paniceae.

SEM studies of the antheria of all species of *Olyra* reveal marked differences among them, including various types of sculpturing such as round, elliptical or hexagonal pits, narrow or broad excavations, and diverse epidermal patterns. The latter vary from relatively smooth to rugose surfaces with hooks and the presence of several kinds of hairs, including round to flattened macrohairs and short, globose bicellular microhairs, unusual in the subfamily. The antherial patterns, as revealed by SEM studies, support the previous arrangement of species in the genus based on exomorphological characters.

SOLTIS, DOUGLAS E. Department of Biology, University of North Carolina, Greensboro, NC 27412. - Allozymic variability in four eastern U. S. species of *Heuchera* (Saxifragaceae).

*Heuchera americana*, *H. parviflora*, *H. pubescens*, and *H. villosa* are diploid ( $2n = 14$ ) herbaceous perennials occurring in the eastern U.S. Individuals from populations representing these four species were investigated utilizing starch gel electrophoresis. Allozymic data were obtained for 14 enzymes apparently encoded by 16 loci. Although low, values of P and H for these species of *Heuchera* are higher than those obtained for species of the related genus *Sullivantia* (Soltis, 1982). The greater genetic variability of *Heuchera* species may be attributable to breeding system; the investigated species of *Heuchera* are obligately outcrossing, whereas species of *Sullivantia* predominantly self. Allozymic data also have taxonomic implications. Rosendahl et al. (1936) assigned *H. pubescens* to section *Heruchea* and placed the remaining three species in separate subsections of section *Americanae*. Based on crossability data, Wells (1979) suggested taxonomic changes at the sectional and subsectional level. Electrophoretic data indicate a high degree of similarity among the species investigated, but clearly define two groups. *Heuchera villosa* and *H. parviflora* form one group, whereas *H. americana* and *H. pubescens* are allozymically more similar to each other. The relationships suggested by allozymic data are not in agreement with the traditional treatment of Rosendahl et al., but do support the taxonomic changes suggested by Wells.

SOLTIS, DOUGLAS E.\* and BRUCE A. BOHM. Department of Biology, University of North Carolina, Greensboro, NC 27412, Botany Department, University of British Columbia, Vancouver, B.C., V6T 1W5 Canada. - Flavonoid chemistry and karyology of the disjunct species of *Tiarella* (Saxifragaceae).

*Tiarella* is a genus of herbaceous perennials, and is generally considered to comprise three species: *T. cordifolia*, *T. trifoliata*, and *T. polyphylla*. These species are distributed in eastern North America, western North America, and eastern Asia, respectively. Numerous other genera of vascular plants similarly display this well-known floristic disjunction (Wood, 1972). Available evidence indicates that this disjunction arose during the late Miocene (10-12 million years B. P.). Prior to the late Miocene, the

northern latitudes were essentially encircled by a Mixed Mesophytic Forest community. Despite information regarding the events that disrupted this once-continuous community, few studies appear to have compared in a biosystematic fashion related species displaying this disjunction. We therefore initiated a flavonoid chemical and karyotypic comparison of the species of *Tiarella* to determine the extent of differentiation among these apparently long isolated species. Chromosome studies have shown all species of *Tiarella* to be characterized by the same chromosome number ( $2n = 14$ ), and essentially identical karyotypes. Although chromosomal evolution in the genus appears to be conservative, flavonoid differentiation has occurred among the species. Each species of *Tiarella* is chemically distinct. Apparently significant differences in monoglycosides exist between the North American species, *T. cordifolia* and *T. trifoliata*. Triglycosides appear to be absent from *T. polyphylla*, whereas they are present in the North American species. Furthermore, *T. polyphylla* displays the simplest array of flavonoids.

SOUKUP, VICTOR G. Herbarium, University of Cincinnati, Cincinnati, OH 45221 & Hormel Institute, Austin, MN 55912. - Leaf Hydrocarbons of *Trillium* (Liliaceae).

The approximately 60 species of *Trillium* are native to eastern and western North America and eastern Asia to the Himalayas. Species vary from about 6 to 55 cm in height with the areas of individual leaves (bracts) ranging from about 4 to 300 cm<sup>2</sup>. Only one bract was collected from each plant but with small species up to 25 bracts were collected from individual plants in a colony to make up a specimen. Total leaf hydrocarbons were determined on representative specimens from various populations of each species. Bracts were collected in early anthesis and comminuted in a blender in chloroform/methanol solvent. Hydrocarbons were obtained from the crude extract by TLC on silica and analytically separated by GLC on an SE-30 25 meter glass capillary column. Normal aliphatic hydrocarbons from C<sub>15</sub> to C<sub>34</sub> were found with C<sub>25</sub>, C<sub>27</sub>, and C<sub>29</sub> predominating. C<sub>15</sub>, C<sub>23</sub>, C<sub>24</sub>, C<sub>25</sub>, C<sub>28</sub>, C<sub>30</sub>, C<sub>31</sub> and C<sub>34</sub> were also important in North American species while C<sub>18</sub>, C<sub>19</sub>, C<sub>21</sub>, C<sub>22</sub>, C<sub>24</sub>, C<sub>26</sub>, and C<sub>28</sub> were also important in Asiatic species. Similarities between species run from a high of 0.955 to a low of 0.345. Results generally support affinities suggested on morphological basis but there are some notable exceptions, e.g. the *T. pusillum* varieties.

SPENCER, KEVIN C.\* and DAVID S. SEIGLER.

Department of Botany, University of Illinois, Urbana, IL 61801. - Systematics of *Adenia*

(Passifloraceae): Numerical Analysis and Chemistry.

In an analysis of the distribution of cyanogenic glycosides in the Violales we discovered that the possession of certain substitutional types of cyclopentenoid cyanogens was indicative of taxonomic relationships at the familial level. In order to test the predictive utility of cyclopentenoids at the generic level and below, we combined a chemical study of the genus *Adenia* with a numerical analysis of its morphological characters. Cladistic and phenetic analyses of up to 80 characters in the 92 described species in the genus using several in- and out-groups yielded a consistent pattern of species association. Application of data on the distribution of the different types and combinations of cyclopentenoid cyanogens within the genus

provided a basis for constructing a reasonable cladogram of *Adenia*. The success we have had with reconstruction of a classification in this genus encouraged us to model a similar approach for use in the analysis of the systematics of the large genus *Passiflora* and the family Flacourtiaceae.

SPOONER, DAVID M. Department of Botany, The Ohio State University, Columbus, OH 43210.  
- Morphological variation and distribution of *Gratiola viscidula* (Scrophulariaceae).

*Gratiola viscidula* Pennell is currently documented from 86 counties in the Piedmont and adjacent Atlantic Coastal Plain and southern section of the Blue Ridge Province. In addition, disjunct populations are located farther west, to the Ozark Plateau in southeastern Missouri and the Allegheny Plateau in southeastern Ohio and adjacent Kentucky and West Virginia. The species was separated into two subspecies by Pennell in 1935: *G. viscidula* subsp. *viscidula*, and *G. viscidula* subsp. *shortii* Durand ex Pennell. The latter subspecies, which was distinguished by its larger calyces, petals, and leaves, was believed to be confined to southeastern Ohio and adjacent Kentucky and West Virginia. In the recent literature it has erroneously been referred to as *G. viscidula* var. *shortii* (Durand) Gleason, and *G. viscidula* var. *shortii* (Pennell) Gleason. Herbarium specimens have been examined from throughout the range of the species, and mass collections were made in Ohio, Kentucky and West Virginia. Examination of this material has demonstrated that the sizes of petals, calyces and leaves are highly variable both throughout the range of the species and within individual populations. Subspecific categories are unwarranted.

STANDLEY, LISA A. Department of Biological Sciences, Wellesley College, Wellesley MA 02181.  
- Ecotypic variation of stomatal distribution in *Carex aquatilis* Wahl.

*Carex aquatilis* Wahl. (section Phacocystis), a widely distributed species of temperate marshes and wet tundra, exhibits morphological and physiological variation across its range. Recent studies of *Carex aquatilis* in the Pacific Northwest have demonstrated that foliar anatomy also varies ecotypically. The majority of species in sect. Phacocystis have stomates restricted to the abaxial surface. The leaves of *C. aquatilis* are typically amphistomous, which is presumed to be an advanced character. The relative distribution of stomates between the adaxial and abaxial surfaces varies between populations; stomates may be entirely or primarily adaxial, or may have an equal density on both surfaces. No significant variation in stomatal distribution occurs within populations, which are also uniform with regard to the thickness of leaves, sizes of stomates, and total numbers of stomates. Climatic factors are strongly correlated with the distribution of stomates. Hyperstomous populations occur where the average annual precipitation exceeds 60 cm and the average July temperature is less than 29°C, and are coastal and montane. Amphistomous populations occur where the climate is drier and warmer and water-stress is presumed to be greater, chiefly in the Columbia Basin. In the absence of physiological adaptation, one way that photosynthetic efficiency may be increased in arid habitats is through a decrease in the intercellular mesophyll resistance to CO<sub>2</sub> diffusion. Amphistomy may be important as a

means of decreasing the CO<sub>2</sub> diffusion distances and increasing the rates of uptake, thus increasing the photosynthetic efficiency of *Carex aquatilis* in more xeric climates.

STANDLEY, LISA A. Department of Biological Sciences, Wellesley College, Wellesley MA 02181.  
- The taxonomy of the *Carex lenticularis* complex in Central and South America.

The *Carex lenticularis* complex forms a distinct and probably paraphyletic subgroup within the section Phacocystis (Acutae). The combination of nerved perigynia with a torulose, stipitate base, irridescent achenes with ornamented silica-bodies, chromosomal numbers of n=42-46, and narrow amphistomous leaves distinguishes this complex. These features are shared with the amphiatlantic *Carex nigra* group, which is distinguished by the hyperstomous leaves. Recent studies have shown that the South and Central American taxa *Carex hermannii*, *C. cuchumatanensis*, and *C. decida* are included in the *C. lenticularis* complex, based on similarity in morphology, foliar anatomy, and the surface patterns of achenes and perigynia. Montane and low elevation populations of *Carex decida*, in South America, and of *C. lenticularis* in North America, show similar patterns of variation with regard to the sizes of plants and colors of pistillate scales and perigynia. Patterns of distribution and variation of morphology and of anatomy in these species provide information on the origin and divergence of taxa of the *Carex lenticularis* complex, which extends along the western Cordillera from Alaska to Tierra del Fuego.

STEBBINS, G. LEDYARD\*, MICHAEL VASEY AND ELIZABETH STEVENS. Department of Genetics, University of California, Davis, CA 95616. - Chromosome numbers and population variation in the *Antennaria alpina* complex in the Sierra Nevada and Cascade ranges.

In the Sierra Nevada of California, diploid populations that were described as *A. pulchella* Greene are sympatric with tetraploid populations that correspond to *A. media* Greene. Diploids are generally smaller in stature and reproductive structures, and differ significantly in other respects. Ecological requirements overlap, but diploids tend to be in soils that are better drained. In most of the Sierra Nevada, populations are sexual with staminate-pistillate ratios approaching 1:1, but some populations, particularly those peripheral to the area, have an excess of pistillates, up to 100%. Populations from the volcanic peaks of the California and Oregon Cascades are entirely pistillate except for those on the Three Sisters, Oregon. Diverse habitats close together favor sexual populations containing staminate plants; smaller more homogeneous habitats widely separated from each other contain only pistillate apomicts.

STEELE, KELLY P. Department of Biological Sciences University of California, Santa Barbara, CA 93106  
- Parallel evolution in two species of *Gilia* (Polemoniaceae)?

Studies by Verne Grant have indicated that *Gilia capitata* and *G. achilleaeifolia* are two closely related species which are genetically isolated. No F<sub>1</sub> hybrids have been produced (few seeds are set) in any experimental crosses between the two species. However, the precise delimitation of the two species

using morphological criteria has always been problematic. *G. capitata* as defined by Grant includes numerous populations formerly included in *G. achilleaeifolia*. Present studies utilizing experimental crosses of previously unstudied populations support Grant's delimitation with one important exception. *G.c.abrotanifolia* occurs in the San Rafael Mts. of coastal southern California about twenty miles east of unambiguous populations of *G. achilleaeifolia* (the species southern limit). The populations from the San Rafael Mts. are strikingly different from the coastal populations of *G. achilleaeifolia* and are similar to populations of *G.c.abrotanifolia* in the Sierra Nevada. However, crossing results indicate that individuals from the San Rafael Mts. set numerous viable seeds with individuals from coastal *G. achilleaeifolia* populations (number of viable seeds/number of flowers pollinated=2.5) but only occasionally set viable seed with individuals from any population of *G. capitata* including *G.c.abrotanifolia* (number of viable seeds/number of flowers pollinated=.4). Results for reciprocal crosses are similar. It appears that populations of *G.c.abrotanifolia* in the San Rafael Mts. may represent *G. achilleaeifolia* which resembles *G.c.abrotanifolia*. This resemblance could result from parallel evolution of similar races within the two species or from the retention of primitive characters from a shared common ancestor. Evidence for each hypothesis will be presented.

SULLIVAN, GENE A.\* & JULIAN A. STEYERMARK. Department of Botany, Louisiana State University, Baton Rouge, LA 70803-1705 & Instituto Botanico, Apartado 2156, Caracas, Venezuela. - Recognition of the genus *Muzonia* (Rubiaceae).

The genus *Muzonia* N. Osorio is described as containing six species. The genus is found in the premontane forests of the northern and central Andes and the coastal ranges of Venezuela. Three species were previously described. Originally placed in *Cinchona*, two Colombian species were transferred to *Muzonia* by Osorio (1874). These same two species were later placed in *Ladenbergia* by Standley, unaware of Osorio's work. Three new species are also described. Morphologically distinct from other *Cinchoneae*, these species are similar in habit, general and pollen morphology, and habitat requirements. However, these species differ in pubescence, bract shape and other specific morphological characters. Although inconclusive, evidence of heterostyly has been noted.

SULLIVAN, JANET R. Bebb Herbarium, Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019 - The questionable status of *Physalis variovestita* (Solanaceae).

The biology of *Physalis variovestita*, a rare Texas endemic, and its relationship to *P. viscosa* were examined as part of a systematic study of *Physalis* section *Viscosae*. Previous studies have noted that *P. variovestita* intergrades morphologically with *P. viscosa* subspecies *mollis* (composed of var. *mollis* and var. *cinerascens*), and that populations of these intergrading forms are found throughout eastern Texas. An investigation of interbreeding capabilities and analysis of the resulting hybrids reveals that

*P. variovestita* is genetically more closely-related to *P. viscosa* var. *mollis* than either taxon is to *P. viscosa* var. *cinerascens*. This is substantiated by pollen ultrastructure and size, flavonoid constituents, and a phenetic analysis of thirty-three morphological features of the three taxa. Based on these studies, *P. variovestita* can no longer be considered a species distinct from *P. viscosa* var. *mollis*. The suggestion that *P. variovestita* is of hybrid origin (*P. viscosa* var. *mollis* X *P. virginiana* var. *subglabrata* f. *macrophyssa*) has been examined but cannot be supported or refuted at this time.

SYTSMA, KENNETH J.\* and RICHARD W. PIPPEN. Biology Departments, Washington University, St. Louis, MO 63130 and Western Michigan University, Kalamazoo, MI 49008 - Pollination biology and hybridization in Neotropical *Costus* (Costaceae).

Pollination biology of three sympatric taxa of *Costus* (Costaceae) was studied in the lowland forest region of southern Belize, Central America. Pollen and nectar collecting visitors were observed. Nectar volumes and sugar concentrations were recorded hourly from pre-dawn to mid-afternoon. Amino acid and sugar composition of nectar samples were determined for each taxon. *Costus guanaiensis* var. *macrostrobilus* (sect. *Costus*) is pollinated exclusively by euglossine bees, especially species of *Eulaema*. *Costus pulverulentus* (sect. *Ornithophilus*) is visited by several vectors but most effectively by several species of territorial and traplining hummingbirds. *Costus* sp. nov. is an undescribed taxon visited by both euglossine bees and hummingbirds. Morphology and certain aspects of its pollination biology indicate that it most likely arose through hybridization between *C. guanaiensis* and *C. pulverulentus*.

SYTSMA, KENNETH J.\* , BARBARA A. SCHAAL, and PETER H. RAVEN. Biology Department, Washington University, St. Louis, MO 63130 and Missouri Botanical Garden, St. Louis, MO 63166 - Phylogenetics of the *Lisianthus skinneri* (Gentianaceae) species complex in Central America.

Phylogenetic relationships within a geographically restricted and morphologically closely related group of tropical forest shrubs in the genus *Lisianthus* were analyzed by endonuclease DNA mapping as well as with morphology, flavonoids, and allozymes. Eighteen populations comprising five species in this group and four outgroup species of related *Gentian* shrubs were examined for variation in ribosomal DNA (rDNA). An entire cloned rDNA repeat of *Glycine* (soybean) was used as a probe to detect restriction site changes and insertions/deletions of DNA. Seven restriction enzymes showed at least one site loss/gain in one or more of the populations investigated. Variation in repeat length among the species is due to insertions up to 300 bp long in the non-transcribed spacer region of rDNA. Both the restriction site changes and the insertions allow construction of a phylogenetic tree for the group. These relationships do not totally agree with those obtained from other methods. All data indicate that evolution within the group has occurred from ancestral, mid-elevation *L. skinneri* populations to higher elevation, cloud forest endemic species at several different times. Evidence for hybridization and introgression between *L. skinneri* and one of the derived species is also documented.

TAYLOR, RONALD J. Department of Biology, Western Washington University, Bellingham, WA 98225 - Patterns and interpretations of variability within and among dandelion populations.

Numerous populations of common dandelions were non-randomly sampled within a broad geographical region encompassing the western states of the U.S. and British Columbia, Canada. Within each population an attempt was made to sample the total range of variation, thus involving biotypes indicative of Taraxacum officinale and T. laevigatum, when available. Morphological and chemical variables of sample specimens were subjected to multivariate analyses to establish the pattern of variation within and among populations. Preliminary results reflect considerable inter- and intrapopulation variability; however, the randomness of the variables indicates that most of the variation is explained by phenotypic plasticity. Also, the range of variability between T. officinale and T. laevigatum was more or less continuous weakening the argument for recognition of distinct species. Field and greenhouse observations suggest that most T. laevigatum characteristics are responses to ecological stresses.

TERRELL, EDWARD E. Plant Exploration and Taxonomy Laboratory, Plant Genetics and Germplasm Institute, U.S. Department of Agriculture, Beltsville, MD 20705.

- Taxonomic implications of spikelet epidermal features in *Leersia* and *Oryza* (Poaceae).

Epidermal features on spikelets of species of *Leersia* and *Oryza* were examined by scanning electron microscopy (SEM). Energy dispersive x-ray analysis was used to detect the presence of silicon. The most important epidermal features of the spikelets occur on lemma and palea surfaces (these are similar). *Leersia* lemmas have numerous siliceous triads, each consisting of a central round silica body flanked by large siliceous tubercles with terminal pits or pores. The African species *Leersia perrieri*, *L. tisserantii*, and *L. nematostachya* originally were described under *Oryza* but later transferred to *Leersia*. This study confirms the placement of the first two of these species in *Leersia*; the third species is more difficult to classify. The approximately 20 species of *Oryza* are more diverse and fall into 5 groups. The principal species-group is the *O. sativa* (rice) complex with approximately 14 species having similar lemmatal epidermal configurations. Six other species from Africa and Asia fall into 4 groups. Data from SEM confirm that two additional species originally in *Oryza* probably belong in separate genera; these are *Porteresia coarctata* and *Rhynchoryza subulata*.

THOMPSON, RAHMONA A. Dept. of Botany-Microbiology, Oklahoma State University, Stillwater, OK 74078. - Generic relationships in the Paniceae: *Urochloa* (Poaceae).

In the Paniceae, 25 genera are characterized primarily by spikelet orientation. The validity of this character has been questioned, thus leading to clouding of generic boundaries. In a continuing biosystematic investigation of this group, 10 species of the morphologically variable *Urochloa* were examined using antherial morphology and epidermal and internal leaf anatomy. *Urochloa* was found to be a distinct taxon, but with some intergradation with species of *Brachiaria*. Antherial sculpturing was highly uniform with the *Urochloa* Pattern predominating. Epidermal features are typically panicoid with narrow inter-

costal regions. *Urochloa* has mestome and parenchyma bundle sheaths characteristic of the C<sub>4</sub> PEP-carboxykinase photosynthetic pathway. Mesophyll tissue is limited to one subradial ring surrounding the vascular bundle. Both laminar surfaces are distinctly ribbed; occasionally bulliform fans occur in the adaxial rib depressions.

TOOLIN, LAURENCE J. Department of Geosciences, University of Arizona, Tucson, Az. 85721  
- Grasses unmoved by glacier's advances.

During the past two decades it has been demonstrated that fossil packrat middens from the western U.S. are an excellent source of plant macrofossils. In dry protected sites these middens can persist for thousands of years. Plant remains thus preserved can be dated by the C-14 method. In the past, grass fragments have been largely overlooked, since they are difficult to recognize and identify. Intensive study reveals, however, that grass florets are well preserved and can be determined with a high degree of accuracy. Recent work has led to the recovery of 65 species in 27 genera. The fossils reported here, ranging in age from more than 35,000 to 350 years, are from the northern Chihuahuan Desert region in western Texas and southern New Mexico. These fossils demonstrate that many of the grasses growing at the sites today have been in place since the pre-full glacial mid-Wisconsin. Species with C<sub>4</sub> photosynthesis were present throughout the record, with little change in the percentage of C<sub>3</sub> species compared with modern assemblages. While non-grass plant remains from the same middens indicate considerable change in other vegetation through time, the grass flora apparently remained relatively stable. It is suggested, therefore, that the growth form and physiology of perennial grasses may make them less sensitive to a given change in a climatic regime than trees, shrubs, or succulents. The presence or absence of C<sub>4</sub> grass species in a fossil record may not be as reliable an indication of past climates in a given area as has been suggested in recent literature. Modern grasslands in the Southwest may represent the present ecological adjustment of very old, relatively stable associations of grasses.

TRUSHEL, NICHOLE, DONALD J. PINKAVA, and MARC A. BAKER\*. Department of Botany & Microbiology, Arizona State University, Tempe, Arizona 85287. - A taxonomic revision of the *Opuntia whipplei* complex, Cactaceae.

*Opuntia whipplei* circumscribes three varieties: var. *whipplei*, var. *viridiflora* and var. *multigeniculata*. The latter two are believed to have arisen through interspecific or possibly intersectional hybridization. We have found good evidence that *O. whipplei* var. *whipplei* hybridizes with *O. leptocaulis* and *O. acanthocarpa* var. *thorneri*. Preliminary data have also revealed *O. whipplei* var. *whipplei* to be involved in intraspecific polyploidy. Most of the plants are diploid, while a tetraploid race exists in northwestern Arizona. Chromosome numbers of the other varieties are yet to be determined. Field and laboratory studies will include character measurement and analysis, cytogenetic analysis, seed viability, pollen stainability and determination of ecological parameters.

## 134 Systematic Section

UMBER, RAY E. Department of Botany, University of Wyoming, Laramie, WY 82071.

- Pollinator size as a factor in *Penstemon strictus* flower evolution.

*Penstemon strictus* Bentham subspecies *strictus* is a plant species found in Wyoming, Colorado, New Mexico, Arizona, and Utah in a wide variety of habitats from about 6,000 to 11,000 feet of elevation. Within this one taxon one can find a great deal of variation in flower size. Corollas can range in size from 21 mm to as much as 45 mm in length. Differences in shape can also be seen. In an effort to understand the diversity in the flower sizes and shapes seen in *P. strictus* field studies were begun to first establish that differences in flower parameters existed between populations and secondly to establish differences between populations in terms of pollinator suites. Significant differences in flower sizes and shapes were found between different populations of *P. strictus* and differences were also found in the pollinator suites. *Penstemon* populations with large pollinators were also characterized by the larger flowers as expected. Pollinator size is then judged to be an important factor in the evolution of the genus *Penstemon*.

VARADARAJAN, G. S.\* and GREGORY K. BROWN. Department of Botany, Ownbey Herbarium, Washington State University, Pullman, WA 99164. - Re-evaluation of the classification of Phytolaccaceae s. lat.

The generic composition of the Phytolaccaceae Lindl. has long been controversial, and past treatments reveal a variety of familial circumscriptions and intrafamilial classifications. Central to the controversy are the genera *Achatocarpus* and *Phaulothamnus*, *Agdestis*, *Barbeuia*, and *Stegnosperma*, which have been treated within the Phytolaccaceae s. lat. or as components of the Achatocarpaceae Heimerl, Agdestidaceae Nak., Barbeuiaceae (Baill.) Nak., and Stegnospermaceae (H. Walter) Nak. respectively. In hope of resolving controversy over the delimitation of Phytolaccaceae, we applied Wagner Network and UPGMA cluster analysis algorithms to a data matrix of 34 characters for each of the 20 genera that comprise Phytolaccaceae s. lat. The results indicate well-defined groups of genera, and suggest the need for recognition of Phytolaccaceae s. str. (*Anisomeria*, *Ercilla*, *Gisekia*, *Phytolacca*), *Petiveriaceae* (*Gallisia*, *Hillieria*, *Ledenbergia*, *Lophiocarpus*, *Microtea*, *Monococcus*, *Petiveria*, *Rivina*, *Schindleria*, *Seguieria*, *Trichostigma*), *Achatocarpaceae* (*Achatocarpus* and *Phaulothamnus*), and the three monogeneric families Agdestidaceae, Barbeuiaceae, and Stegnospermaceae. The analysis also points out the need for further research regarding the treatment of *Microtea*, *Lophiocarpus* and *Monococcus*, genera tentatively included within the *Petiveriaceae*.

VODICKA-ASBURY, MARGARET R. L. H. Bailey Hortorium, Cornell University, Ithaca, NY 14853. - Preliminary investigations into the systematics of the tribe Prockieae (Flacoutiaceae).

The tribe Prockieae, as recently circumscribed by Sleumer, comprises eight neotropical genera. This circumscription has a historical basis in Warburg and Gilg (Engler) although alternative classifications have

been proposed. Those of Bentham and Hooker and of Hutchinson divide the genera into two groups, one assigned to the Flacoutiaceae and the other, to the Tiliaceae. A range of placentation types from parietal to intruded parietal to secondarily axile has played a too important role in placement of the genera. Distributions of character states determined from detailed anatomical studies of leaves (especially stomate characters) and from anatomical studies of ovary development, as well as characters in the literature on wood anatomy (Miller) and pollen morphology (Keating) are not congruent with distributions of placentation type. Resolution of the problem of placement of these genera can only be accomplished in a phylogenetic context, based on a wide array of characters.

WALLACE, ROBERT S.\* and DAVID E. FAIRBROTHERS Department of Biological Sciences - Botany Unit Rutgers University, Piscataway, N.J. 08854. - Population comparisons using isoelectrically focused seed storage proteins of *Opuntia humifusa* (Raf.) Raf.

Morphological studies of the eastern prickly-pear cactus, *Opuntia humifusa* show it to be a highly polymorphic species. To determine the similarity indices between closely and widely distributed populations having morphological differences, the use of isoelectric focusing electrophoresis was chosen because of the high resolution capability of this separation method. Seeds of fifteen populations of *O. humifusa* were collected ranging from Long Island, NY to northern Florida representing different physiographic areas. The seeds were de-coated by hand in a mortar and pestle and the resulting endosperm - embryo containing meal was de-lipidified in cold (0°C) acetone. Proteins were extracted in a TRIS-glycine buffer (pH 8.4) and separated in a 7% polyacrylamide gel in which BioLyte ampholytes were added to produce an anode to cathode pH gradient from 3 to 10 respectively. Staining was accomplished using Coomassie Brilliant Blue general protein stain and enzymatic stains for EST, APH, and ADH. In comparisons between the populations, high (>0.80) indices of similarity were found when based on isoelectrically focused proteins. The resolution obtainable with this method also was sufficient to detect differences between nearby populations having slight or no apparent morphological differences. It can be concluded that *O. humifusa* is a single species throughout its range and that isoelectric focusing electrophoresis may be used as a high resolution separation tool for analysis and comparison of seed storage proteins in the Cactaceae.

WARNOCK, MICHAEL J. Department of Biology, Sam Houston State University, Huntsville, Texas 77341. - Natural hybridization between *Delphinium treleasei* and *D. carolinianum* (Ranunculaceae). *Delphinium treleasei* Bush ex Davis and *D. carolinianum* occur sympatrically on the Ozark Plateau of southwestern Missouri and northwestern Arkansas. *Delphinium treleasei* is a locally common endemic to the region, occurring only in juniper "glades" on outcrops of Cotter dolomite. *Delphinium carolinianum* is a widespread species found from the south Atlantic states to the foothills of the Rocky Mountains as well as in the Ozarks. Ecologically,

considerable overlap is observed between the species. Although *D. treleasei* is usually found in slightly thinner, rockier soils than *D. carolinianum*, mixed populations are occasionally seen and discrete populations within 100 m of each other are common. Phenologically, the period of overlap of anthesis is about two weeks. Visitors to both species include bumblebees, butterflies and hawkmoths. Over the last five years, four putative natural hybrid plants have been discovered. These putative hybrids show intermediacy in morphological and flavonoid characters as well as nearly completely unsharable pollen and no seed set. The intermediate plants were each found in populations of *D. treleasei* with nearby populations of *D. carolinianum*. Artificial crosses were attempted using each species as a pollen donor. All attempts were unsuccessful. A substantial genetic barrier between the species is indicated. This is quite unlike results by other workers (Epling & Lewis) on hybridization in *Delphinium*. A third species, *D. tricorne* Michaux, also occurs in the region, with populations often quite near those of *D. treleasei* and *D. carolinianum*. Due to differences in flowering phenology, no opportunity for hybridization between *D. tricorne* and the other taxa was seen.

WARWICK, S.I. and L.D. BLACK. Biosystematics Res. Inst., Agriculture Canada, Ottawa, Ontario KIA 0C6.  
- Genecological studies of a new problem-weed in Canada, *Sorghum halepense* (Johnson grass).

Thirteen populations of *Sorghum halepense* were sampled from fields in Ontario, Canada and Ohio and New York in the U.S.A. Four populations were reported to overwinter as rhizomes but the others do not. The morphology, phenology, resource allocation patterns and growth of seedling and mature plants grown in a 5-month greenhouse cultivation trial were examined for differences between the overwintering and the non-overwintering biotypes and between populations within biotypes. Fifty characters were scored, 7 from field collected material and the rest from plants grown in the greenhouse. Field collected specimens showed phenotypic differences between biotypes, with the non-overwintering populations having larger seeds, wider culms, and leaves, and larger inflorescences ( $p < 0.05$ ). Results from the greenhouse trial indicated similar differences. Plants from the non-overwintering populations had greater germination, larger and faster growing seedlings, were earlier to flower, had taller and wider culms, larger seeds, greater reproductive and crown dry weights per plant and about 1/10th the rhizome dry weight of overwintering plants ( $p < 0.05$ ). Differences between populations within biotype were evident for both biotypes, with greater variability among the overwintering populations. Plants from the only known overwintering population in Ontario were later to flower and generally smaller than the overwintering populations from the U.S.A. There was little evidence of heterogeneity within populations, except in rhizome production where certain individuals of some non-overwintering populations did not produce extended rhizomes.

WELLS, MARISA\* and RAY E. UMBER. Department of Botany, University of Wyoming, Laramie, WY 82071.  
- A systematic study of *Penstemon glaber* (Scrophulariaceae).

*Penstemon glaber* (Pursh) Crosswhite is a member of the subgenus *Habroanthus* Crosswhite section *Glabri*

(Rydberg) Pennell series *Habroanthus* Crosswhite. This taxon occurs in southern Montana, Wyoming, the western portions of North and South Dakota and Nebraska and along the Front Range of Colorado in northeastern New Mexico. *Penstemon glaber* now includes *P. alpinus* Torr. with three subspecies; ssp. *magnus* (Pennell) Penland, ssp. *brandegei* (Porter) Penland and *alpinus* (Torr.) Penland and varieties *riparius* (A. Nels.) Pennell and var. *pubicaulis* Pennell. The variation (both floral and vegetative) observed throughout the range is great and warrants re-examination. This study was undertaken to better understand this taxon. A detailed morphometric analysis was conducted using field collections and dried herbarium specimens. Comparative flavonoid chemistry was also utilized as it has proven useful in the genus. The result of this study was that two distinct taxa were recognized.

WYNIA, RICHARD\*, and ARVID BOE. Plant Science Department, South Dakota State University, Brookings, SD 57007.

- The occurrence of bi-flowered spikelets in *Beckmannia syzigachne* (Steud.) Fern.

*Beckmannia syzigachne* is common in wet meadows and on shores of lakes and ponds in North America. Its value as a nutritious and palatable forage and wildlife food is well documented. Numerous regional floras have stated that *B. syzigachne* spikelets contain a single floret. Observation of its mating system, as part of our evaluation of its potential as a cultivated forage crop, revealed the presence of bi-flowered spikelets in plants grown in the greenhouse from spikelets collected in northeastern Montana and eastern South Dakota. In summer 1982, caryopses were germinated under an alternating temperature and light regime (16 hours dark at 7°C, 8 hours ambient light at 21°C). Seedlings were planted in the greenhouse when plumules reached 2.5 cm. Spikelets obtained from 360 plants from three Montana collections and 270 plants from four South Dakota collections indicated a percentage of bi-flowered spikelets ranging from 41 to 4% for collections from Arlington, South Dakota and Outlook, Montana, respectively. Similar percentages were observed for primary culm subsamples within each collection. Caryopses from Montana collections were significantly heavier than those from South Dakota. Mean 100-caryopse weights were  $30.4 \pm 0.5$  and  $23.5 \pm 0.4$  mg for Montana and South Dakota collections, respectively. Ecotypic variability for bi-flowered spikelet production and caryopsis weight was found among seven collections from South Dakota and Montana. Taxonomists, in the preparation of future floras, may want to investigate the occurrence of bi-flowered spikelets in *Beckmannia syzigachne* populations in regions covered by their treatises.

WYSS, ANDRE\*, MICHAEL DONOGHUE, KEVIN DEQUEIROZ and MARK NORELL. Department of Biology, San Diego State University, San Diego, CA 92182-0058.

- Reticulation and hierarchy in phylogenetic systematics.

Cladists have generally assumed that hierarchy is the predominant pattern in nature and cladistic methods are designed to recover this hierarchy. However, it is important to consider alternative patterns and exactly how these can be discovered and incorporated in cladistic analysis. We consider when (if ever) one would be justified in invoking a hypothesis of reticulation (e.g., hybridization) to

explain the available data. Normally cladists prefer the hypothesis of relationship requiring the fewest character state transformations, i.e. the most "parsimonious" hypothesis. We demonstrate that it is sometimes possible to reduce the total number of steps by introducing one or more reticulations into an otherwise hierarchic cladogram. If one is allowed to invent "donor organisms" then all incongruence in data sets can be explained as having resulted from reticulation. These observations focus attention on the need to consider what additional information or criteria can be used to decide when it is appropriate to invoke hierarchy and when reticulation. Information concerning geographic ranges, the constitution of genomes, and experimental hybridizations can all bear on this decision, but it is unclear exactly how these data should be added to the character data in arriving at an overall parsimony decision. To clearly formulate this problem we contrast a case in which reticulation is an implausible explanation with one in which it seems highly likely. Although it may be impossible to develop any universally applicable rules, we can formulate a set of general guidelines for deciding when reticulation should be considered.

YOUNG, DAVID A. L. H. Bailey Hortorium,  
Cornell University, Ithaca, New York 14853  
- Vesselless Angiosperms: Character  
weighting and the pan-parallelism paradigm.  
Resurrection of the hypothesis that woody  
members of the Magnolianaes (sensu Takhtajan)  
are not primitively vesselless has, as expected,  
generated considerable controversy, and criticisms  
of the hypothesis recently have appeared in various  
publications. Most of the criticisms leveled so far  
have focused on three principal areas: 1) disagreement  
with the assumptions and methods of Hennigian  
cladistic analyses; 2) disagreement with circumscription  
of the original study group and character delimitation;  
and 3) the apparent lack of adaptive value of losing  
the "highly adaptive" vessel (i.e., vessel member).  
Each of these areas of disagreement will be addressed  
in the context of a cladistic analysis of the  
Magnolianaes. It is suggested that the vesselless con-

dition belongs to a unique class of weighted characters in that it is not used by evolutionary systematists to define higher taxonomic groups within the angiosperms (i.e., it is a weighted plesiomorphic feature). Assumptions inherent in assuming plesiomorphic vessellessness within the angiosperms will be considered in the context of the "pan-parallelism" paradigm that seems to prevail in angiosperm systematics. It will be argued that parsimony should prevail over either a priori or a posteriori character weighting. Finally, the "adaptive value" of vessellessness will be considered.

ZULOAGA, FERNANDO O. \* and THOMAS R. SODERSTROM.  
Instituto de Botanica Darwinion, San Isidro,  
Republica Argentina and Department of Botany,  
Smithsonian Institution, Washington, D.C. 20560.  
- Disposition of the "outlying" species of the  
genus Panicum (Poaceae: Paniceae) from tropical  
America.

During studies leading to a revision of the species of Panicum from Central and South America, we analyzed the following taxa of dubious placement within the genus: P.glutinatum Swartz, P.villaricense Mez, P.macranthum Trinius, P.aristellum Doell, P.arnacites Trinius, P.megastachyum Nees and P.grandifolium Doell. Our findings indicate that  
- P.glutinatum & P.villaricense should be transferred to Homolepis, bringing the number of species in the genus to five;  
- P.macranthum should be included in Streptostachys, a genus previously consisting of one species and now comprising S.macrantha, S.asperifolia and a new species;  
- P.grandifolium should be transferred to Ichnanthus;  
- P.aristellum & P.arnacites present clearly different characteristics in relation to Panicum and should be considered as two new genera in the Paniceae; and  
- P.megastachyum includes two species under the same name, both of which should be transferred to Brachiaria.  
The correct disposition of these outlying species allows a further clarification of the genus Panicum itself.

## TEACHING SECTION

### Luella Weresub Memorial Lecture: Fungi as Botanists

PIROZYNSKI, K.A. National Museums of Canada (NMNS), Ottawa, Ont. K1A 0M8, Canada.  
- Fungi as botanists.

All living organisms are taxonomists, and the biotrophs, like human taxonomists, are concerned with systematics of living organisms. However, unlike a human taxonomist, they cannot afford to make mistakes, but have had millions of years of experience in discovering morphological, physiological, biochemical and ecological characters which often remain hidden to our eyes and minds.

As obligate carbon heterotrophs the fungi have been intimately linked with plants throughout their long history, and provide particularly good examples of tightly co-evolved biotrophic relationships, both parasitic and mutualistic. How meaningful the associations are will depend on how well we can distinguish between the biotroph as a taxonomist and the biotroph as an opportunist. Nevertheless, taxonomic data derived from studies of such complex interactions are likely to be more critical and objective than those based on a systematist's morphological interpretations which are the traditional tools of systematics and biogeography.

## Special Lecture: Reproductive Biology of the Flowering Plants

MEYER, BASTIAAN J. D. Department of Botany, University of Washington, Seattle, WA. 98195.

- Reproductive biology of the flowering plants. The study of pollination and seed-dispersal, once considered an innocent pastime for retired school-teachers, now occupies a central position in biology, providing new concepts as well as demonstration-material to such diverse areas of investigation as co-evolution, morphogenesis, entomology, ethology, population-dynamics, biochemistry, animal & plant physiology, foraging-strategies, cost-benefit relationships, and others. In the present symposium, emphasis will be placed upon some case-histories which each have contributed to various disciplines in a significant manner. The arm lily family has provided the classical and most spectacular examples of cyanide-resistant and thermogenic respiration; some of its members, pollinated by fungus-gnats, display mushroom-mimicry; in the genus Arisaema, sex-change can be studied experimentally. In the Orchidaceae, the recent discovery that the odor of the flowers of Orchis galilaea mimics that of the females of certain wild bees and attracts the males (but not the females!) of these insects justifies the conclusion that O. galilaea can be seen as a "stepping-stone" on the path which in geological history has led to pseudocopulation between insects and orchids. In the genus Ficus (figs), pollination by minute gall-wasps has long been recognized as one of the most extreme examples of co-evolution. Recent studies have shown that figs can also provide magnificent material for the study of sex-ratios and timing-mechanisms. In the realm of fruit- and seed-dispersal, considerable attention will be given to the role of aardvarks in the dispersal of Cucumis humifructus, which has subterranean fruits, and to that of Clark's nutcracker, the major dispersal-agent in pine-species with wingless seeds.

## Special Lecture: Plants, Science and Teaching—A Wonderful Opportunity

POSTLETHWAIT, S.N. Department of Biological Sciences, Purdue University, West Lafayette, IN 47907. - Plants, Science and Teaching - A Wonderful Opportunity.

The nation is experiencing a re-awakening to the significance of science to our well being both individually and as a nation. Leaders of professional societies, governmental officials and news media are joining in an intense effort to identify the problems of science education and the search for solutions. What is the role of botany teachers in this movement? Is the study of plants important in the lives of a TV and computer generation? Can the methods of science be incorporated into student activities in a botany course? The potential of botanists and botany is almost unlimited!!

## Laboratory Workshops

DEYRUP-OLSEN, INGRITH J. Department of Zoology, University of Washington, Seattle, WA 98195.

### - The use of lectins to study cell surfaces.

Lectins are proteins which combine specifically with carbohydrate molecules, or with carbohydrate groups in such complex molecules as glycoproteins and glycolipids. Because carbohydrates are universally present on the outer surfaces of cells, lectins can be used as tools to manipulate and mark cells at the levels of the cell wall or cell membrane. Experiments with lectins are easily carried out by students in elementary classes, and offer investigative challenges to students at more advanced stages. Work with lectins directs the student's attention to the diverse and crucial roles in physiological processes of the cell surface. In the present workshop, some basic systems will be demonstrated (yeast; vertebrate erythrocytes; lectins from various plant and animal sources) as appropriate for use in the student laboratory.

ERBISCH, FREDERIC H. Research Division, Michigan Technological University, Houghton, MI 49931.

### - Workshop in Light Microscopy.

The brightfield microscope is commonly used in the biological sciences teaching laboratory. This type of microscope is often well suited for many of the exercises students perform because they are studying prepared microscope slides of suitably stained materials. However, with unstained biological materials these microscopes perform poorly because sufficient contrast between the material and its background is lacking. Phase contrast microscopes are sometimes used to overcome this lack of contrast problem. Unfortunately, most laboratories do not have enough phase contrast microscopes for routine student use.

Fortunately, though the brightfield microscope can be easily and inexpensively modified so it can meet the students' needs in most laboratory situations, even with unstained materials. The aim of this Workshop is to demonstrate how these modifications can be made. This entire exercise will concentrate on those microscopy modifications which can be done by students during the course of their laboratory study. Each Workshop participant will, with materials costing less than one dollar, convert an ordinary brightfield microscope to a polarizing and a darkfield microscope and achieve rhinberg and oblique illumination. Each of these modifications does, in its own way, increase contrast between the specimens and its background. A sample botany laboratory exercise will be performed by the participants so each can evaluate the advantages and disadvantages of these modifications in the study of plant materials. Handouts describing the modifications and the exercise will be available for each participant.

GREYSON, RICHARD I. Department of Plant Sciences, University of Western Ontario, London, Ontario, N6A 5B7. - Some laboratory exercises with gibberellins and cytokinins.

In order to document some chemical properties along with biological responses to gibberellins and cytokinins we have prepared the following set of demonstrations and "hands-on" experiments.

GIBBERELLINS. A) Thin layer chromatography. A

## 138 Teaching Section

comparison of the TLC behavior of three gibberellins run on i) normal phase silicic acid adsorbant and ii) reverse-phase material. Visualization of chromatograms and calculation of Rf values of the separated components will be by UV fluorescence. B) Bioassay. Two bioassay systems will be demonstrated i) Lettuce hypocotyl and ii) Dwarf rice. Dose-responses to both unchromatographed and TLC chromatographed standards will be presented for both assays. Dose-response curves for both assays will be prepared. C) Extraction. A very rich, easily extracted source of gibberellins is the immature fruits of Scarlet Runner or Kentucky Wonder beans. The preparation of the extract and its assay will be described. CYTOKININS. Bioassay. Two bioassay systems will be demonstrated. i) Soybean hypocotyl slice assay and ii) Amaranthus betacyanin synthesis assay. The latter system calculates betacyanin levels through measures of spectrophotometric absorbance at 542 and 620 m $\mu$ . Dose-response curves will be prepared.

### Contributed Papers

GERRATH, JEAN M.\* and U. POSLUSZNY. Department of Botany and Genetics, University of Guelph, Guelph, Ontario, Canada N1G 2W1.  
- The use of videotape introductions to facilitate consistency in multi-sectioned laboratories.

In response to some of the problems of ensuring consistency in teaching a large laboratory course in introductory botany, a series of videotape introductions to labs was made. In these, the work to be covered is outlined, the main objectives are stressed, and techniques such as freehand sectioning are demonstrated. These tapes have meant that students can now see and hear the introductions clearly, and that all sections are given the same information. Students are apparently more able to work independently through their lab manual exercises and to perform the necessary techniques more easily than they did under the more traditional system. Demonstrators with varying proficiencies in public speaking are no longer required to give the introductions. A demonstration of one of the tapes will take place and a discussion of the procedures used to produce them will ensue.

DWIGHT T. KINCAID. Depart. of Biol. Sciences. Lehman College, CUNY, Bronx, NY 10468 - Micro-computer assisted instruction in biometry using botanical data.

I present programs which teach biometry by using my research data to illustrate topics in frequency distributions, derived variables, data smoothing, correlation, regression, ANOVA, and nonparametric methods. Our graduate students relate well to statistical treatments of data bases including morphometrics of leaves, quadrats, distribution of tree size, and micro-meteorology. The programs are largely in BASIC, are implemented on the Apple II, and are available free on discs. Students are given these programs and told to use them as supplement and drill following class lectures. Each program takes about 30 minutes with timing under student and program control; scrolls text; provides graphic images and questions graded by the program; and provides bibliographies. To operate them requires no more than to type, run. While the same raw information could be given by mimeographed handouts, students find it more fascinating to watch text scroll and graphics fade-in, overlay, and fade-out.

Timing and pause are crucial. Program execution halts until students enter their guess for say, the correlation coefficient of a scatterplot, the influence of an outlier on a regression line, whether 2 frequency distributions are different, or whether a histogram has a normal distribution. Drill is important in learning how to analyze biological data, so during program execution there are opportunities to backup; and at the end, all graphs used to illustrate various points, fade in and out sequentially. While computer assisted instruction is not difficult to code, it is indeed time consuming for the programmer. However, the structure one adopts can then be modified to create computer assisted instruction in other subjects. These programs are compatible with my menu-driven package of programs presented to the teaching section at AIBS last year. A new release is available since corrections; improvements in speed, memory utilization, and program executed documentation; and new programs have been added.

KRUPP, JONATHAN M. Department of Botany, University of California, Davis, California 95616. - The selection and operation of color television equipment for use in botany laboratory courses.

Color television systems for use in botany laboratory courses must be selected with an understanding of the capabilities of the equipment and the abilities of the potential users. Basic equipment for such a system consists of a color video camera and lens, a trinocular compound microscope with a C-mount camera adapter and light balanced objectives, a video tape recorder, and a color monitor / receiver. In addition, a wide variety of equipment is available which can provide pointers, text, or other markers on the TV screen. Specifically, cameras with automatic white balance and video output controls and separate, low mass pick-up tubes are the most suitable. Due to its greater resolution and compatibility with other video media, the 3/4", U-matic cassette is the most useful tape format. Compact equipment, mounted on portable carts allows greater flexibility and utilization of the system without the need for extensive dedicated space. Applications for such a system include the production of review tapes for use by students and faculty, use as a multiple viewer microscope system for group discussions, and as a medium for preserving and exchanging images of rare and/or ephemeral specimens over time and distance. Sample tapes produced during laboratory courses will be available for review and the possibility of establishing a video tape exchange network will be considered.

MULLINS, JEWANETTE S.\* and JOHN A. NOVAK. Biological and Environmental Sciences, California University of Pennsylvania, California, PA 15419 and Science and Math Education, The Ohio State University, Columbus, OH 43210.

- The hay infusion - a teaching tool for mastery learning in freshman botany.  
Bloom's Mastery Learning technique forms the framework in which freshman botany is taught at California University of Pennsylvania. Lecture subject matter is arranged in learning units which are reinforced in the laboratory. Augmentation of lecture material is primarily by means of the hay infusion, which each student cultures as a semester-long project. Learning units illustrated by the infusion are: 1) succession 2) abiotic factors 3) organism interactions 4) food chains 5) aseptic technique 6) living bacteria 7) bacterial cultures 8) bacterial identification, 9) blue-green bacteria 10) diatoms 11) green algae.

Students are required to write a term paper, in scientific format on their own hay infusion. In keeping with Bloom's tenets, students score high on these term papers. Bloom's curve of extinction is achieved for all lecture exam grades.

ORR, ALAN R. Department of Biology,  
University of Northern Iowa, Cedar Falls,  
IA 50614.

- Microscopic identification of metabolic pathways in plant tissues.

Metabolic pathways are the means by which cells obtain their building block molecules and their energy of life to do the work of living. Often it is difficult for the student to relate lectures about energy transducing pathways to the actual plant tissues. Microscopic "visualization" of biochemical pathways offers a challenging way for students to better comprehend plant metabolism. Techniques will be described for the preparation of fresh-frozen cryostat sections of plant tissues and the localization of enzymes as markers for the pentose phosphate pathway, citric acid cycle pathway and the electron transport pathway. Some basic relationships to plant development will be presented.

PLATT, ROBERT S., JR. Department of Botany, Ohio  
State University. Columbus, OH 43210.

- The fixation of carbon and nitrogen: flawed gas-grabbing systems.

Botany courses today can make a major contribution to the understanding of energy-efficient food production in our energy-limited world. Two botanical processes are fundamental in this discussion: the photosynthetic fixation of carbon dioxide, and the fixation of dinitrogen, particularly that by legume root nodules and blue-green algae. These processes have interesting similarities. Both start with a complex enzyme (RuBP carboxylase and nitrogenase) that has an affinity for specific atmospheric gases ( $\text{CO}_2$  and  $\text{N}_2$ ), and both reactions are driven by ATP and a strong reductant. Furthermore, the efficiency of both enzymes is severely inhibited by molecular oxygen. Neither enzyme appears to be well adapted to modern atmospheres. (The parallel ends, of course, with an analysis of the specific mechanisms of oxygen inhibition.) The development of strategies to overcome this systematic flaw, however, would appear to be a primary objective both in natural selection, as evidenced in the recent

evolution of  $\text{C}_4$  photosynthesis, and for the genetic engineering of nitrogen fixing systems into plants other than legumes and algae.

SUNDBERG, MARSHALL D. Department of Biology,  
University of Wisconsin, Eau Claire, WI 54701  
- Stereological analysis of sun and shade leaves in general botany.

Stereology is the study of three dimensional objects through the interpretation of two dimensional images. Its primary use in biology has been to analyze ultrastructural aspects of plant and animal cells. The basic techniques of stereology are simple and may be applied to the analysis of cells with the light microscope. The paper describes the procedure used in a general botany course to quantitatively analyze the volumes of different cell types in sun and shade leaves. These data support the qualitative descriptions of sun and shade leaf anatomy found in most general botany texts.

WESTERLING, KARIN E.\* and THOMAS C. WILSON.  
Department of Developmental and Cell Biology and  
Instructional Development Services, University of  
California, Irvine, CA 92717. - Some factors affecting student perceptions of instructor teaching ability.

End-of-term teaching evaluations by students are used extensively as a measure of instructor teaching ability. Since information concerning instructor proficiency may then be used as a basis for course assignments, promotion, and/or rehiring decisions, it is important to determine whether student evaluations are valid and reliable. Fortunately, reliability is amenable to statistical analysis. End-of-term teaching evaluation instruments for biology teaching assistants were administered to undergraduate students. The students' evaluation of instructor performance is correlated with factors which are often thought to affect student perceptions of teaching quality. Students' expectation of course grade, perceptions of course difficulty, and estimation of gained reasoning skill are correlated with their impressions of instructor ability.