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Trends in the Development of Geographic Botany

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Source: *Annals of the Association of American Geographers*, Vol. 32, No. 4 (Dec., 1942), pp. 319-354

Published by: [Taylor & Francis, Ltd.](#) on behalf of the [Association of American Geographers](#)

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**ANNALS**  
of the  
**Association of American Geographers**

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Volume XXXII    DECEMBER, 1942

No. 4

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Trends in the Development of Geographic  
Botany

HUGH M. RAUP

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INTRODUCTION

Plant geographers have devoted a great deal of attention during the past two or three decades to consideration of the methodology of their field. Their literature is copiously supplied with both short and long papers dealing with methods: all the way from descriptions of highly involved measurements of plant reactions and statistical methods for the study of plant communities, to the long and acrimonious debate over "Age and Area." Likewise there is a large and controversial literature on ecological concepts. Some ecologists recognize plant communities as highly organized entities, while others are doubtful whether the communities exist at all. With all this discussion of methods and concepts, the basic ideas upon which all of plant

geography rests have either been taken for granted or considered to have only academic, historical significance.

The present paper is not concerned with the details of these methods and concepts, therefore, so much as with some trends in what might be termed the logical approach to plant geography. The ideas involved are not new in the fields from which they are drawn, but it is hoped that they will gain some significance from being arranged in a pattern which will take them out of their separate fields and hold them up to light for comparison and correlation.

Plant geography, as we now know it, exists in compartments, though to a lesser extent among some European students than in America. Perhaps the greatest need with which we have to deal is the correlation and integration of work in these compartments, and the final breakdown of the barriers that separate them. It is the purpose of this paper to point out what some of the barriers are and how they arose, on the general principle that an understanding of them will go a long way toward their elimination. If the paper possesses an "argument," it is that geographic botanists stand in need of a critical examination of the premises from which they reason; and it is suggested that a revival of more purely inductive methods might serve not only to unify varying points of view but also to clarify objectives for the whole field.

#### THEOPHRASTUS TO HUMBOLDT: FLORISTIC PLANT GEOGRAPHY

The first plant geographers were the "proto-botanists" who first learned how to use plants for food and shelter. In addition to knowing the kinds of plants that were useful, they had to know where they could be found. Later on, when men learned to cultivate plants, it was necessary to learn enough about natural habitats to construct a fair approximation of these habitats, and to arrange their materials so as to bring about a happy coincidence of plant, soil and climate that would produce the desired results. The botany of the Greek natural philosophers, such as Theophrastus, was the culmination of untold generations of effort among primitive men along these lines. Since the botany of the ancient Greeks remained effective for a thousand years and was the starting level from which the modern science "took off," as it were, during the Renaissance, it will be well to look into it for ideas that could form the background for our concepts of plant geography.

Theophrastus was, above all, a practical gardener; but his knowledge of the Greek countryside as well as information and materials brought to him by contemporary travellers and conquerors in southern Asia supplied him with an abundance of problems concerned with the general distribution of vegetation. His writings are filled with observations that show a keen and vital interest in the geographic distribution of plants and their local selection

of habitats. His classification of the plants he knew was based in part upon form (trees, shrubs, undershrubs, and herbs), and in part upon position or habitat selection (Greene, 1909). His gardening experience made him conscious of geographic zones of hardiness in the region he knew. He returns to this theme repeatedly, usually correlating the observed phenomena with climate; and in one place (1: 115), we find the flat statement “. . . that the locality is more important than cultivation and tendence.” He recognized plants that preferred shade and others that lived mostly in bright sun. Likewise he wrote of differences in the kinds and habits of plants that grew on the north and south slopes of hills, and he realized the significance of the mountains as producers of more different kinds of plants and habitats than the plains. He knew the difference between wind and frost damage to plants. In spite of his preoccupation with cultivated things, in one place he devotes no less than eight chapters to the description of natural aquatic vegetation which he divides into communities on a physiographic basis. He wondered about range discontinuities, and the absence of plants from certain places, noting that the cypress was peculiar to Mt. Ida in Crete, and the Syrian cedar to the hills of Cilicia and Syria. He speaks of competition for nourishment among trees in a forest, and discusses the dispersal of plants by wind and water; and finally, in discussing the generation of plants, he describes what would now be termed “successions” on river flood plains and on stirred soils.

Theophrastus's approach was fresh and naïve, unencumbered with anything resembling geographic dogma or theory. He described the phenomena of plant life as he saw them, and likewise the phenomena of plant habitats. Wherever he could find a simple factual coincidence between the two he stated it, usually as merely another observed fact, but sometimes with the implication of cause and effect relations. His knowledge was empirical, and in spite of the prevailing deductive logic of his time his conclusions seem to have been arrived at by simple inductive reasoning. Furthermore, it is impossible to separate his plant geography from his systematic knowledge of the kinds of plants.

No tangible advance was made either in the classification of plants or in knowledge of their distribution until the period of the Herbalists in the 15th and 16th centuries. The fortunate coincidence of events which produced a *renaissance in the arts had its influence in botanical science as well*. Travel and exploration brought knowledge of plants from many parts of the world, and the invention of printing and illustration began to diffuse the knowledge. Under these and other like stimuli, men revived a naïve interest in the plants that grew about them, writing fresh descriptions of them and automatically becoming conscious of differences among kinds of plants never before noticed.

It is unnecessary, in the present discussion, to trace the development of systematic botany from these early beginnings down to Linnaeus and his successors. But it should be emphasized that the geographic botany of the period remained inseparable from it. The discovery of the New World, and such botanical travels as that of Tournefort to the Near East (1717), together with the invention of a usable system of botanical nomenclature and diagnostic description (Linnaeus, 1753), gave to students a vast amount of new empirical knowledge with which to think new thoughts about distribution. Naturally, the first ones to do this were the systematic botanists who had the requisite knowledge; and there finally appears the roster of illustrious 19th-century floristic plant geographers which begins, perhaps, with Willdenow (1792, 1805) and culminates with Joseph Dalton Hooker, Asa Gray (1859, 1884), and Engler (1879–82).

Floristic plant geography has dealt primarily with the distribution over the earth's surface of the kinds, or species of plants. The arrangement of its vast body of knowledge rests, first, upon a clear understanding of the kinds of plants. Having delineated the kinds, it has aimed to outline all the peculiarities of their geographic distribution. Attempts to explain this distribution have been almost entirely historical. At first the explanations consisted in assumptions of special creation, or the study of dispersal mechanisms and the making or breaking of land connections between different floristic regions. Later, with accumulating evidence for the mutability of species, it became necessary to involve the evolution of genera and species in the explanations of distributional phenomena. It must not be assumed that floristic students have disregarded correlations of plant distribution with that of other, physical features such as climate, soil and local physiography. The studies of Willdenow (1792) and Wahlenberg (1813, 1814) on the plant geography of the European Alps indicate a keen interest in such matters; but already some of the larger patterns of world distribution, such as the similarity of eastern Asiatic and eastern North American floras, were beginning to take form, producing problems that seemed far beyond the scope of any existing knowledge of climatic relationships or the abilities of plants to migrate.

Phytogeographic knowledge remained empirical, as did also that of the physical habitat. It had been achieved naïvely, as had that of Theophrastus; and the methods of reasoning with it were essentially inductive—from observation to observation, with a keen lookout for coincidence among facts. So was built up the mass of solid factual material that forms the basis for what we know of the geography of the species of plants. In the nature of things it cannot at present be separated from taxonomy any more than it could in the time of Linnaeus and Willdenow. It is practiced now almost

entirely by those who are especially trained for taxonomy and for problems of speciation. Because a large percentage of the active taxonomists are now engaged in problems of the tropics or of the southern hemisphere, where floristic knowledge is yet far from complete, there we find a large part of the work in floristic plant geography. That this is not entirely the case, however, is shown by the recent papers on north temperate and boreal regions by Hultén (1937) and Fernald (1925).

Of the accomplishments and problems in floristic plant geography only a small part need be mentioned here. Predominantly floristic were the works of Gray on the affinities of the North American flora (1884), of Darwin on the influence of Pleistocene Glaciation and the significance of barriers (1859), and of J. D. Hooker on the distribution of Arctic plants (1862). Also to J. D. Hooker (1847-60), and to Robert Brown (1814) we owe some of our basic generalizations on the botanical affinities of the Antarctic and Australasian regions. A classic study of insular floras and their geographic significance was that of Hemsley (1885). Willis's theories of "Age and Area" (1922), with the great volume of stimulating criticism and controversy which they have brought out, are grounded in floristics and speciation. Floristic geography is being used effectively on both sides of the controversial hypothesis of continental drift (See Wulff, 1932; Irmscher, 1922, 1929; Steffen, 1938). The enigma of bipolar distribution (DuRietz, 1940) is as yet primarily a floristic problem. Not the least of values in floristic geography is to be found in its significance as a tool for modern students of taxonomy and phylogeny. The use of areal criteria in the delineation of taxonomic units, so admirably enunciated by Wettstein (1898), has become an essential of sound research in these fields.

Floristic geography, like other phases of the science, has suffered from being compartmentalized. In its simplest form it might be likened to the "place geography" of the field as a whole. As such it can easily become the mere cataloguing of facts, entirely out of contact with geographic reality in the broad sense. Its greatest limitation, however, is probably the inherent presumption that it rests upon correctly defined taxonomic units. The definition of these units is often so complex and problematical, and so dependent in many cases upon "taxonomic judgement," that generalization from them becomes difficult. Furthermore, the proper definition of the units requires such a broad knowledge and practice in taxonomy and floristics that only a few students are sufficiently trained to work with them. Another source of error in floristic plant geography lies in its inevitable use of negative evidence. Many of its conclusions rest upon the *absence* of plants from certain regions as well as upon their presence in others. Ac-

curacy rests in this case upon the care that has been devoted to exploration as well as upon the proper delineation of species.

#### HUMBOLDT TO DARWIN

In the early part of the 19th century there appeared an interesting diversion in phytogeographic thought. The famous explorer-naturalist, Alexander von Humboldt, published a short "Essay on the Geography of Plants" (1805) in which he proposed to discuss the world's plant life, not in terms of species, but in terms of masses of vegetation-forms. His extensive travels in Europe, north Africa, and in the Americas led him to believe that he could thus find better coincidences between botanical features and those of climate and topography than by using species. The idea for such a classification was not new, for we have seen that Theophrastus used it as an essential part of his primitive arrangement of plants; but Humboldt greatly elaborated it by inventing fifteen structural categories into which he arranged all the species of plants he knew. Some of these categories, such as Palms, Arborescent Ferns, Conifers, Orchids, Mosses and Lichens, coincided with those of the systematic botanists, while others cut across the recognized orders and families so as to bring together species of the most diverse taxonomic relationship. As an adjunct to his system Humboldt wrote vivid descriptions of plant communities, and made determined efforts to find correlations between their distribution and that of the physical features of the landscape (1817). Plant geography was only one of his many interests, for, with Carl Ritter, he was busy at laying the foundations for all of modern geography, and at preparations for his ambitious scheme of writing a description of the Universe (1845-62).

For present considerations the essential fact about Humboldt's plant geography is that it was entirely upon a morphological, or rather a physiognomic basis. He made no serious effort to relate his "life-forms" to the functions of the plants involved. They were simply physiognomic categories which enabled him to prepare an intelligible description of the vegetational features of the landscape without the necessity of going into taxonomic detail. As such it proved eminently useful, and was perpetuated by a number of subsequent students. The most important of these was probably Grisebach, whose "Vegetation der Erde" appeared in 1872, and contained descriptions of no less than 54 form categories of plants. Both Grisebach and Schouw (1822), an earlier follower of Humboldt, elaborated extensively the possible relationships between distribution and physical phenomena. Alphonse de Candolle likewise attempted to draw up limits for the distribution of species in relation to climate, particularly in terms of temperature. Like Humboldt, he used statistical methods in the comparison

of floras. De Candolle's method of defining temperature climates by the summation of degrees of heat useful to the plant was later utilized, with some modification, by Merriam (1895) in his effort to find determining factors for the distribution of life zones in North America.

Humboldt's primary purpose in phytogeography was a description of the areal differentiation of the world of plants; but the plant world was only one facet of the picture, one pattern on the canvas. He conceived of geographic areas as *wholes*, within which the total effects were produced by the balanced interplay of many causes. His approach to the solution of these causal problems was almost entirely empirical, following purely inductive methods of reasoning. He was but little concerned with the formulation of hypotheses and assumptions of cause and effect between plant reactions and environmental factors; rather he sought to accumulate factual patterns which could be selected and superposed inductively to show possible relationships (1817). He apparently despaired of ever solving the actual, complex problems of cause and effect within areas. This is suggested by a statement that appears in the first volume of his "Cosmos" (1845, p. 75): "We are still very far from the time when it will be possible to reduce, by the operation of thought, all that we perceive by the senses, to the unity of a rational principle. It may even be doubted if such a victory could ever be achieved in the field of natural philosophy."

His reasoning, therefore, was identical in method and aims to that of the floristic plant geographers. He differed from them principally in using other forms for vegetational description, and in his conception of areally and structurally differentiated, highly complex communities of organisms composed of many species.

Alphonse de Candolle, in his classic treatise on plant geography published in 1855, gave expression to the problem of causation in this way: (p. 594) "... I have considered plants in groups, according to their structure, or their habitats, or according to their occurrence in this or that part of the world, and I have tried to find the average areas of species in each of these groups. By this method one arrives at proofs of the coincidence of facts, not of causes." After presenting some examples to illustrate this he goes on to say: (p. 595) "Thus, in establishing the average range of species according to their structure or their station or their habitat, we have accomplished only half of our research. It is necessary to establish also the causes of extension or nonextension of range which can have affected the species, and to see if they can be applied to each in detail. One discovers thus that there are causes of great significance and others of little influence, botanical or physiological causes within the plants themselves, and physical or geographic

causes dependent upon the country; actual causes that are easily comprehended, and unknown causes that have perhaps long since ceased to be effective." And again: (p. 598) "It is necessary, therefore, to be content with explaining vast ranges on the surfaces of continents first by considerations of structure and physiology if possible, and then by having recourse to the hypothesis of anterior causes as a last resource which is very frequently indispensable." De Candolle's definition of what he means by "present" and "anterior causes" is clarified by the following passage: (pp. 601-2) "It will not have escaped the reader that most of the causes designated as 'present,' for example the nature of seeds, the ability to resist immersion, etc., began to be effective long before our time, ever since the date of origin of each species; so that if one will use the words 'anterior causes' in the larger sense, these causes prevail greatly over the present causes." He expresses his skepticism of the outcome as follows: (p. 601) "Considering the interplay of all these causes, the ones which are anterior apparently have the most weight, perhaps because they are more varied and have been in operation over a longer series of centuries. I do not know if we will achieve an understanding of the nature and extent of these diverse anterior causes. . . ."

Any discussion of pre-Darwinian plant geography would be incomplete without consideration of the work of Edward Forbes; for it is clear that much of Darwin's own reasoning was based directly upon it. Forbes put into practice, in a study of the flora of the British Isles, ideas of "anterior cause," or "historical cause," that were rather nebulous in writings of Willdenow and more clearly formulated by de Candolle. He conceived of the British flora as composed of elements whose affinities were with the floras of neighboring parts of Europe, some northern and others southern. In comparatively recent geologic time, with suitable changes of climate and land connections, these contributing floras had had access to the British Isles; but with later separation by ocean barriers, remnants of them had been isolated there, and were now persisting in the habitats most suitable to them. This "theory of persistence" became an important part of Darwinian biogeography, and has since been greatly elaborated, especially by recent students. It has acquired added significance through genetic studies of the effects of isolation.

At the advent of Darwinian thought there could be noted, following the above discussion, three points of view in plant geography. The first was floristic in nature, using the distribution of taxonomically determined species as units of study. The second utilized form categories of plants which might or might not coincide with taxonomic divisions. The third dealt with

communities of plants which live together in supposedly more or less balanced economies. The second and third of the three were rather closely related, since communities were commonly defined on the basis of physiognomy. All three sought for explanations of plant distribution by similar methods of reasoning. They looked into the fields of climatology and geology, and into other phases of biological science, for patterns of distribution which could be compared with their own, and which might throw light on their problems.

#### THE EFFECTS OF DARWINISM UPON PLANT GEOGRAPHY

The ideas outlined by Darwin (1859) and by the geologist Lyell (1853) not only produced sweeping changes in all of these points of view, but also led to notable innovations in the methods of reasoning. One can scarcely improve upon the words of Sir Joseph Hooker in stating the revolutionary effects of these ideas. In his address to the Geographical Section of the British Association in 1881 Hooker (1882) said, "Before the publication of the doctrine of the origin of species by variation and natural selection, all reasoning on their distribution was in subordination to the idea that these were permanent and special creations; just as before it was shown that species were often older than the islands and mountains they inhabited naturalists had to make their theories accord with the idea that all migration took place under existing conditions of land and sea." Thus a new element was injected into every line of biogeographic thought—that species or vegetations could be considered not as static things, but as mutable entities of which one could see only an existing expression, and which possessed a past and presumably a future development during which their reactions and forms could be different. Likewise the world in which they lived during the past was shown to have been different from the existing one.

At the very outset Darwin formulated the assumption of a more or less direct cause and effect relation between the existing form of a plant and its physical surroundings. The core of the argument was to be found in the idea of *adjustment*, for if the theory of natural selection were to be effective in the evolution of species, then it would be impossible to admit that a plant could continue to live if it were not adjusted structurally and functionally to its environment.

Owing to the fact that floristic plant geography was so intimately related to taxonomic botany, the impact of Darwinian ideas upon it first became effective through the field of taxonomy. A so-called "natural" system of classification had been developing slowly from the early beginnings of Jung, Ray and Linnaeus. Although this had achieved much of its present form before Darwin, phylogeny as we know it did not exist. Phylogeny rests

upon the idea of mutability and upon a concept of time in a changing world during which development could occur. These ideas did not become crystallized until Darwin's time. Needless to say, they vastly complicated the problems of the plant geographer. Up to this time he had always had recourse to special or parallel creation to explain his disjunct ranges, or else he fell back upon hypothetical "anterior causes" which he dimly sensed. There was also the unproved possibility that dispersal was efficient enough to account for long jumps. Darwin now eliminated special creation, and threw very serious doubt upon the possibility that identical species could have *evolved* in more than one place at the same time. Furthermore, his geographic studies had led him to a clear understanding of barriers to migration, and after extensive investigations of the means of dispersal among plants he was left with a large and imposing residue of unsolved geographic problems. Here he followed the lead of Willdenow, de Candolle and Forbes, and retreated to "anterior causes," but now with greater hope of success because of advances in the study of geological history. In brief, plants with disjunct ranges must have been at some time continuous in their distribution, later to be divided by changing external conditions. Darwin's outline of the effects of the last glaciation upon the vegetation of the boreal regions still forms the basis for much of our thinking along these lines.

It has already been noted that attempts to explain the distribution of plants on a floristic basis had always been largely historical; and floristic plant geographers quickly adjusted their thinking to the Darwinian ideas of development. The classic works of Hooker on Arctic floras (1862), and of Asa Gray on the affinities of the North American flora (1884) set a standard of excellence that is ably maintained by such present-day students as Skottsberg (1910-38, 1929), Nordhagen (1935), Van Steenis (1934-36), Fernald (1918, 1925, 1926), Hultén (1937), Du Rietz (1940), and many others.

In spite of these changes in perspective the effect of Darwinism upon the floristic view of plant geography was not so great as upon other views. The reasoning remained inductive in large measure, with conclusions growing slowly out of masses of fact which were sorted laboriously into patterns of coincidence and suspected actual relationship. The assumption of adjustment, inherent in the theory of natural selection, was incidental to the hard facts of taxonomic relationship and distribution with which the floristic geographer had to deal.

Plant geography in terms of the forms of plants, on the other hand, immediately underwent revolutionary changes. This has been stated excellently by Du Rietz (1931) as follows: "The physiognomy of plants was now more

and more looked upon as a direct or indirect product of the environment, and gradually there developed a tendency to a valuation of physiognomic characters according to their supposed importance in the process of natural selection—or for the antiselectionists according to their supposed direct causal relation to the environment.” Such students as Warming, Kerner, Drude and others quickly discarded the old systems based upon pure form in favor of systems that would involve the biological or functional significance of structures. These systems involved many characters, most or all of them chosen, as Du Rietz says, for whatever contribution they were thought to make toward the adjustment of the plant to its environment. There arose the lively problem as to what characters were to be considered significant “adjustment, or epharmonic, characters,” and what were merely “indifferent.” The amount of teleology that then developed in efforts to find functions for plant parts has probably never been surpassed. Perhaps the best of the new systems was that proposed by Warming. It classified plants according to the duration of life (annual, biennial or perennial), the power of vegetative propagation, the duration of shoots, the relation of shoots to the surface of the earth, etc.

The development of biological life-form systems has found its highest development in the work of the Danish botanist Raunkiaer (1907, 1908). Raunkiaer's system is the one most widely used at the present time. It has had great popularity among some European students; but, like other life-form systems, it has been applied in America only in a few places. It is a relatively simple system, based upon a single complex of plant structures which is selected because of its presumed high survival value, namely, the position with relation to the surface of the ground of buds or growing points by which the plant survives the unfavorable seasons of the year. Raunkiaer made a further contribution by placing the use of his life-forms upon a statistical basis. He constructed so-called “biological spectra” (1908) for various regions by making comparative tables of the percentages of the total floras which fell into his form categories. He then tried to correlate these spectra with the climatic features of the world.

Closely related to the origin of biological life-form systems was that of another view of plant geography, based upon the physiological relationships of the plant to its environment. The ideological forbears of this view are, like those of the former, rooted in the assumption of *adjustment* to environment. When Humboldt, Schouw, and de Candolle tried to draw up relations between the distribution of plants and temperatures they made no pretense that they had found actual *causal* relations, only coincidences which, if they could find enough of them, might lead to sound generalizations. The

physiological plant geography which now developed under the stimulus of new discoveries in physiology *started* with the assumption of causal relations. It very quickly took over much of the factual material accumulated by the students of physiognomy, both as to the forms of individual plants and of plant communities. The new physiology was in terms of the functional reactions of plants to the various separate parts of the environment such as water, light, and nutrient elements. It dealt in parts that could be measured, and was strongly influenced by the methods of research in physics and chemistry. Consequently the new physiological plant geography began to be concerned with the isolation and measurement of the *factors* of the habitat. From the basic assumption of adjustment it was but a logical step to another assumption: that a plant could continue to live in a given place only so long as none of the environmental factors varied beyond certain limits which were set by the physiological requirements of the plant. Since the factors could be measured with some degree of accuracy, it was expected that with some experiment on the plant's requirements it would be possible to find what factor or factors were actually limiting distribution.

These views were crystallized in two classic works, the first by Warming on the "Ecology of Plants" (1895, 1909) and the second by A. F. W. Schimper on "Plant Geography on a Physiological Basis" (1898, 1903). Both began with more or less detailed discussions of the factors of the environment, and of the structural and physiological peculiarities by which plants are adjusted to them, and both did all they could to eliminate the mass of teleology that had already grown up around the idea of adaptation. They then proceeded to interpretive descriptions of the plant life of the world in terms of the great plant-environment complexes that could be recognized in deserts, marshes, tropical rainforests, etc. Both of these authors were at some pains to state, at the beginning, the philosophical basis for their arguments. Adaptation and natural selection were essential in both, and in both is stated the necessity of investigating the physiological requirements of plants. Schimper emphasizes the latter point particularly: "The ecology of plant distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology, for it presupposes an accurate knowledge of the conditions of the life of plants which experiment alone can bestow."

Physiological plant geography, with its later emphasis upon the structure, history and significance of plant communities, soon became widely accepted as the most promising field in which contributions to the science as a whole could be expected. It greatly influenced the Scandinavian and Swiss schools of thought in Europe, and the British school under the leadership of Tansley. In America it gave rise to the plant ecology of Cowles (1901, 1911), Clem-

ents (1905, 1916), Transeau (1903, 1905), Livingston and Shreve (1921). The most recent comprehensive textbook we have in this country on plant ecology and plant geography, that of Weaver and Clements, rests almost entirely upon a physiological or ecological basis.

Ecological plant geographers usually go back to Humboldt, Schouw and Grisebach for the classic foundation of their view. This seems to be due to the fact that these students broke away from the purely floristic idea of plant geography and set up descriptive units based upon pure form and community structure, thus releasing themselves at least in part from the problems of speciation that were becoming increasingly difficult in floristics. We have already seen, however, that in spite of these changes, the processes of logic had, for the older men, remained identical with those of the floristic geographers. Humboldt and his followers set themselves to describe the world of plants empirically, dealing with the relationships of plants to environment only on a comparative basis. They purposely refrained from plunging into problems of actual cause and effect, apparently because they had arrived logically at a strong presentiment that they could not solve such problems then, and probably never would. Ecological geographers, on the other hand, starting with the assumption of a causal relation between plant and environment, have built the entire structure of their science upon efforts to prove its significance and to interpret the distribution of plants on the basis of it. The initial reasoning, therefore, has not been by simple induction from a body of empirically and naïvely determined facts, but from a system of working hypotheses based upon assumptions of actual cause and effect.

It has already been noted that Warming and Schimper very carefully stated these conditions at the outset, and the same procedure was followed by Livingston and Shreve in their studies of climatic relations to vegetation (1921). Cowles (1911) attempted to do the same in a brief discussion of adaptation at the close of his textbook of plant ecology. In his earlier work on *Research Methods in Plant Ecology* (1905) Clements stated clearly that his premises were in environmental determinism. In the latest textbook of Weaver and Clements (1929, 1938), however, the causal relation is obviously no longer an assumption but an established fact, and no apology for it is given.

A striking corollary to the development of physiological plant geography has been its antipathy toward floristic views. This has been particularly true in America, although the vogue was probably set for it by Schimper. Floristic geography was regarded as primitive and outmoded, useful only for the mass of facts it had accumulated. Clements was inclined to discount even a part of this value, for we find the following attitude expressed by him

in 1905 (p. 2) : "Geographical distribution was grounded upon the species, a fact which early caused it to become stereotyped as a statistical study of little value;" and again, "The fixed character of the subject is conclusively shown by the fact that it still persists in almost the original form more than half a century after Grisebach pointed out that the formation was the real unit of vegetation, and hence of distribution." Livingston and Shreve expressed the same view in a different way, but, if anything, more pointedly, in 1921 (p. xii) : "The investigation of the causes which determine the distribution of plants and plant communities is essentially a physiological task, in which it is necessary for us to regard the plant as a functioning organism and to give little attention, for the time being, to the fact that it has a descent-kinship with other plants. We must keep the plant in mind as an aggregation of coordinated physiological processes, continually controlled by a complex of environmental conditions. It is only by a sharp separation of the phylogenetic and the physiological considerations of the plant that we can hope to investigate with success the relation of plants to their environmental controls." In another place (pp. 4-5) they have the following: "The study of vegetation *as such* has been, on the whole, greatly obscured by the fact that it has never been completely divorced from the study of the flora. Too much emphasis cannot be laid, at the present time, on the radical distinctness of the work of physiological plant geography, on the one hand, which attempts to relate the occurrence and distribution of species as physiological entities to the factors of environment, and the work of floristic plant geography, on the other hand—which attempts to reveal the geological history, the movements, the vicissitudes of species as phylogenetic entities. . . . Nevertheless, in order to come squarely to face with the problems of physiological plant geography, we have to lay aside much that floristics has taught us, and shall have to ignore phylogeny, except in so far as it shows us that plants of close kinship often have the same or similar anatomical and physiological characteristics."

The net result of these attitudes of mind has been the sharp division between physiological and floristic plant geography which now exists in this country. Adherents of the first consider the second to be well past its usefulness and already semi-fossilized; in fact they often do not recognize its existence. A very recent treatise on the history of the plant sciences (Reed, 1942) has a brief but splendidly informative chapter on geographic botany, in which about equal space is given to both phases; but in noting American contributions made after 1900 only Clements and Cowles are mentioned! Floristic students, on the other hand, are apt to be impatient with ecologists because of their reliance upon unproved assumptions and general disregard

of taxonomic problems; but the indictment is partly justified that all too few floristic workers are aware of the useful material developed by plant sociologists and students of life forms.

#### CURRENT TRENDS IN PLANT GEOGRAPHY

Some attempt must be made here to evaluate the different views in plant geography and to describe some current trends.

#### *Floristic Geography*

Floristic plant geography, far from being the sterile, unchanging drudge it has been assumed to be, has given unmistakable evidence of virility during the present century. It is unnecessary to review its recent history in detail, but two or three trends appear to have particular significance.

Many floristic students, especially in Europe, have shown a willingness to utilize the geographic findings of workers in the field of plant communities. Nordhagen's work (1935) on the floras of some of the Norwegian forelands and fiords affords an instance, as do also the series of studies by the Danish botanists in Greenland (See Böcher, 1933; Gelting, 1934; Porsild, 1922, 1932; Sørensen, 1933). Here the floristic and ecological work has been rather closely coordinated. European plant geography, especially in Scandinavia, was never so sharply divided between these two fields as it has been in America. This may be due to the influence of Warming, who, although subscribing to many of the major tenets of the environmentalist view, was still conscious of historical aspects in vegetation which could only be got at through the floristic, phylogenetic field. Efforts on the part of Du Rietz (1921) and other floristic students in Scandinavia to place the study of plant communities on a foundation of more inductive reasoning also suggest a broadening of floristic points of view.

One of the most important developments in floristic geography since the time of Forbes, Darwin and Hooker is the extension of the theory of persistence by Fernald (1925). Professor Fernald's conclusions were arrived at entirely by the old technique of the comparative study of range patterns, unencumbered by assumptions of a physiological causal relation with external environments. Faced with the peculiar limitation and discontinuity of many ranges, even within restricted areas, he suggested that some species of plants must be inherently conservative or nonaggressive. He thought that this might be due to senescence—that the species as phylogenetic units were "running down." This is the central theme of much of Fernald's reasoning with problems of boreal American distribution. He correlated the present ranges of many species in this region with the effects of the later episodes of

the Pleistocene Glaciation, and accounted for the persistence of such ranges to the present with his idea of conservatism.

The theory of conservatism in species lacked any material support for several years except for additions to the sustaining evidence from plant ranges, which had already been raised to imposing proportions by Fernald himself. Then Anderson (1936, 1937) directed attention to genetic studies in species of *Iris* that seemed to give positive evidence that the idea of conservatism was sound. It was to be interpreted, not as a function of age necessarily, but rather as a result of reduction in genetic variability. Since then a rather formidable array of material from the fields of genetics and cytology has been brought together and seems to have firmly established the idea as a promising one for geographic research. A recent paper by Stebbins (1942) contains an excellent review of this evidence, and it will not be discussed in detail here. The theory of conservatism vs. aggressiveness has recently been applied by Hultén to all of boreal floristic geography, with striking and stimulating results (1937).

The main point to be made here is that floristic geography has been enormously enriched by genetic views in the study of populations, and by the contributions of genetics and cytology to the problems of taxonomy. These views are remarkably free from environmental determinism, and the reasoning is rigorously inductive, without pretense of a direct attack upon the ultimate complex causal relationships. Physiological plant geography, on the other hand, has been rather resistant to the inroads of genetical ideas, perhaps owing to its inherent preoccupation with the external environment of plants. One of its basic ideas has always been a causal sequence in which the habitat comes first, but the field of floristics now comes forward, aided and abetted by students of genetics, with the idea that the plant itself, by its inherited existence, contains causal elements which cannot be readily subordinated to the external environment. Some recent work by Cain (1940) indicates the beginning of an effort to coordinate these points of view (see also Griggs, 1940).

#### *Life Forms in Plant Geography*

It has already been noted that the development of life-form classification was placed upon a purely functional, or "biological" basis by Raunkiaer early in the present century. Only a single character complex was used, and this was selected for its assumed survival significance. Because of its obvious simplicity and the ease with which it can be applied to large and complex floras, Raunkiaer's system has had a wide vogue and is still used extensively. It soon incurred severe criticism, however, because it was too simple to describe adequately the complex nature of vegetation. This was probably due

to the fact that it was so one-sidedly functional and "epharmonic" in its interpretations. Structural characters for which no function could be found had been regarded as of little importance, and, as DuRietz remarks (1931), it was thought that ". . . the old physiognomic period in the study of life forms marked a very low and primitive stage compared to the modern 'biological' period." Du Rietz suggests that: "It never occurred to them that also another conclusion could be drawn from the lack of parallelism between physiognomic and biological types, namely that the purely 'biological' types were insufficient for one of the most important tasks of plant geography, namely the accurate and objective picturing of the morphology of vegetations." Drude (1913) attempted to correct this in part by a new system which, like Warming's, involved enough characters to make it more flexible. Although it was primarily functional, it involved a number of elements whose survival value was in question.

Even with more elaborated systems, there has been a general adherence among ecological plant geographers to biological interpretation in the selection of characters. Braun-Blanquet has merely enlarged upon the scheme of Raunkiaer (1928; 1932, pp. 289-96). Livingston and Shreve (1921) considered Drude's system best adapted to their uses, and have the following significant comment upon life-form methods in general: "Whatever features of the gross anatomy of plants may be discovered to have no apparent importance in any aspect of their adjustment to environment will have no place in shaping our ultimate system of growth-forms." The same general views are held by Weaver and Clements (1929, 1938), Tansley and Chipp (1923, 1926), and many others.

One of the more interesting recent trends in modern plant geography has been a determined reaction against the biological life-form systems. Du Rietz (1931) has presented an excellent review of this trend, in which he has played an important part. In 1921 he published a proposed system for use in Scandinavian studies of vegetation based upon pure physiognomy. It grew out of impatience with hypothetical division lines between indifferent and adjustment characters—lines that could be shifted back and forth according to the region, the flora, or the opinions of the student. He went directly to the old views of Humboldt and Grisebach, and maintained that the only sound basis for an objective classification of life-forms would have to be built upon pure form, with the complete elimination of all assumptions of causation between environment and plant. He suggested that the forms which brought about the convergence of adapted types should be looked for not in processes of adaptation, but in the "homologous variations" of Bauer (1919) (see also Vavilov, 1922).

Du Rietz's system has apparently gained considerable acceptance in

Europe. Independently, Cockayne (1921) formulated a system for use in his New Zealand studies which was based essentially upon physiognomy. He was doubtful of the significance of adaptive structures as geographic criteria, and preferred to leave these assumptions out of his reasoning. Skottsberg likewise used a physiognomic system in describing the vegetation of Juan Fernandez Island (1929). In 1931 Du Rietz published a revision of his earlier system, but maintained essentially the same philosophical views, which he clearly stated as follows: “. . . only life-forms delimited independently of any adaptation theory can be of any use at all as units for the inductive study of the adaptation problem and of the actual correlation between life-form and environment.”

### *Physiological Plant Geography*

American physiological plant geography has remained strongly environmentalist, as already stated, though a few voices have been raised in protest. These protests appear not to have been directed so much at the environmentalist view, however, as at some of its interpretations. There have been two outstanding concepts in synecology which have had their highest development in America. The first is what may be called the “organismic” concept of the plant community. It is one of the foundation stones of the plant ecology and geography of Clements. The second is the idea of plant succession, or the “dynamic” view of plant communities. This has become the cornerstone of the whole study so far as most American students are concerned.

Ecological plant geographers set out with high hopes of solving all the real problems of distribution on a physiological basis. The starting points for most of this work have been either among plants under cultivation or tending, or among those that live on what might be termed the “physiological fringes” of the world habitat. The discovery, in the management of crop plants, of soil deficiencies that could be defined and corrected with fair precision has lent a great deal of weight to the theory of limiting factors. The finding that even the rarer elements in the soil could be significant has complicated the problem, but at the same time has seemed to emphasize the necessity for further extension of the factorial approach. In the realm of natural vegetation, the obvious suitability, structural and physiological, of aquatic and desert plants for their habitats has given an abundance of *cases* wherein the assumption of physiological causation could not readily be disproved, and the environmental complex was apparently simplified by being one-sided. There are also the large and apparently safe generalizations regarding a causal relation between climates and some of the great vegetation types and barren areas of the world. It is difficult to think of any other reason for the

absence of plants from central Greenland than the rigor of the climate there; and the excess of moisture and heat in tropical lowlands is sufficient to preclude the development of grasslands or deserts in those regions. Likewise, in the study of plant communities, the starting points have been in the more obviously ecotonal habitats such as on pond and lake shores, prairie or forest margins, arctic and alpine timberlines. In all of these situations there has been thought to be a possibility of reducing the causes to one or two factors. The material basis for the study of dynamic ecology also rests in these ecotonal areas, or in areas of naturally or artificially disturbed soil.

It has been the hope of the physiological plant geographer that, armed with causal relations derived from experiment or from these fringes, he could slowly work back into the great masses of the world's mesophytic vegetation, solving his causal problems in parts, as they arose. The literature of the attempt to do this has become extremely voluminous; but since the technique has involved a deliberate partition of the problem, the results are also in parts, the integration of which is a discouraging task. One of the few exhaustive attempts at the correlation of plant distribution with a complex of factors was that of Livingston and Shreve on "The Distribution of Vegetation in the United States as Related to Climatic Conditions" (1921). While it was admittedly only a partial treatment of the total habitat complex, the results achieved will serve to illustrate the nature of the problem.

The philosophical grounds for this study were clearly in environmental causation. The authors drew inspiration directly from Schimper, whose work, they say, "has done much to stimulate interest and activity in what we may designate as causational or etiological plant geography" (pp. 24-25). Some other quotations will further bear this out: "We have approached our problems in plant geography with the mental conception that they are merely problems in physiology. . . ." (pp. 24-25); "Our attitude toward plants has been that of the physiologist, and we have tried to bear constantly in mind the conception that vegetational characters are simply expressions of the activities of individual plants. We maintain that all discovery of true causal relations in ecology must depend finally upon this point of view" (p. xiv); "Plant geography can progress but little further by qualitative observational methods, and the physiological and quantitative point of view must, of necessity, finally prevail" (p. xv); "In an etiological study of plant distribution, either natural or artificial, the conception of physiological limits must hold a very prominent place" (p. 99); and finally, "The existence of a causal relation between climatic conditions and the vegetation of any given region is so well known as to have become practically axiomatic" (p. 581).

Livingston and Shreve's statement of the net results of their work may

be summarized with two brief quotations. "A relation between climate and the distribution of the common species which dominate the principal vegetations is . . . well-established fact. But the relations between climate and the distribution of the generality of individual species is indirect and is obscured by many considerations" (p. 581). With regard to the prime requisite of the physiological approach—experiment, they have the following remarks: "The problem of the rôle of climatic conditions in determining plant distribution is essentially a physiological one, since it rests, in ultimate analysis, upon the influence exerted by environmental conditions on the activities of individual plants. The attack upon this problem must, however, be made by methods quite different from those employed in purely physiological investigations. The conditions must be measured rather than controlled, and the plant material must be examined throughout its range of occurrence. . . . The methods that must be employed hinge very largely upon the interpretation of a vast series of uncontrolled experiments under the varying conditions of natural environment. It is to the geographic aspects of the problem that we must ascribe many of its complexities and much of its difficult nature" (pp. 581–2).

Thus, in spite of repeated statements of faith in the initial assumption of environmental control in the distribution of vegetation, the authors could present as evidence only a coincidence between climate and the distribution of a few common species. They were left with not even good coincidence for the "generality of individual species." Their conclusion with regard to the experimental method was even more striking. It should be remembered that the prosecution of research in this field was predicated upon an experimental knowledge of plant reactions to environmental factors, as Schimper stated at the beginning (1898, 1903). We can measure the factors after a fashion, but we have no way of knowing whether they are in terms significant to the plant until we know the plant's reactions to their values. This, if we use ordinary physiological method, involves experiment, and experiment involves control; but when we control the life of a plant, no matter what the results of the experiment they become greatly limited in their value for the original purpose—that of solving the environmental relationship. Ecologists realized this long ago, and devised means of approximating conditions of naturalness in the laboratory or partial control in the field, but they could not eliminate control or their experiments would no longer be experiments. Even under rigidly controlled conditions the solution of one problem only leads to another fully as complex as the first if not more so. These students have been faced with the same problem of the complex causal system which was recognized and appreciated by

Humboldt and de Candolle, whose incisive logic warned them that the problem was probably unsolvable by any means then conceivable. Ecologists have tried to simplify the problem with the theory of limiting factors, but the isolation of such factors for most plants is almost as complex as the original cosmos.

Livingston and Shreve's conclusion with regard to the use of experiment in attacking the complex environmental relation is strongly reflected in the following statement found in the preface to their work, "On the whole, then, our aim has not been to discover true causal relationships between the two categories of observations here considered, but rather, simply to describe some of the vegetational and climatic features of the country. . . . Our work is primarily descriptive, as most ecological work must be for a long time to come, and the discovery of simple concomitancy is our nearest approach toward the establishment of causal relations. We have been led to the view that ecological science can be most rapidly advanced through this general method of quantitative comparison and by the placing upon record of such cases of concomitancy (between plants and their surroundings) as this method is able to bring forth" (pp. xiii-xiv).

This is sound method—simple inductive reasoning from empirically gathered facts—identical with that of Humboldt and the outstanding floristic geographers. As stated it involves no assumption of a causal sequence from habitat to plant. It is hardly consistent with some of the authors' later statements noted above, which place some of these elusive causal relations in the category of axioms; nor is it consistent with one in their introduction: "We can, in brief, put it down as a law of plant geography that the existence, limits, and movements of plant communities are controlled by physical conditions."

If all this be true, it would seem to reorient the experimental method, in the commonly accepted sense of the term, for physiological plant geography. The latter then becomes, as floristic geography always has been, a search for what Livingston and Shreve call "simple concomitancy," with no particular prospect of finding causal relations except by approximation. The chief advantage of the physiological approach becomes its promise of presenting new kinds of factual patterns for comparison. Who shall say whether they are better or worse patterns than those presented by the field of morphology, especially in view of all the latter's ramifications in cytogenetics? Experimental physiological techniques, used with complete realization of their limitations, will make valuable contributions to these patterns; but they do not seem to show any greater promise of solving the complex plant-environment relation than do other techniques such as are in use by students of floristics or genetics.

A more or less stable community of plants living together in an area can hardly be an "organism" in the sense of an individual, but Clements has insisted that its analogy with an individual is so close that many of the characteristics of an individual (growth, maturity, death) may be attributed to it. Gleason's criticism of the concept has probably been the most effective (1926, 1939). He maintains that the idea is untenable because the plant community cannot actually be defined in space—that the community is made up of individuals whose presence there depends so much upon chance as to render a finite description impossible. Clements's use of the concept has of necessity been limited to analogy, and his reasoning has thereby repeatedly fallen into error, as pointed out by Cooper (1926) and others (see also Phillips, 1935, for a review of this matter).

The organismic theory has had a wide acceptance in the field of geography as a whole. Hartshorne, in his recent survey of the whole field (1939), devotes a long chapter to a critical discussion of it, with arguments that are strongly reminiscent of those advanced by Gleason for geographic botany (see below).

Although the organismic concept has had many critics, the theory of succession, or at least of vegetational change, is almost universally accepted, especially among American students. It is looked upon as essential to an understanding of the plant world, and most of the organization of our material is based upon it. This received a clear statement by Cooper, in 1926. "One fundamental premise must dominate the whole, almost axiomatic, and yet needing constant emphasis—the universality of change. It follows from this that to confine our field to the present, or to include only the easily accessible portions of the immediate past, will seriously damage the prospect of valuable results. Notwithstanding the fact that the present must always furnish the bulk of our knowledge, the only truly scientific viewpoint is that which opens up the whole vista of vegetational history." In brief, it is urged that the student of plant succession should attempt to integrate the geography and history of the plant life of any given area.

Gleason is one of the few who have been so bold as to question the proposition that the present distribution and nature of vegetation can only be studied properly with the aid of its successional history (1927). His argument is simple and proceeds directly from his attitude toward the plant community. If a community cannot be defined in *space*, neither can it be in *time*. Here again, as will be noted later, the general geographers have had to deal with similar problems.

It is of interest to note in this connection that Braun-Blanquet has made an effort to organize the study of plant sociology around the static

community (1928), and to keep the developmental concept in a secondary position. In a brief criticism of Clements's methods Braun-Blanquet says, "He worked out methods for investigating the dynamic processes and sought to place the classification of communities on a dynamogenetic foundation. He has been criticized . . . for neglecting the static features of vegetation. His dynamics are often hypothetical, and the static social units are indispensable as a foundation for the study of vegetation" (p. 305).

#### DEVELOPMENT OF GEOGRAPHY AS A WHOLE

Before attempting to summarize the recent trends in plant geography it will be well to look briefly at developments in the field of geography as a whole. Here we have the advantage of the recent and highly critical review by Richard Hartshorne (1939) called "The Nature of Geography." This paper recounts the history of modern geography, with a rigorous examination of the philosophical grounds upon which it rests. The close parallels that exist between its problems and vicissitudes and those of biogeography should make the book "required reading" for any biologist whose work takes him into the geographic field.

Modern geography is regarded as having its origin in the work of the German masters, Alexander von Humboldt (1845-62) and Carl Ritter (1822-59). We have already discussed Humboldt's points of view in plant geography, and we have noted that they were only a reflection of his views on geography as a whole. Ritter was in substantial agreement. His first principle "was that geography must be an empirical science rather than one deduced from rational principles—from philosophy—or from *a priori* theories of general 'geography'" (Hartshorne, 1939, p. 230). In his own words "The fundamental rule which should assure truth to the whole work is to proceed from observation to observation, not from opinion or hypothesis to observation" (1822, 1: 23). With neither Humboldt nor Ritter, however, did this degenerate into mere fact-gathering. Both were deeply conscious of the close interdependence of phenomena in a given area. They sorted their facts areally, and sought, through comparative studies, to arrive at some approximation to causal relationships, and at characterizations of different areas by outstanding factual complexes. Like Humboldt, Ritter thought that laws of interrelationship existed, but he felt that they could better be worked out inductively than by starting with assumptions. He thought we should "ask the earth itself for its laws" (1822, 1: 4).

After Humboldt and Ritter the next outstanding geographer whose work has large significance for biogeography was Friedrich Ratzel. Ratzel's first volume, significantly entitled *Anthropogeographie*, was published in

1882. It contained something of a new departure in that it began with the "natural" conditions of the earth and then related them to human cultures by way of their influences on these cultures. By this turn geography became, for the time, environmentalist, with the assumption that human culture was principally the product of the "natural" conditions which surrounded it. In a second volume of his work, published in 1891, Ratzel largely reversed this view, but a strong tendency to invoke environmental causation directly in human geography became deeply embedded in geographic thought. The implications of Ratzel's work were brought to America by Ellen C. Semple who published, in 1911, her book on the "Influences of Geographic Environment." Guided by Semple's writings, and modified by the school of "physiography" centering in the work of W. M. Davis, American geography continued to reflect this environmental determinism for two decades. Semple, and especially Barrows (1923), who treated geography as "Human Ecology," did not look for all ultimate causation in the external environment, but rather in an "adjustment between man and the earth." They sought thus to eliminate some of the one-sidedness in the study of environmental relations, but they did not at the same time clarify a reasoning which began with the assumption of human adjustment to environment.

Only a small and relatively inarticulate minority knew of or cared for contemporary developments in nonenvironmentalist schools. Then in 1925 Carl Sauer, impressed with some works by the German students, published a short paper called "The Morphology of Landscape." Sauer advocated, on logical grounds, a return to the earlier reasoning of Humboldt and Ritter and to that of some later German geographers: namely, that assumptions of environmental determinism should be eliminated, that geography should endeavor to ground itself upon safer, inductive methods.

These views have made notable changes in American geographic thought. They have apparently achieved wide acceptance, and are greatly elaborated and clarified by the work of Hartshorne already mentioned.

The similarity between the general outline of the history of geographic thought, and that of its special part, plant geography, is obvious. In both, the initial impulses for modern development occurred in the time of Humboldt, with their reasoning based upon inductive logic. Certain phases of plant geography, notably in the fields of life-form and physiological studies, became strongly environmentalist under the influence of the theory of adaptation which grew out of Darwinian thought. Although Hartshorne makes no mention of it, the equivalent movement in human geography reflected by Ratzel probably arose from the same inspiration. In both cases the followers of environmentalism became remarkably one-sided and confident in

their reasoning, failing to use the results developed from other points of view; and in each case there has been either a contemporary persistence of the older, more conservative reasoning, as in floristic plant geography, or an early revival of it as in the German school of geographers. The movement centering in the works of Warming and Schimper, who attempted to eliminate some of the post-Darwinian teleology from studies of structural adaptation to environment, trying at the same time to fix the geography of plants upon a basis of physiological adjustment, probably had its counterpart in the later work of Ratzel and in that of Semple and Barrows.

Here the comparison stops except for a few recent developments in plant geography, some of which have already been noted. The outspoken reaction of some Scandinavian and English botanists against the current functional interpretations in life-form classification, and their advocacy of return to a purely physiognomic basis, form a close parallel to the revolutionary geographic movement started in America by Carl Sauer. There are some further parallels among recent trends that also deserve attention. Gleason's criticism of the organismic concept of the plant association has its counterpart among general geographers, as shown in the following statement by Hartshorne: "In organic growth, all the individual parts develop from a common origin . . . , are nourished from a common food supply, and are controlled in their growth by some common directive agency. External elements introduced into a single part of the organism are either converted into materials that are spread through the whole, or are expelled, or in the abnormal case, are immediately recognized as 'foreign bodies' and isolated, as in a cyst. What do we find comparable to this in the alteration of an area of the earth? The soil erosion of any single slope may be entirely independent of all conditions in other parts of the area; the growth of a single tree is dependent only on the immediately surrounding conditions; what takes place in all the rest of the area may be of no importance to it whatever. The rainfall conditions are largely the result of external forces quite independent of changes in the area itself. Finally the cultural landscape developed by man cannot be understood either as a growth within the area nor as a process of digestion of external materials by the area as an organism: cultivated plants are introduced not into the area as a whole, nor into any common digestive organ, but first into some particular field. Foreign capitalists and engineers may insert factories into a region of primitive subsistence economy, as though a surgeon were to put a backbone in a starfish" (p. 259). Hartshorne concludes that regions cannot be defined as units of reality, and cannot be considered as concrete individual objects (p. 281). It is not difficult for us to apply this conclusion to our concepts of the plant association.

Related to the primary significance of succession in the organization of plant geography, also questioned by Gleason, Hartshorne has described a similar problem in geography as a whole: "The various forces that alter the landscape of an area, whether they are internal or external, recognize no common limits to the area. It follows therefore, that, in whatever manner we may consider a particular area as a definite unit, that unity can be established only as of a given time. . . . Any study of the development of the cultural landscape of an area . . . is legitimate only if we remember that the area considered through a sequence of periods is an arbitrary unit. Whatever interest there may be in studying the combination of processes of changes in an arbitrary unit of area, there can be no logical requirement that geography must make such studies." Hartshorne thinks that underlying the thesis of the essential significance of development in a geographic area is the assumption—"commonly unmentioned, and even denied"—that the unit area will remain unchanged during the process. He thinks that this concept is, "in principle, a survival of the idea of environmental control" (Broek, 1938, in Hartshorne, 1939, p. 182). Unit areas do not, of course, maintain themselves thus in reality.

Again, the charge is commonly made that a geography that does not emphasize change would be *static* and unimportant—that *becoming* is more important than *being*. To this Hartshorne (p. 183) replies that "If . . . one examines the question of what 'is important' objectively, one must ask what importance *becoming* can have, if the state of *being* is unimportant." In this view history as applied to geography becomes a systematic study of any particular feature of the area under consideration. Hartshorne also calls attention to the inherent complexity of any proposed integration of history and geography, which, he maintains, appears "beyond the limitations of human thought" (p. 463).

Anyone who has tried to define a plant community and to solve the impenetrable maze of cause and effect relations that exist in it at a point in time must have wondered how he could ever hope to project it backward into history without either losing it completely or merely compounding his unsolved problems. Yet we find that the developmental view of vegetation is confidently pushed back even into remote geologic time, and both complex communities and successions are reconstructed on meager paleontological evidence.

#### THE NATURE OF PLANT GEOGRAPHY

Having sketched briefly what appear to be the principal trends of development in phytogeography, and having drawn up some parallels with the

history of all modern geographic thought, it seems worth while to look ahead for possible courses into which existing trends may lead us. It is impossible to do this without raising controversial issues and expressing a certain amount of personal opinion.

For the plant geographer, by far the most significant feature of the recent developments in geography as a whole is the complete re-evaluation of the environmentalist view, and with it the insistence that geography is an empirical, integrating science, proceeding by inductive reasoning from circles of facts, rather than from assumptions of causal sequences of relationship among facts. The effects of these ideas, as they impinge individually upon the several existing viewpoints in plant geography previously noted, are more or less far-reaching, depending upon the extent to which these viewpoints have been diverted into environmental determinism. As the effects touch the whole of plant geography, moreover, their influence may become even greater.

Floristic plant geography should be least affected. Its distribution problems have always had such a wide scope, and the inherent uncertainties in its taxonomic and phylogenetic concepts have been so great, that it has been forced to remain conservative in its assignment of causes. This effect has been increased by the studies of geneticists on the species problem. The morphological boundaries of species, and thus their actual geographic boundaries, have always been more or less obscured by the question of what were *good* characters and what were temporal, *ecological* ones. The transplant studies of Turesson (1922) in Europe and of Clausen, Keck and Heisey (1940) in America, as well as investigations of polyploidy (see Stebbins, 1940), have tended to increase the systematist's respect for many kinds of characters that he formerly thought were direct responses to environment. The tendency in such recent work has been to raise rather than lower the plant in the scale of cause and effect. Evidence of the deep penetration of this idea into floristic plant geography is to be found in such work as that of Lam (1938) on the Burseraceae, and of Anderson (1941) and Fassett (1941) on mass collection techniques.

A revision of environmentalist views in the study of life forms appears already well under way in Europe although it has not yet shown itself among the few American students that have gone into this field. Here again there have been inherent reasons for conservatism, for it has never been possible to divorce the study from problems of speciation. Form, whether it was to be interpreted one way or another, still had to be examined in detail, and sooner or later brought the student into contact with hard facts of plant structure that would not admit of causal explanation. Furthermore, there were always in the background those old physiognomic systems of Humboldt

and Grisebach which, after all, had proved useful. A revision of views was probably hastened by the extremely one-sided, epharmonic Raunkiaer system which soon proved to have serious and obvious flaws in its delineation of reality.

The greatest effect of a change to more inductive methods should be found in physiological plant geography. Du Rietz has already noted a start in this direction (1921), and it is possible to see it in the work of Braun-Blanquet (1928) and his followers in European schools. The factors of the external habitat are there considered, not as the starting point for the investigation of the plant life of a given area, but as elements in the economy of the plant communities that live there. Braun-Blanquet's approach to the whole subject of plant community structure and relationship is largely inductive, but that environmental determinism still persists in his work is shown, among other ways, by his treatment of Raunkiaer's life-form classification.

By analogy with geography as a whole, as it has been outlined in the preceding discussion, plant geography becomes simply a study of the areal differentiation of the world of plants. It may be looked upon as a chorographic, integrating study which attempts to consider, not only particular kinds of phenomena in reality, but actual sections of reality itself. It may organize its material in two ways, systematically and regionally. "In systematic geography each particular element, or element complex, that is geographically significant is studied in terms of its relation to the total differentiation of areas, as it varies from place to place over the world. . . . This is in no sense the complete study of that particular phenomenon, such as would be made in the appropriate systematic science, but the study of it solely in its geographic significance. . . . In regional geography all the knowledge of the interrelations of all features at given places—obtained in part from the different systems of systematic geography—is integrated . . . to provide the total geography of those places" (Hartshorne, 1939, p. 465).

Plant geography may be said to have systematic phases in floristic geography, in the distribution of life-forms and plant communities, and in the distribution of such behavior patterns as might be definitely determined to have geographic significance. It may expect to find many such patterns in the fields of physiology and cytogenetics. It should draw upon the other systematic sciences such as geology, meteorology, zoölogy, and human geography for still other patterns of fact. Its nearest approach to regional geography would be an attempt at the integration of all these patterns in any given area, with an effort to relate the area to all the others in the world in such a way as to define useful divisions of the world on a botanical basis. It is difficult to conceive of a regional plant geography in a strict botanical

sense, for a botanical problem of integration in any given area cannot be separated from the total complex of geographic phenomena.

We have seen that the problem of establishing the "natural" geographic areas with which the student must deal is fraught with difficulties, and that areas, like species, are bounded by arbitrarily drawn limits. Hartshorne's statement here is to the point:

"The problem of establishing the boundaries of a geographic region . . . presents a problem for which we have no reason to even hope for an objective solution. . . . The most that we can say is that any particular unit of land has significant relations with all the neighboring units and that in certain respects it may be more closely related with a particular group of units than with others, but not necessarily in all respects. The regional entities which we construct on this basis are therefore in the full sense mental constructions . . . even though we find them to be constructions that provide some sort of intelligent basis for organizing our knowledge of reality" (1939, p. 275).

Gleason arrives at a somewhat similar conclusion on the basis of his "Individualistic Concept of the Plant Association": "Since every community varies in structure, and since no two communities are precisely alike, or have genetic or dynamic connection, a precisely logical classification of communities is not possible" (1939, p. 108; see also 1926, p. 26).

With so much difficulty in setting up natural unit areas it seems entirely illogical to liken them in any way to individual organisms, either in space or time. With so small a knowledge of the relationships at a given time within an area or community as we now possess, it seems extremely difficult to derive principles by which we could reconstruct the area for past times. Above all it appears unnecessary and misleading to construct a classification of plant communities upon such a historical or successional basis. The study of development might better be relegated largely to the history of regional cross-sections or of individual features that might be encompassed in space. It would become, then, a part of systematic plant geography. No one familiar with geographic field problems will deny the significance and universality of successional change in the vegetable world, but it probably can be said that we know too little about it to use it as a framework upon which to hang all our knowledge and problems in plant geography.

Our present ideas of the development of vegetation are based to a surprising extent upon inference—upon deduced facts rather than upon observed facts. We have fair notions of what has actually happened in the recent past on areas of cleared land, on new flood plains, or on lake shores, but these are "marginal" to the "generality" of vegetation, for which we can only infer the nature of the change. We would be better advised, therefore,

to base our study of plant geography, and any system of classification for botanical regions that we may hope to devise, upon the existing plant life rather than upon partially hypothetical trends of development. A system "based on primary facts, facts of observation . . . provides a more solid basis for scientific work than a system based partially on deduced facts" (Hartshorne, 1939, p. 364).

What is to be the logic of the geographer's method if current trends are followed? He should approach his problem naïvely, by studying "a particular circle of facts which [he] first establishes and describes in order to search for causal relationships" (Hettner, 1907, quoted in Hartshorne, 1939, p. 126). He is not to attack his causal problems directly as an end in themselves, on the general principle that ". . . a definition of a field of science in terms of causal relationships *instructs* its student to seek and find such relationships, robs him of his impartiality, and easily leads to dogma; for 'success lies most apparently, or at least most easily, in the demonstration of an environmental adjustment'" (Michotte, 1921; Sauer, 1927, 1931; Schlüter, 1906, quoted in Hartshorne, 1939, p. 302).

The inductive logic proposed here was that of Humboldt and Ritter, Grisebach, Darwin, Hooker and Gray; and it is being used effectively today by our modern floristic geographers and a few plant sociologists. It is the logic which underlies the technique of comparing maps of the ranges of species and other phenomena. It can probably be said of plant geography, as of geography as a whole, that "The most important contributions of geography to the world's knowledge have come from an application of the technique of mapping distributions and of comparing and generalizing the patterns of distribution" (James, 1935). This does not mean that we should fail to make full use of the method of "multiple working hypotheses," which has been so clearly defined, and put to such excellent use in the field of geology (Chamberlin, 1897). But hypothesis should be an aid to the interpretation of observed facts rather than a basis upon which to build a science.

The advent of an environmentalism which tended to exclude other attitudes in geographic thought occurred at about the same time in the field as a whole and in the various phases of plant geography. Likewise at the same time there appeared a tendency to reason, not from a "circle of facts," but from an assumed causal relation between environment and organism. As this tendency gathered headway the fission between our two principal viewpoints in plant geography became evident—floristic vs. ecological. It seems reasonable to suspect that an actual barrier between them is the fundamental one of a difference in logical method. The current trend among some ecological plant geographers to return to more inductive reasoning, and a

definite trend in that direction among general geographers, suggest that the barrier is on the way to dissolution. Much of it will remain standing, however, as long as there are many ecologists who have no working knowledge of methods and materials in the floristic field, and many floristic students who know nothing and care less about the structure and behavior of plant communities.

What are the prospects of formulating principles and generic concepts in plant geography as it is here conceived? In short, what prospect is there of reaching a resolution of the complex interplay of influences in a geographic area? We can expect such principles and concepts in some of the systematic elements which contribute to the complex. There are some generalizations with regard to climatic and edaphic factors, physiological requirements of plants, organizational and developmental characteristics of communities, and habits of variation among species—all of which supply materials and inspiration for study of the regional or areal unit. But it seems necessary to realize that in regional studies principles may be arrived at with great difficulty or not at all. Inductive logic gives us no expectation of anything beyond approximation.

Hartshorne has stated our limitations very clearly: "One major difficulty lies in the fact that the integration of phenomena which we must study in areas is an integration of a large number of independent, or semi-independent factors. Consequently we seldom have to do with simple relationships—e.g., rainfall to soil, temperature to crops, etc. Theoretically we might follow the logic of the systematic sciences, by assuming that all other conditions remain the same, but we have only the laboratory of reality in which to study these features, and in that laboratory the other elements do not remain the same, except perhaps in a very small number of cases, and we have no way of making them remain the same. Indeed, even if we knew the theoretical principles governing the relation of each individual factor to the total resultant, in the case of such complex resultants as cultural features, a principle which attempted to state the sum total of all the relationships, each in its proper proportion, would be far too complicated for us to be able to use. This is a general difficulty that applies not only to all the more complicated aspects of the social sciences, but also to many phenomena in the natural sciences. Even if one knew all the principles and had all the data, the solution would be involved in a mathematical equation so complicated that no finite mind could solve it" (1939, p. 385).

It may be said that this is a defeatist view—that by denying so much of the expectation of final solution in the complex problems of causation we would eliminate much of the inspiration and incentive to further research.

It would have to be admitted, however, that one of the most active, productive and persistent phases of plant geography has been thriving upon inductive methods for many generations. It has never hoped for more than an approximate solution to the problem of ultimate causation. The same would have to be said of other natural sciences such as geology and meteorology, and of most of the broad field of plant and animal morphology. To hold that the logical methods of these sciences were "defeatist" would be denying the quality of logic that gave us the Renaissance and the development of nearly all of modern science.

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*August, 1942.*