

E. Physiological Ecology, Disturbance, and Ecosystem Recovery

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I. Introduction

During the last decade ecologists seem to have reached a plateau in the attempt to construct a body of theory that is realistic and general enough to serve as a paradigm for their science. The effectiveness of major generalizations concerning such topics as succession, competitive niche divergence, diversity-stability, and r-K selection has been questioned by theoretical disproof or frequent case exception (Harper 1980; McIntosh 1980a). Few concepts of similar stature have been developed since about 1975, though there are current heavily researched issues (for example, disturbance and plant-herbivore interactions). During this period, we have learned much about the workings of populations, communities, and ecosystems, but we may have learned even more about the limitations of our traditional ways of viewing and studying ecological interactions (Saarinen 1980; Levin 1981; Salt 1983; Strong et al. 1984).

Ecologists are gradually becoming more comfortable with the heterogeneity, stochasticity, and ungeneralizability of many ecological phenomena (Johnson 1977; Simberloff 1980; Strong 1983). A few ecologists have recently suggested new ways of thinking about the complexity of ecological systems that are largely borrowed from the physical sciences. Examples are diffusion theory (Levin 1981), the environ concept (Patten 1982), hierarchy theory (Allen and Starr 1982), and strange attractors (Schaffer 1984). At the same time, others emphasize that more traditional approaches are suitable, but only if we appreciate that there are distinct *kinds* of communities, that most generalizing statements will be conditional, and that ecology is a pluralistic discipline (Diamond and Case 1986).

Our goal in this chapter is to describe ways in which our understanding of population, community, and ecosystem behavior can be unified through an emphasis on microsite physical/chemical fluxes and the physiological ecology of resource processing by individual organisms. Though terrestrial plant communities are used as examples, we believe that this functional approach is flexible enough to apply to other community types. We discuss this approach in Section II, apply the ideas to forest disturbance and recovery as an example in Section III, and conclude in Section IV with a general research strategy for understanding the physiological and demographic bases of community structure and dynamics.

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II. Physiological Ecology and Ecosystem Complexity

1. Scales and Process Versus State

The scales of space and time for living systems cover 14 orders of magnitude (Osmond et al. 1980; Delcourt et al. 1983, see also Part 1-B). Ecologists usually must consider interacting units that are simultaneously processing energy and resources on widely different scales. As a result, familiar complications arise when we (1) fail to define or communicate our scales, (2) observe and conclude on scales that are not appropriate for the questions at hand, and/or (3) use higher-level observations of state to infer lower-level process (Wiens et al. 1986). For example, much of the debate over succession and climax concepts since about 1920 could be viewed as examples of (1) and (2) (Pickett 1976; McIntosh 1980b; Shugart 1984). The problems imbedded in (3) can be quite deceptive. Do we really understand how or why succession occurs by repeatedly measuring biomass, density, or cover at designated points in the sere? Do we understand competition between plants when we construct uniform density replacement experiments and weigh biomass at the end of the season? Have we measured reproductive effort correctly by calculating ratios of vegetative and reproductive dry weights?

Prediction across hierarchical levels, be it upward or downward, requires a knowledge of process at each level and the scales of interaction and regulation between levels. The behavior of parts both drives and is constrained by the whole. Reductionist and holist viewpoints are thereby revealed as artificial breakages of a fundamental inseparable duality (Levin 1976a; Levins and Lewontin 1980; Allen and Starr 1982).

It is instructive to consider how subdisciplines of ecology have dealt with state versus process and space-time scales in the past. Ecosystem and physiological ecology have focused on similar processes but on widely different scales: ecosystem energy balance/leaf energy balance; system productivity/leaf and whole-plant carbon gain; system compartments and material transfer/whole-plant allocation; biogeochemical cycling/leaf and whole-plant water and nutrient economies; efficiencies (both); and homeostasis (both). Population and community ecology are more difficult to characterize, but many of the concepts are based either on static descriptions (population age and size structure, community classification, community diversity) or on complex phenomena that span several interactive hierarchical levels (population demography, competition, trophic level interactions, succession).

In our view, the traditional breakdown between community and ecosystem "levels of organization" is unfortunately divisive. The community is usually defined as the species populations on a site and their interactions, while ecosystem is defined as the community plus the abiotic environment. This isolates two perspectives on the same biotic system: state (community) and process (ecosystem). Do community snapshots in the form of species lists, relative abundances, or food webs mean much if such static descriptions are dissected away from the dynamic patterns of physical and chemical fluxes in the biotic-abiotic system? With their emphasis on trophic interactions, transfer efficiencies, and pyramids, animal ecologists have come closer than plant ecologists to a unified community-ecosystem understanding based on resource processing. Perhaps because of this original distancing of population-community versus ecosystem perspectives, population and ecosystem ecologists have disagreed vigorously

on which level of organization controls the other (Levin 1976a; McIntosh 1980a). Our viewpoint is this: the community does not *become* an ecosystem by adding the abiotic environment, it *is* an ecosystem because it is inseparable from the abiotic environment. The community (= ecosystem) is simply one level in the hierarchy of open living systems, from cell to planet, that transform energy and resources.

Ecosystem and physiological ecologists have been successful in answering many of their respective questions for at least three reasons:

1. These subdisciplines have tended to avoid the problems of middle-number systems (Weinberg 1975, cited in Allen and Starr 1982) by reducing the number of interacting components or relying on statistical summarizations of high-number processes. For example, plant physiological ecologists have concentrated on adaptation to environmental conditions on narrowly defined spatial and temporal scales, usually individual plant organs, for a short period of time relative to organ or organism longevity. They have also relied on the statistical laws of gaseous diffusion for carbon dioxide and water vapor transfer, and on unifying concepts such as water potential. Ecosystem ecologists have built successful models of carbon, water, and nutrient dynamics by aggregating organisms into a smaller number of functional categories (such as "herbaceous producers") and stratifying system components into variables and constants according to change rates, making analytical solutions and error control feasible.

2. For the most part, physiological and ecosystem ecologists have worked within their appropriate hierarchical levels. Few ecosystem ecologists would argue that biogeochemical models can be used to predict lower-level details such as community composition. Plant physiological ecologists are only now beginning to work upward mechanistically from single-leaf net photosynthesis and transpiration to whole-plant carbon balance and water use, explicitly considering variability in the microenvironments around plant parts and the variability (in age, condition, and position) of the parts themselves (Schulze 1982; Mooney and Chiariello 1984). But there are practical limits to this upward construction, and it may not be necessary to base ecosystem models on leaf-level behavior (Foin and Jain 1977). Shugart (1984) states: "It is not that the mechanisms of photosynthesis are not important in tree growth; it is that the explicit phenomena involved in photosynthesis at a leaf's surface are lost in the higher space/time scale."

3. Finally, *within their respective scales*, ecosystem and physiological ecologists have generally tried to understand system dynamics by studying processes, rather than just resulting end-states.

In contrast, population and especially community ecology have confronted middle-number systems, due to the questions asked, and have often relied on observations of state to infer process. To be sure, many questions can be satisfactorily answered by measuring only end-states. But the questions typically asked by population and community ecologists, and about which generalizations are sought, require a simultaneous knowledge of both lower-scale process and higher-scale regulation. The clearest demonstrations of this dual causality in population and community organization have been achieved through careful comprehensive experimentation (e.g., Connell 1961; Paine 1974; Harper 1977).

2. Microenvironmental Fluxes and Resource Transformation: A Unifying Perspective

A useful approach to ecological interactions is through the relative costs and benefits of alternative resource transformation strategies, an explicit emphasis on how organisms acquire and use the materials they need to grow and produce offspring (Orians and Solbrig 1977a; Schulze 1982). This must include a knowledge of the ranges and flexibilities of resource use in changing environments by individuals within populations and communities, as well as the effects of different patterns of use on short-term and long-term differential survival and reproduction.

Such an approach is not new, since ecologists have long recognized the significance of variation in resource acquisition and use, as related to heritable traits and thus natural selection. Optimal foraging theory is the most recent and most rigorous expression of this approach in animal ecology (E.E. Werner and Mittelbach 1981). Plant physiological ecologists have made tremendous advances with this perspective (Lange et al. 1981, 1982, 1983a,b; Chabot and Mooney 1985). Nevertheless, it can be argued that the potential of resource relationships has not been fully exploited in the attempt to understand complex ecological interactions, particularly in terrestrial plant communities. Complicated phenomena like competition and succession are still studied most often by measuring state variables such as plant dimensions, plant weight, or seed number, the final higher-level outputs of black-boxed processes, and disturbance is often defined in terms of biomass destruction and/or available space (Grime 1979; Sousa 1984), rather than changing resource patterns (Vitousek and White 1981; Bazzaz 1983).

We believe that a more satisfying mechanistic understanding of such phenomena can be achieved by viewing the interactions between plants through their mutual influences on the physical and chemical fluxes (resources and modifiers) that comprise their shared microenvironment (see also Part 2-A). We are *not* arguing that predictions of plant community behavior must incorporate explicit formulations of individual or organ-level process, but rather that higher-level modeling and prediction may be weakened substantially without a clear understanding of these details. Plant-animal interactions, such as herbivory, pollination, seed predation, dispersal, and mycorrhizal relations may also be viewed profitably from cost-benefit accounting of limited resources (Mooney and Gulmon 1982; Coley et al. 1985).

Individual traits or organisms should not be isolated from their respective ecological and evolutionary contexts (Gould and Lewontin 1979; Harper 1980) and it can be misleading to over-emphasize a single criterion of performance as opposed to a balanced suite of criteria. The allocation of carbon, water, and nutrients to a particular growth or behavioral pattern may not maximize a specific criterion of efficiency, but nonetheless represent an *effective* overall strategy, given the ever-shifting pressures of the biotic-abiotic environment. Furthermore, organisms are rarely selected by one or two overriding factors, and we should not be surprised if plants and animals act suboptimally, from the "peak performance" viewpoint, most of the time (Lewontin 1979; Harper 1980, see also Parts 2-A and 2-B). Optimal combinations of resources and modifiers occur relatively infrequently and occupy only a narrow range of the broad microenvironmental fluctuations that most terrestrial plants routinely experience and

survive. In addition, there may be underlying genetic constraints on selection for a given trait, such that further increase in performance for that trait would be offset by decreased performance in another (Antonovics 1976; Wright 1977; Via and Lande 1985). On the whole, terrestrial plants are remarkably flexible in their responses, relying on several individual and population-level characteristics to buffer them from environmental unpredictability. These include modular construction, dormancy, phenotypic plasticity, and/or genotypic diversity (Allard and Bradshaw 1964).

Therefore it is not wise to apply specific performance criteria for resource use to all communities, and not even within a more restricted category of systems like terrestrial plant communities. The plasticity of plant responses and the unpredictability of community interactions make this tenuous. A thorough knowledge of the short- and long-term dynamical pressures of a system is necessary to interpret the relative effectiveness of a given pattern of response (Wiens 1986).

Spatial heterogeneity and plasticity are largely responsible for the difficulties plant ecologists face in formalizing community interactions (Levin 1976b; Schaffer and Leigh 1976; Pacala and Silander 1985). These and other problems have led Botkin (1981) to suggest that there are fundamental limits to what is knowable about community interactions as complex as succession, and he favors theoretical constructs and mathematical models over field and laboratory experiments for exploring these limits. We agree on the potential existence of limits to our predictive knowledge and that quantitative models are powerful tools. However, we would argue that an equally productive method of exploring the certainties and uncertainties of community interactions is to precisely describe the patterns of resource use by participating species in the context of how the mosaic of microenvironments in the community changes in predictable and unpredictable ways under the influences of external forces and the community itself. The research strategy presented in Section IV is developed from this proposition.

The birth, growth, and death of a single plant in an operationally defined microsite can be modeled conceptually in a manner that illustrates this perspective. We can consider the target plant and its microenvironment to be an open system, which at this scale is designated as a microsystem. The microsystem is operationally bounded where the influence of the target plant on its neighbors is judged by the observer to be insignificant. The microsystem boundaries for a given plant must be flexible, since they will vary with the status of the target plant and neighbors, as well as with the interaction that is being studied. Aboveground and belowground boundaries may differ depending on root and shoot architectures and the importance of competition for different resources. If processes such as pollination and gene flow are in question, microsystem boundaries will be less distinct since plant-plant interactions are regulated less by plant positions and the number of plants interacting may be larger. In this discussion, we will emphasize interactions between adjacent plants.

The target plant and neighbors acquire and allocate resources through whole-plant integration of physiology, module morphology, and architecture. They interact through mutually influenced aboveground and belowground fluxes in physical and chemical factors. The mutual microenvironment is affected not only by the plants, but also by direct microsystem inputs and outputs (incident solar radiation, water drainage out of the rooting zone, etc.), physical disturbance, and within-microsystem death and

mineralization. Animals and microbes influence, and are influenced by, the micro-environment. Other outputs from the microsystem include gamete and propagule dispersal during reproduction, as well as the loss of tissue to herbivores.

Nothing in this model is earth-shaking. However, the advantages of such a formulation are that it views the target plant and its environment as a dynamic open system (Levin and Paine 1974; Whittaker and Levin 1977) and explicitly considers plant-plant interactions as occurring through mutually affected physical and chemical fluxes (Wu et al. 1985, see also Part 2-C). Models of plant interactions that use empirical predictors of single plant performance are based on essentially the same concept of the target plant in a neighborhood (Weiner and Conte 1981; Weiner 1982; Pacala and Silander 1985).

In some cases, it will be more useful to consider the microsystems of morphological subunits of the target plant, rather than the entire phenotype. Modular construction permits a realistic breakdown. Thus shoot or root branches may interact with neighboring branches of several species, with potentially different competitive outcomes (Küppers 1985). The reciprocal effects of each species on the shared branch environment can be modeled. Ramet interactions among clonal species may also be described more precisely if the ramet microsystem is used rather than the genet microsystem (Hartnett and Bazzaz 1985).

The model can be expanded to consider a population of genotypes of the same species. The target population now has age, size, and spatial structure, and thus distributions of the states and potential responses of individuals. We recognize that quantifying these dynamic distributions is more difficult than it sounds, but suggest that this upward construction of a population's status at any point in time is, in principle, the logical connection between physiological ecology and population biology. Once again, we are not suggesting that leaf-level physiological rates should be the basis of integration at higher levels. In this model, whole-plant microsystems are the focus, and the population is a spatial mosaic of individual plant microsystems. The microsystem boundaries of adjacent target genotypes in the population will usually overlap to produce "interlocking spheres of influence" (Gleason 1975). This yields intraspecific interaction and the possibility that an individual of a second species located in the neighborhood overlap zone can simultaneously affect two or more target genotypes.

Adjacent microsystems of one or more species that are similar in plant status and physical and chemical fluxes may be grouped into units that are distinct from neighboring units. This is frequently what is meant by "patches" in the literature. The criteria and scale used for grouping will vary with the system and questions addressed. Regardless of whether individual microsystems or patches of similar microsystems are used, we agree with Levin and Paine (1974) that it may be useful, if not necessary, to quantify the statistical properties of such mosaics in order to understand overall community behavior. This has been attempted for individual plant microsystems in some of the work on size hierarchies (Weiner 1985) and in Silander and Pacala's (1985) neighborhood predictors. Transition matrices (Stephens and Waggoner 1980), demographic functions (Levin 1976b), and the FORET gap models (Shugart 1984) have been used to explore patch dynamics.

Intraspecific or interspecific competition can be modeled in this manner at the level of either individual plants or populations (Caldwell et al. 1983; Küppers 1984,

1985). Succession is explored through differential recruitment, resource acquisition and allocation, and mortality under shared microenvironmental influences, and by simultaneously considering each participating species as a target population. The actions of physical disturbance, herbivores, predators, pathogens, pollinators, dispersers, and other agents may alter the outcomes of either competitive or successional series of events. Conversely, the trajectories of plant interactions may differentially affect animals that reside in or pass through the microsystem. The effects of genetic identity (in the individual model) and genetic structure (in the population model) can be considered where desirable. Finally, from the viewpoint of ecosystem function, the inputs and outputs of each microsystem and the pattern of energy and resource exchange between microsystems in the community mosaic can be expressed.

3. Cross-Level Integration and the Role of Physiological Ecology

The foregoing discussion can be distilled to two major points:

1. Complex ecological phenomena are best studied through investigation at several hierarchical levels on appropriate spatial and temporal scales, with attention paid to both lower-level driving processes and higher-level regulating processes.
2. With specific reference to terrestrial plant communities, a unifying way to view the mechanisms of plant-environment, plant-plant, and plant-animal interactions is through precise knowledge of resource use by interacting individuals or populations.

Any disharmony in these statements can be resolved by carefully circumscribing the role of physiological ecology in understanding higher-level organization and dynamics. First, our comments on historical state versus process emphases within ecology suggest that physiological ecology and ecosystem analysis can be linked in concept and quantification due to the common focus on physical and chemical fluxes (see also Part 1-A), and this has proven to be true. Within the constraints set by overriding physical forces in each ecosystem, a knowledge of the physiological behavior of individual plants can contribute to the explanation of major components of ecosystem function (Miller 1979; Lange et al. 1983b; Billings 1985). The reciprocal effects of larger-scale ecosystem forces (bedrock geology, regional climate, etc.) on the success of alternative strategies, such as evergreen versus deciduous habit, can also be explored. The projects on convergent evolution in mediterranean and desert ecosystems are classic examples of this kind of integration (Mooney 1977; Orians and Solbrig 1977b).

Second, there are numerous examples of how a knowledge of physiological and life historical behavior can provide a mechanistic understanding of population growth, size and age structure, optimal reproductive and defensive allocation, coexistence, competitive outcome, or successional turnover (e.g., Foin and Jain 1977; Bazzaz 1984a; Mooney and Chiariello 1984; Bazzaz et al. 1986).

The potential explanatory power of physiological ecology at the community (= ecosystem) level will vary with the dynamics of the system in question. Higher-level behavior cannot be fully captured by reductionist assembly of lower components; neither can it be fully understood in most cases without the mechanistic detail of

physiology. Physiological ecology and population biology can jointly clarify this interdependence if community interactions are viewed through the costs and benefits of alternative strategies of resource use as related to reproductive success.

III. Disturbance and Response in Closed Forests: an Example

The surging interest in disturbance in the last few years (reviewed in Sousa 1984; Pickett and White 1985) reflects the shifting expectations of ecologists about community organization and provides an example for applying the ideas developed in Section II. We will first discuss our view of disturbance as changes in physical and chemical fluxes, and then suggest how the physiological and life historical strategies of species may serve as a starting point for understanding population and community (= ecosystem) behavior in moist, close-canopied forests. Elements of this discussion have been treated in previous papers (Bazzaz 1983, general considerations; Bazzaz 1984b, wet tropical forests specifically).

1. Disturbance from the Perspective of Individual Organisms and Physical/Chemical Fluxes

Much of the recent literature portrays disturbances as exterior forces that disrupt community structure and function. To be sure, disturbances are sometimes classified as "exogenous" versus "endogenous" (Bormann and Likens 1979), and it is now more widely accepted that disturbance is an integral feature of most communities (White 1979; Sousa 1984; Pickett and White 1985). However, there is a strong tendency to define and describe disturbances as sudden changes in system states (community composition and structure) rather than processes (physical/chemical fluxes and organismal responses). As they are usually regarded, disturbances cause changes that are recognizably different from nondisturbed community behavior. This may be useful for certain questions, but it is not free from problems.

For example, storm winds may fell trees in a mature forest, allow shade-intolerant pioneers to colonize larger gaps, and initiate a successional turnover of dominance to primary species as the gap community matures. In contrast, the same storm winds could topple pioneer dominants in a young forest, release shade-tolerant seedlings, and hasten the normal successional turnover. The same physical fluctuation, increased windspeed, may cause a different direction of community change in the mature forest (a qualitative shift) or a different rate of change in the young forest (quantitative shift). Aside from the question of whether or not acceleration of a normal pattern of community change should be considered a disturbance, how do we reconcile individual tree responses with the different community effects to produce a unified definition of disturbance?

The key point is that communities do not respond to environmental shifts; individual organisms do. To the individual plant, disturbance events are quantitatively, but not qualitatively, different from other shifts in physical and chemical fluxes. The fol-

lowing discussion attempts to clarify our understanding of disturbance by focusing on the responses of individuals to disturbance-altered environments.

The pattern of concentrations and fluxes of physical and chemical factors forms the microenvironment of a plant at a given point in time. Based on the identity and status of the plant at this point, some of these factors will be consumable resources, some will be modifiers of consumable resource uptake and utilization (including toxins), and still others may have no detectable influence on the plant. Since most factors can act as either a resource or a modifier, often simultaneously, flexibility in factor categorization is necessary.

Individual resources and modifiers may behave synchronously or asynchronously, due to the physics and chemistry of their interactions as well as site conditions. The effects of spatial and temporal differences in resource packaging on plants are, in general, poorly understood (P.A. Werner 1976). The pattern of physical and chemical fluxes on a given microsite depends on external inputs to the microsystem and modification by neighborhood community structure. Changes in the fluxes of a specific factor have three components: direction, magnitude, and rate.

A disturbance can then be thought of as a change in physical and chemical flux patterns (see also Part 1-A) that is *judged by an observer* to influence target organisms in a manner significantly different from normally experienced fluctuations. This judgment is not arbitrary, since it must be based on a thorough knowledge of target organism responses. The influence of such a shift on the target organisms may vary from being highly positive (enhanced reproductive success) to highly negative (death), and may be due to the direction, magnitude, and/or rate of change.

Disturbances will usually consist of two phases of environmental fluctuations. In the first phase, a relatively rapid, large shift in one or more factors causes unusually high growth or death rates of parts of individuals, whole individuals, populations, or even most of the community. Community structure is thus changed, which results in a second, longer-lasting phase of altered microenvironmental fluxes. For example, a phase 1 increase in windspeed during a thunderstorm falls an overstory tree. After the storm, the changed microenvironmental fluxes in the gap initiate phase 2. This second phase will last much longer than the first, as fluxes return gradually to pre-disturbance levels during patch regrowth and maturation.

Disturbances have often been categorized as environmental fluctuations versus destructive events (e.g., White and Pickett 1985). This distinction is confusing for at least three reasons. First, some disturbances may initially operate through a sudden shift in the relative growth rates of populations rather than immediate mortality. For example, the addition of phosphorus (phase 1 shift) to a stable lake community may change community composition, structure, and physical/chemical fluxes significantly (phase 2) due to the growth and crash of algal populations. Second, when mortality does occur, the destruction of organisms is *caused* by extreme fluctuations in environmental factors (high temperatures, wave energies, soil salinity, etc.). This is true even for biological agents of disturbance. For example, the chewing by insect mandibles is, to the plant, nothing more than very intense localized pressure that severs or crushes cell walls. Likewise, organisms that rely on secreted enzymes or other compounds for external digestion change the chemical environment around plant epidermal tissues. Though plants may respond in specific ways to biological disturbance agents, the

interaction is always through physical and chemical forces that, if necessary, can be quantified. Third, destructive events *are* environmental fluctuations for the plants that are not killed in phase 1 and live to experience phase 2. The reason is that a plant does not "see" surrounding community structure, either intact or heavily disturbed. Rather, it responds to the physical and chemical fluxes of its microsite as they are altered by healthy, damaged, or dead neighbors. The "structure" of a plant's neighborhood is simultaneously (1) a modifier of unbound resources, through architectural and physiological effects on such variables as temperature, irradiance, and ion gradients in the soil, and (2) a pattern of temporarily unavailable, "slow-moving" resources, those absorbed or bound up in the biomass of competitors. The structure of the community is both the collective result of individual plant responses to previous microsite mosaics, and the cause of present microenvironmental mosaics to which plants are responding.

The problem is no longer that of categorizing disturbances as environmental fluctuations or destructive events, but rather defining the criteria whereby "normal environmental fluctuations" are distinguished from "disturbance fluctuations". If we persist in regarding disturbances as events that are in some way not normal, then we cannot define disturbance until we face the troublesome task of defining normal (undisturbed) individual or community behavior. This is analogous to the problem of defining community stability. Both concepts are scale-dependent. They are functions of the questions we ask, not of the system itself, since the appropriate scale and system boundaries are not defined until we pose the question. This is why a discrete event such as the burning of 100 hectares of forest can be simultaneously "normal" for the species at the regional/millennial scale, and "disturbance" for the individual at the microsite/lifespan scale. Likewise, the local stand of trees may be in successional transition following fire (unstable), while the landscape mosaic of stands is in equilibrium (stable).

At the microsite scale, populations and communities are composed of individuals that respond uniquely to any given shift in energy and resource fluxes. This uniqueness is due to genetic individuality, developmental status, and/or the differing attributes of each plant's neighborhood. These individual responses will vary with organism stature, longevity, life history, and physiology. Thus a single disturbance may be imperceptible for one organism (or population) and disastrous for a second organism (or population) on the same site.

Differential perception of disturbance events by organisms or populations may result in parts of the system responding to environmental shifts on quite different scales than the rest. Community properties like species richness and the distribution of relative abundance among species can respond in complex ways to different disturbance frequencies (Allen and Starr 1982; Sommer 1985).

Subsequent interactions (during phase 2) between organisms that have been differentially affected by a disturbance event in this manner may be quite different as compared to pre-disturbance dynamics. The natural or intentional elimination of keystone predators (Paine 1974), herbivores (Tansley and Adamson 1925), or superior competitors (Abui-Fatih and Bazzaz 1979) may significantly alter the composition and developmental patterns of the remaining community. In contrast, the loss of a numerically important species from a community that is less tightly structured may not be so

significant. The dramatic decline of American chestnut (*Castanea dentata*) in the eastern U.S. was followed by some shifts in the abundance of other tree species, but the tree community absorbed the disturbance without major ordered change (McCormick and Platt 1980).

The result is that any physical and chemical shift classified as a disturbance must also be community-defined, even though it is initially measured as a set of changes in fluxes relevant to target organisms. The effect of the disturbance on ecosystem properties then depends on the relative role of the disturbed organisms in energy flow and nutrient cycling, and on the altered interactions among survivors. Cyclic regularity of disturbance, community status, and ecosystem functions may be fostered by, and favor, the target species themselves. Examples are fire in boreal (Heinselman 1981) and western montane (Romme 1982) coniferous forests, and in chaparral (Mooney and Conrad 1977). Such cases epitomize the need for a community scope in determining the events that should be regarded as disturbances.

The preceding discussion clearly emphasizes the role of the observer in defining scale, and suggests that there are no easy ways to divide the continuum of environmental fluctuations into normal and disturbance (abnormal) regions. We should not be surprised that generalizations about disturbance across widely different scales and community types encounter difficulties. We may have to regard disturbance on a case-by-case basis and rely on operational definitions of "normal" that express something like "statistically most probable". A disturbance is then a shift in physical and chemical fluxes that affects individual organism behavior and community composition and structure by deflecting them from the most probable state or series of transitions.

The advantage of defining disturbance in these terms is that we can directly assess the effects of disturbance-altered physical and chemical fluxes on the physiological ecology of individual organisms, their interactions, and cumulative ecosystem response. We can also consider the implications of disturbed environments for the evolution of physiological strategies. Though elements of the following discussion apply to other communities, we will focus on tree physiological and reproductive strategies as related to disturbance in moist temperate and tropical forests.

2. Microenvironmental Patterns in Forest Gaps Versus Understory

The effects of closed canopies on the complex microenvironmental gradient from the disturbed areas of large natural gaps to the intact forest understory are pervasive. A multi-layered structure alters the ranges and spatial-temporal variations in air and soil temperatures; windspeed; ambient [CO_2]; irradiance; species distribution; soil moisture; nutrients; and relative humidity. The breadth and steepness of gap-understory microenvironmental gradients are functions of disturbance frequency, size, and magnitude. Gap size, shape, orientation, and the remnant community interact to produce enormous heterogeneity among forest gaps in patterns of physical and chemical fluxes (Ricklefs 1977; Bazzaz and Pickett 1980; Denslow 1980; Bazzaz 1983, 1984b; Pickett 1983; Brokaw 1985).

Both ends of this complex gradient impose constraints on suitable physiology, morphology, and architecture. Though early successional environments are often con-

sidered to be the most "rigorous", especially due to the ranges of physical factor variation, the deep shade produced by trees of mature forests may be just as "rigorous" as gap environments because of the lean carbon budgets and the limited allocation options that are imposed by the canopy.

The radiation environments of mature forest and conifer plantation understories have been studied extensively through field sampling (e.g., Anderson 1964; Hutchison and Matt 1977) and theoretical models (e.g., Jarvis and Leverenz 1983). The water environment has also been monitored (e.g., Minckler et al. 1973; Patric 1973; Landsberg 1984). However, in spite of the long-standing debate over root versus shoot competition in the understory (Pearson 1930; Korstian and Coile 1938; Shirley 1945), the interactions between light, moisture, and nutrient limitations are only partially understood. High soil water potentials should reduce the need for a more extensive root system and allow greater resource allocation to stems and leaves. Even small differences in height growth that result may be important during early seedling growth due to competition for light in the herbaceous stratum.

The microenvironments of temperate and tropical understories differ in many ways that suggest sunflecks may be more important for suppressed seedling carbon gain in the latter. Temperate broadleaved forests have generally higher diffuse irradiance on the forest floor and a seasonally leafless canopy that, in the spring at least, offers the possibility of high net assimilation by species that break dormancy early. However, the water environments may also be influential. There are two ways in which stomata may operate to take advantage of temporarily high photon flux densities. They may open quickly in response to increased irradiance or remain open continuously. The stomata of some shade-tolerant temperate species respond faster than co-occurring shade-intolerant species to changing irradiance, suggesting that the former profit more from sunflecks (Woods and Turner 1971). However, ample soil moisture and low vapor pressure deficits may permit continuously high stomatal conductance by shade-tolerant species in tropical wet forest understories (Mooney et al. 1984). If this proves to be common in these forests, it will stand in contrast to most of the temperate zone, where suppressed shade-tolerant seedlings experience lower soil water potentials and higher vapor pressure deficits, particularly in middle to late summer. Available data are sparse on the relative role of sunflecks, but the prediction is true for *Claoxylon sandwichense* (Pearcy and Calkin 1983) versus *Acer saccharum* (Weber et al. 1985).

The potential for shoot thermal and water stresses is greater in gaps because of the increased radiation loads. Large gap pioneer species no doubt experience lowered leaf water potentials at midday, and this may increase in daily duration if allocation to roots does not keep pace with shoot height growth as saplings compete for gap space. They probably must tolerate lower tissue water potentials than species in the understory, since excessive leaf temperatures would result if stomata were to close and leaf orientations remained the same. However, gaps consistently contain more water in addition to the radiation, and actual water stresses may be less significant than commonly assumed. High assimilation and growth rates can be supported by the available soil moisture, and affordable allocation of carbon to root systems can increase access to water deeper in the soil, at least until competition in the developing gap community becomes intense. Some data exist on microenvironmental patterns in natural gaps, as well as models of direct beam and diffuse radiation. But a great

deal of work is in order before we will understand the variations in physical and chemical fluxes between and within gaps differing in size, shape, orientation, remnant community, and age. The general changes in fluxes brought about by a multiple-tree windthrow are suggested in Fig. 1.

3. Plant Performance as Responses to System Fluxes

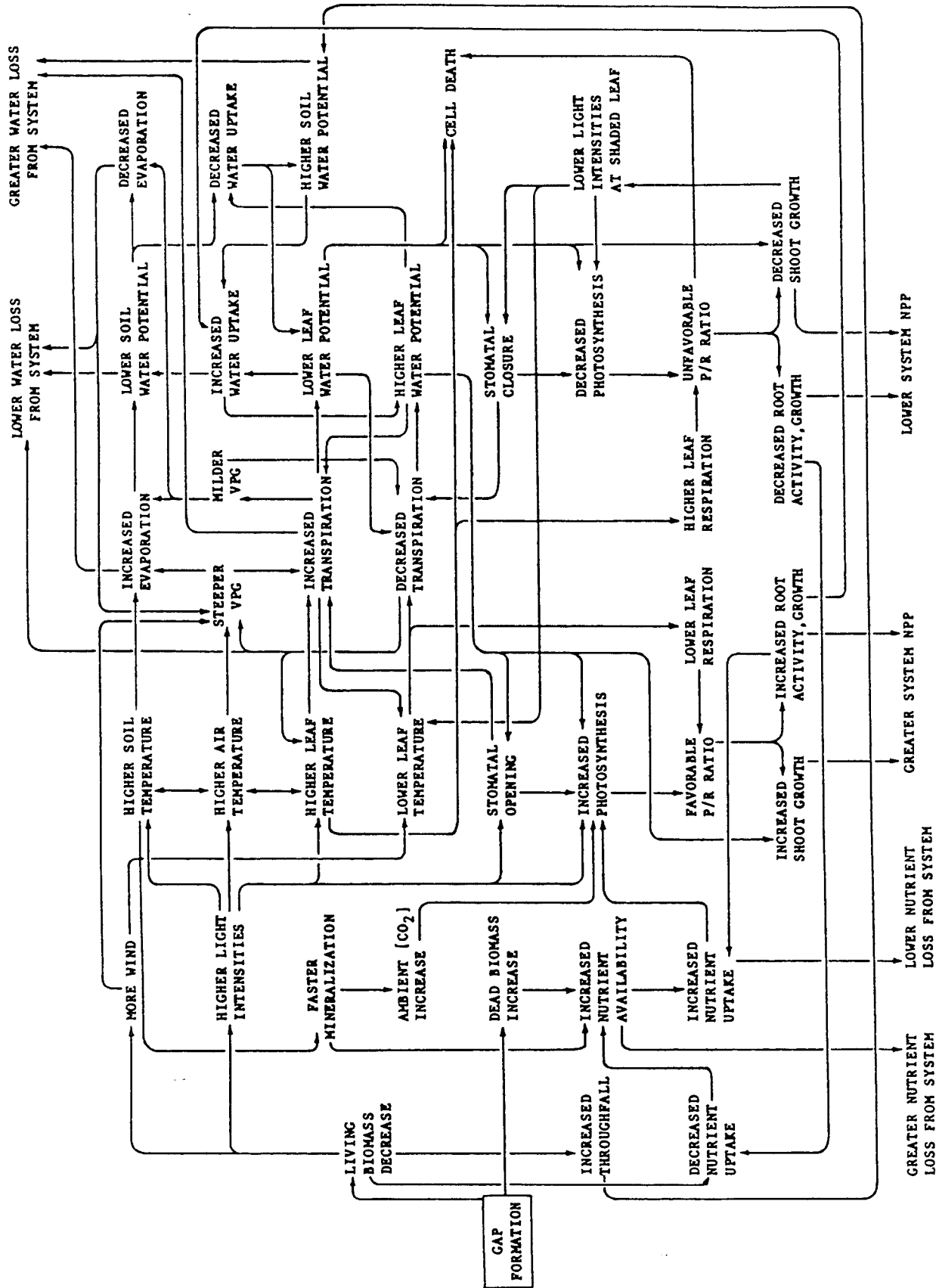
Potential responses of plant shoots and roots to forest gap environments are shown in Fig. 1. The interactions between light, water, and nutrient availabilities are suggested along with the effects of differential allocation of carbon to roots and shoots. To simplify the diagram, only plant-environment interactions are shown. Obviously, it is necessary to consider the influences of biotic agents (herbivores, pollinators, pathogens, mycorrhizae, and competitors) on plant physiological performance, and vice versa, and these could be added where desired.

Though plants can be widely plastic in physiology and architecture (see Part 2-A), the divergent problems posed by gap versus understory environments apparently exceed the capacity for any single species or group of species to grow rapidly at all points along the gap-understory gradient (Bormann and Likens 1979; Canham and Marks 1985). This may be largely due to the extensive differences in photosynthetic machinery that are required for survival and growth at the gradient extremes (Bjorkman 1981).

In the absence of competition, even a poor growth rate could result in maturation to reproductive status in all but the smallest gaps, where lateral growth of surrounding canopy trees can close the opening. But competition occurs in all gaps not caused by catastrophic large-scale disturbance. A distinct advantage may result for any species with traits that allow it to establish sooner and/or grow faster under at least some of the environments produced by the current forest structure and disturbance regime (see also Part 2-C). The hypothesis (now being tested in the wet tropics. C.B. Field, pers. commun.) is that there is no super generalist that can outcompete potential specialists at their preferred points along the gap-understory continuum. Thus species with recognizable "sun versus shade", "exploitive versus conservative", or "small-gap versus large-gap specialist" traits would result (Bazzaz 1979; Bormann and Likens 1979; Bazzaz and Pickett 1980; Denslow 1980; Pickett 1983; Bazzaz 1984b; Hubbell and Foster 1986).

This does not mean that generalists will be eliminated, even if many specialists were to finely divide the gap-understory gradient. The reason is that stochastic disturbance timing and propagule availability may frequently allow generalists to establish before specialists. Then prior occupancy can reverse the normal order of competitive superiority and permit the generalist to succeed often enough to avoid local or regional extinction.

For sessile organisms, natural selection will favor genotypes that (1) modify their environment such as to benefit their own offspring, or (2) are able to disperse in space and/or time from one suitable but ephemeral habitat patch to another. Since architecture and physiology are jointly responsible for the acquisition of resources and the relative influence exerted by a terrestrial plant over its microsystem, there is a tendency



for dominant plant species in a community to possess the largest above- and below-ground structure, which sequesters and regulates resources, and to be long-lived. The tree life form epitomizes this tendency (Schulze 1982). This may increase reproductive success at the expense of competitors that are poorer environmental modifiers. However, a community dominated by such pervasive resource users may be quite stressful (*sensu* Grime 1979), and require conservative carbon, water and nutrient use, even by adults.

If offspring are to be successful in the environment altered by large old adults, they must be able to either: (1) tolerate lower levels of light, water, and nutrients as juveniles and then respond to disturbance of conspecific adults by using the advantage of advance establishment and capturing overstory space; or (2) germinate and grow quickly after disturbance and then switch to a more conservative mode of resource use typical of adults. The ability of trees to make this physiological switch is apparently limited. Though many species can develop sun or shade leaves and adjust overall architecture and physiology following environmental shifts (e.g., Schulze 1972; Wallace and Dunn 1980; Fetcher et al. 1983; Langenheim et al. 1984), there seem to be genetically based resource acquisition and growth rate strategies that cannot be modified enough to yield success on both ends of the gap-understory gradient, particularly under competitive conditions (Bazzaz and Pickett 1980). Therefore the first alternative above, conservative growth patterns and tolerance of low resource levels, results in the classic strategy of extreme understory (shade) tolerance typified in temperate forests by *Acer saccharum* and in wet tropical forests by some species of *Shorea*.

The logic of structural dominance over microenvironments in forests can thus be summarized. Organisms with large, long-lived structures extensively modify local resource availability, thereby suppressing or eliminating weaker competitors, but this requires inherently conservative growth by adults and advance-established juveniles if the strategy is to succeed. Conservative resource use is attained by lowering energy and nutrient expenditure (respiration rates) to match prolonged periods of low resource flux, rather than brief periods of peak flux, such as sunflecks (Bormann and Likens 1979; Grime 1979, see also Part 2-A). Lower respiration rates are feasible due to the ameliorated understory environment, and are enforced by limited carbon and nutrient acquisition. In addition, acquired resources are valuable due to the difficulty of replacing them. Thus allocation to defensive structures or chemistry may be more cost-effective, per unit resource defended, than in resource-rich environments (Bryant et al. 1985).

This strategy is geared toward the relatively steady understory environment produced by adults, and to the shifts in physical and chemical fluxes brought about by less

Fig. 1. Plant physiological responses to microenvironments in the forest gap ecosystem. The shifts in physical and chemical fluxes caused by a multiple-tree windthrow, and the physiological and growth responses by plants, are shown at a useful intermediate level of resolution. Chains of causation feed back to yield either homeostasis, positive resource gain and growth, or suppression and death. Plant responses that influence system variables such as NPP and nutrient loss are included. Liquid water losses from the system include dissolved, adsorbed, and suspended materials. This will be the major route of nutrient loss, unless nitrogen is volatilized by fire. Interactions with animals and microbes, and the finer details of several processes (such as stomatal control), are left out for clarity

destructive disturbances, such as branch falls, standing death, and single-tree wind-throws. In spite of their ability to survive prolonged understory suppression, even the most shade-tolerant overstory species appear to require the resources released by these smaller disturbances for attaining reproductive status as a canopy dominant or co-dominant (Schulze 1972; Whitmore 1983; Canham and Marks 1985). Advance establishment presumably provides a competitive edge in these situations. The degree to which understory trees, shrubs, and herbs rely on gaps of varying size for greater reproductive success, if not reproductive maturation, has received much less attention (Hibbs et al. 1980; Collins et al. 1985).

Most close-canopied forests regularly experience larger disturbances. Even the communities in which understory tolerance is a common strategy are occasionally ravaged by wind, fire, drought, pathogens, insects, or combinations of these factors. Larger gap disturbances increase physical and chemical fluxes to levels that overwhelm the conservative usage by shade-tolerant species. If the patches produced by the regional disturbance regime exhibit fluxes that are sufficiently high and prolonged, a rapid growth (exploitive, opportunistic) strategy may be successful. This strategy usually involves fast resource acquisition and growth, early reproduction, adequate seed dispersal in space or time, and relatively quick replacement by other species. In some cases (e.g., *Liriodendron tulipifera*; some species of *Ceiba*), swift attainment of competitive adult size and lengthy occupation of overstory space occurs.

In closed forest systems, the exploitive strategy is geared to the high fluxes of resources in the heavily disturbed environments of large gaps. However, plants growing in these environments must be able to tolerate extreme levels of physical factors while accumulating resources: high and low temperatures, steep vapor pressure gradients, greater windspeeds, low tissue water potentials, and potentially destructive irradiances. Fast growth and the repair of biochemical and cellular damage caused by physical extremes require a high respiration rate, which seems to be a relatively inflexible trait of these species. Thus rapid growers exhibit an unfavorable carbon balance in the resource-limited intact understory. Conversely, conservative shade-tolerant species often cannot cope with these stresses and experience high mortality when released in larger gaps (Richards 1952; Whitmore 1978).

To the extent that temperate and tropical tree species are specialized to varying degrees on different portions of the gap-understory gradient for establishment and early growth (Ricklefs 1977; Denslow 1980; Pickett 1983), the disturbance regime of a forest regulates opportunities for regeneration (Whitmore 1982, 1983). Tolerance of dense shade does not guarantee reproductive success and the potential advantages of predisturbance (advance) regeneration, such as prior occupation of space and initial competitive advantage, must be weighed against the necessity of undergoing a major shift in microenvironment as the shade-tolerant seedling responds to canopy removal. Likewise, the advantages of post-gap establishment and avoidance of such an environmental shift must be balanced against the obstacles to shade-intolerant seedling success in heterogeneous gaps. The gap-understory microenvironmental gradient and the remnant community jointly determine the potential success of different regeneration tactics and gap community development on a site-to-site basis.

The relative importance of exploitive and conservative species groups across a forested region will therefore depend on the regional disturbance regime, overall

resource levels (precipitation, soil fertility, etc.), and current species ranges. If any of these are altered, the dominance among strategies may also shift. Because overstory trees strongly influence microenvironments and possess long lifespans, there is an inertia in community change both on short-term (successional) and longterm (e.g., glacial) time scales, such that community composition may be out of phase with local or regional environmental changes (Davis 1986). The interpretation of both the present and future success of tree strategies in a given system must allow for this syn- copation.

4. Life History Traits and Reproductive Strategies

The life history features of exploitive and conservative tree species groups have been discussed elsewhere (Bazzaz 1979; Bormann and Likens 1979; Bazzaz and Pickett 1980; Lechowicz 1984; for examples of species categorizations, see Bormann and Likens 1979; Denslow 1980). Much is known about breeding systems, seed biology (fecundity, periodicity, viability, dispersal, dormancy, predation, germination cues, longevity, seed size, seed banks), leaf and shoot growth phenology, tree longevity (genet and shoot), tree architecture, and the ability to reproduce vegetatively (e.g., Fowells 1965; U.S. Forest Service 1974). The connections between these traits, the physiological attributes discussed in Section III.3, and different forest disturbance regimes are becoming clearer (Oliver 1981; Bazzaz 1983, 1984b; Brokaw 1985; Canham and Marks 1985). In fact, Whitmore (1982) suggests that basic similarities exist among the close-canopied forests of the world in patterns of disturbance and regeneration.

We wish to add only a few comments to this body of observations and hypotheses. Growth rates based on dry weight gain are often designated or implied as the most critical measure of plant success in competitive situations. However, the effectiveness of biomass allocation may be just as important for clarifying the differences between species as absolute leaf-level or whole-plant carbon gain (Küppers 1984, 1985). For example, allocation to nonphotosynthetic defensive structures may enhance longterm survival and growth even though initial investment seems costly in terms of immediate growth (Küppers 1985). Many tropical pioneer trees, typified by species of *Ochroma*, produce stems made of metabolically inexpensive, low-density wood, resulting in low stem strength. There is a tendency among these species for the branching architecture to maximize leaf area supported per unit nonphotosynthetic weight, after allowing for allocation to defensive structures. The rapid attainment of suitable canopy height and reproductive status in an ephemeral, resource-rich environment has been favored over the construction of a more massive, longer-lived shoot. Growth rates based solely on biomass gain may not be any higher for these species as for competitors that would build more compact tissues and increase the volume of occupied space more slowly on the same site, especially if roots are taken into account. The higher probability of earlier death and replacement by slower-growing competitors is outweighed evolutionarily as long as sufficient seed production and dispersal in space or time occurs.

There is yet another level of effectiveness that must be considered. Unless growth is related to reproductive strategy, even a thorough knowledge of growth performance may be insufficient to understand species' behaviors. For example, the reproductive

success of some permanent understory tree, shrub, and herbaceous species may depend on canopy gaps as much as overstory trees. The understory species may reproduce sparingly while suppressed but increase seed production when released by mild disturbances. Large fractions of successful lifetime progeny could be produced by a parent during brief periods of canopy gap formation and closure, due to the windfall of resources and attraction of dispersers to gap environments (Thompson and Willson 1978). If these species allocate most of their newly acquired resources to seed production, their measure of reproductive effectiveness may be higher than their competitors, even though vegetative biomass or dimension growth rates are lower. The question is one of the reciprocal relationship between investment and return *as related to reproductive strategy*, and cannot be simplified to measures of weight or size alone.

This raises a fundamental point concerning our usual ideas of plant success. Canham and Marks (1985) correctly extend comparisons between species from absolute growth rates under specific conditions to relative "growth efficiency" over a wide range of environments related to the disturbance regime. Still, growth (especially biomass) is used as an indicator of success. We are suggesting that our perception of success is recast in evolutionary terms by (1) translating growth efficiency into reproductive effectiveness on a given site, and (2) considering that site in the context of potential reproductive performance by each species over the mosaic of patches generated by the regional disturbance regime. The scope has been enlarged from comparative growth in a particular patch to regional maintenance of population size and age structure by each species through adequate reproduction across patches. This modification of perception can then encompass situations where hierarchies of growth efficiency do not match up with reproductive effectiveness, as well as where they (usually) do. It also highlights the fact that the ultimate indicator of success is not dominance, but persistence, even in low numbers, as an evolutionarily viable species.

5. System Properties as Affected by Plant Performance

Examples of interactions that link whole-plant physiology to ecosystem properties such as net primary productivity and water and nutrient output are included in Fig. 1. Additional comments can be made about the relationship between physiological strategies and ecosystem (= community) behavior.

Net primary productivity for the community increases to a maximum and then declines in larger gaps because exploitive species are gradually replaced by conservative species as available resources are claimed and the gap community establishes control over microenvironmental fluxes. As discussed above, rapid growth (high P/R) is characteristic of large gap pioneers, while conservative growth (low P/R) is typical of the late successional species that produce and maintain large, environment-controlling structures. The behaviors of system trophic parameters such as this are byproducts of turnover in dominant strategy (Bormann and Likens 1979).

Species with exploitive growth and reproductive strategies exist not to repair ecosystem damage or to serve as stopgaps for water and nutrient loss until climax species control the site, but only because disturbance increases resource fluxes and evolution produces effective resource-users. Thus the remarkable influences that pioneer trees

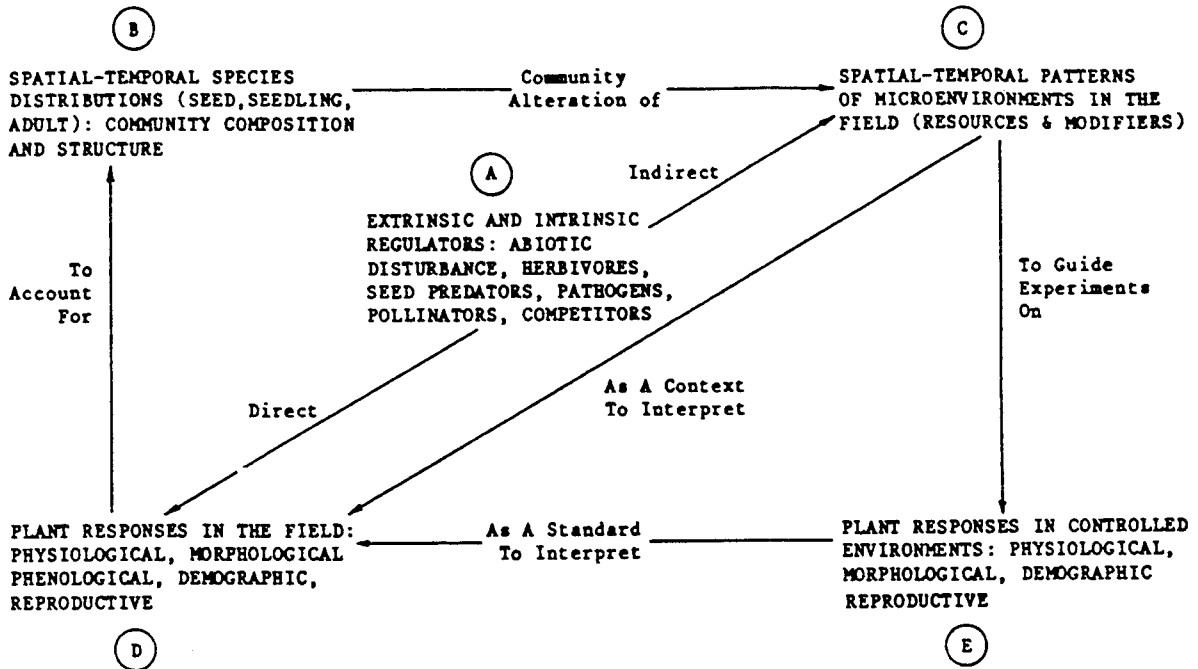
may have on ecosystem properties (e.g., Marks 1974) are explained most parsimoniously by selection for resource acquisition and growth rates that yield reproductive success in the regional pattern of climate, physiography, and disturbance. This is not to say that evolution molds perfect resource-users, nor that the actual community on a site is the best combination of species to efficiently and completely use the resource fluxes of the system.

The strategies of dispersal, dormancy, resource gain and allocation, response to competitors, and defense acquired by species through evolution on a regional scale are thrust together probabilistically on a disturbed site (Pickett 1976), and community-level results are determined in a vast number of loosely coupled microsystems. Where disturbance is not catastrophic, the fecundity and regrowth of competing species saturates potential microsites many times over and virtually assures restoration of productivity, standing crop, and nutrient circulation, even though community composition may be much different.

Community dynamics, during either normal or post-disturbance conditions, is therefore the winnowing out of a few successes from an enormous number of failures. *On average*, these successes are individuals of species better equipped than competitors for using and modifying the pattern of physical and chemical fluxes that has previously characterized the site. Plant communities differ greatly in the precision with which populations are organized by competitive interactions. In general, they are less ordered than animal communities. Stochastic patterns of propagule dispersal and seed bank storage, microsite suitability, prior occupancy, and interactions with animals and microbes generate multiple potential trajectories of community response. In all communities, the trajectories may be described as the pattern of variation around the average collective behavior of populations. When the trajectories converge to a highly probable configuration of composition and structure, "climax" is a centroid that has meaning for the demography and evolution of populations. In other systems, perhaps typified by tropical wet forests (Hubbell and Foster 1986), the variation is so large on the spatial and temporal scales that are relevant to the size and lifespan of the dominant organisms (overstory trees) that the centroid is only an abstraction. In either case, ecosystem recovery, regardless of how it is defined or measured, is a statistical byproduct of the Darwinian fitnesses of individuals and populations (Orians 1974).

IV. Conclusions

Attempts to understand the physiological processes underlying population or community (= ecosystem) structure and dynamics must be detailed and comprehensive. To this end, we offer a general research strategy that combines controlled field and laboratory experiments with observations of natural patterns of microenvironments and community structure (Fig. 2). Though it is framed in terms of plant populations and communities, the strategy can also apply to animal interactions, with modification of terms. For example, the microenvironment of an animal may include not only physical and chemical fluxes, but also "fluxes" of behavioral cues that can be quantified as to frequency, duration, spatial orientation, etc. The community of



- B + C alone: Correlation without mechanistic understanding
- B + E alone: No field verification of autecology and microenvironmental context
- C + D alone: No controlled understanding of autecology
- C + E alone: No field verification of autecology
- C + D + E alone: No field validation of microenvironmental/physiological model of species' behaviors
- B-E alone: Isolated understanding of autecological potential, without natural regulation

Fig. 2. Research strategy: physiological ecology of community structure and dynamics

animals alters this pattern of behavioral cues in a manner analogous to the alteration of physical and chemical fluxes by plant community structure. The regulators of individual animal behavior will include plant community composition and three-dimensional structure in addition to physical disturbance and interactions with other animals. Pursued diligently, this strategy may avoid the incomplete kinds of understanding shown below the diagram.

Research on higher-level ecological interactions must (1) pose testable assertions, (2) comprehensively consider alternative explanations, (3) combine studies of process and state on appropriate interactive scales, (4) avoid adaptationism, and (5) appreciate the fundamental open-endedness of community interactions. The very core of physiological ecology has been the integration of well-understood processes to explain differential higher-level responses. When the population biology of interacting species is firmly rooted in physiological ecology, community behavior is more clearly understood (Orians 1974; Foin and Jain 1977; Bazzaz 1984a). The results underscore the principle that process precedes pattern (Watt 1947).

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