The individualistic concept of the plant association *

H. A. Gleason

The continued activity of European ecologists, and to a somewhat smaller extent of American ecologists as well, in discussing the fundamental nature, structure, and classification of plant associations, and their apparently chronic inability to come to any general agreement on these matters, make it evident that the last word has not yet been said on the subject. Indeed, the constant disagreement of ecologists, the readiness with which flaws are found by one in the proposals of another, and the wide range of opinions which have been ably presented by careful observers, lead one to the suspicion that possibly many of them are somewhat mistaken in their concepts, or are attacking the problem from the wrong angle.

It is not proposed to cite any of the extensive recent literature on these general subjects, since it is well known to all working ecologists. Neither is it necessary to single out particular contributions for special criticism, nor to point out what may appear to us as errors in methods or conclusions.

It is a fact, as Dr. W. S. Cooper has brought out so clearly in a manuscript which he has allowed me to read, and which will doubtless be in print before this, that the tendency of the human species is to crystallize and to classify his knowledge; to arrange it in pigeon-holes, if I may borrow Dr. Cooper's metaphor. As accumulation of knowledge continues, we eventually find facts that will not fit properly into any established pigeon-hole. This should at once be the sign that possibly our original arrangement of pigeon-holes was insufficient and should lead us to a careful examination of our accumulated data. Then we may conclude that we would better demolish our whole system of arrangement and classification and start anew with hope of better success.

Is it not possible that the study of synecology suffers at the present time from this sort of trouble? Is it not conceivable that, as the study of plant associations has progressed from its originally simple condition into its present highly organized and complex state, we have attempted to arrange all our facts in ac-

* Contributions from The New York Botanical Garden, No. 279.

cordance with older ideas, and have come as a result into a tangle of conflicting ideas and theories?

No one can doubt for a moment that there is a solid basis of fact on which to build our study of synecology, or that the study is well worth building. It is the duty of the botanist to translate into intelligible words the various phenomena of plant life, and there are few phenomena more apparent than those of their spatial relations. Plant associations exist; we can walk over them, we can measure their extent, we can describe their structure in terms of their component species, we can correlate them with their environment, we can frequently discover their past history and make inferences about their future. For more than a century a general progress in these features of synecology can be traced.

It has been, and still is, the duty of the plant ecologist to furnish clear and accurate descriptions of these plant communities, so that by them the nature of the world's vegetation may be understood. Whether such a description places its emphasis chiefly on the general appearance of the association, on a list of its component species, on its broader successional relations, or on its gross environment, or whether it enters into far greater detail by use of the quadrat method, statistical analysis,[1] or exact environometry, it nevertheless contributes in every case to the advancement of our understanding of each association in detail and of vegetation in all its aspects in general.

It is only natural that we should tend to depart from the various conclusions which we have reached by direct observation or experiment, and to attempt other more general deductions as well. So we invent special terms and methods for indicating the differences between associations and the variation of the plant life within a single community. We draw conclusions for ourselves, and attempt to lay down rules for others as to ways and means of defining single associations, by character species, by statistical studies, by environmental relations, or by successional history. We attempt to classify associations, as individual

[1] Pavillard has cast serious doubt on the efficiency of the statistical method in answering questions of synecology. His argument, based solely on European conditions, needs of course no reply from America, but it may properly be pointed out that the intimate knowledge of vegetational structure obtained in this way may easily lead to a much fuller appreciation of synecological structure, entirely aside from any merits of the actual statistical results.

examples of vegetation, into broader groups, again basing our methods on various observable features and arriving accordingly at various results. We even enter the domain of philosophy, and speculate on the fundamental nature of the association, regard it as the basic unit of vegetation, call it an organism, and compare different areas of the same sort of vegetation to a species.

The numerous conclusions in synecology which depend directly upon observation or experiment are in the vast majority of cases entirely dependable. Ecologists are trained to be accurate in their observations, and it is highly improbable that any have erred purposely in order to substantiate a conclusion not entirely supported by facts. But our various theories on the fundamental nature, definition, and classification of associations extend largely beyond the bounds of experiment and observation and represent merely abstract extrapolations of the ecologist's mind. They are not based on a pure and rigid logic, and suffer regularly from the vagaries and errors of human reason. A geneticist can base a whole system of evolution on his observations of a single species: ecologists are certainly equally gifted with imagination, and their theories are prone to surpass by far the extent warranted by observation.

Let us then throw aside for the moment all our pre-conceived ideas as to the definition, fundamental nature, structure, and classification of plant associations, and examine step by step some of the various facts pertinent to the subject which we actually know. It will not be necessary to illustrate them by reference to definite vegetational conditions, although a few instances will be cited merely to make our meaning clear. Other illustrations will doubtless occur to every reader from his own field experience.

We all readily grant that there are areas of vegetation, having a measurable extent, in each of which there is a high degree of structural uniformity throughout, so that any two small portions of one of them look reasonably alike. Such an area is a plant association, but different ecologists may disagree on a number of matters connected with such an apparently simple condition. More careful examination of one of these areas, especially when conducted by some statistical method, will show that the uniformity is only a matter of degree, and that two sample quadrats with precisely the same structure can scarcely be discovered.

Consequently an area of vegetation which one ecologist regards as a single association may by another be considered as a mosaic or mixture of several, depending on their individual differences in definition. Some of these variations in structure (if one takes the broader view of the association) or smaller associations (if one prefers the narrower view) may be correlated with differences in the environment. For example, the lichens on a tree-trunk enjoy a different environment from the adjacent herbs growing in the forest floor. A prostrate decaying log is covered with herbs which differ from the ground flora in species or in relative numbers of individuals of each species. A shallow depression in the forest, occupied by the same species of trees as the surroundings, may support several species of moisture-loving herbs in the lower stratum of vegetation. In other cases, the variations in vegetational structure may show no relation whatever to the environment, as in the case of a dense patch of some species which spreads by rhizomes and accordingly comes to dominate its own small area. The essential point is that precise structural uniformity[2] of vegetation does not exist, and that we have no general agreement of opinion as to how much variation may be permitted within the scope of a single association.

In our attempts to define the limits of the association, we have but two actually observable features which may be used as a basis, the environment and the vegetation. Logically enough, most ecologists prefer the latter, and have developed a system based on character-species. In northern latitudes, and particularly in glaciated regions, where most of this work has been done, there is a wide diversity in environment and a comparatively limited number of species in the flora. A single association is therefore occupied by few species, with large numbers of individuals of each, and it has not been difficult to select from most associations a set of species which are not only fairly common and abundant, but which are strictly limited to the one association. But in many parts of the tropics, where diversity of environment has been reduced to a minimum by the practical completion of most physiographic processes and by the long-continued cumulation of plant reactions, and where the flora is

[2] It has often occurred to the writer that much of the structural variation in an association would disappear if those taxonomic units which have the same vegetational form and behavior could be considered as a single ecological unit.

extraordinarily rich in species, such a procedure is impracticable or even impossible. Where a single hectare may contain a hundred species of trees, not one of which can be found in an adjacent hectare, where a hundred quadrats may never exhibit the same herbaceous species twice, it is obvious that the method of characteristic species is difficult or impracticable.

It is also apparent that different areas of what are generally called the same association do not always have precisely the same environment. A grove of *Pinus Strobus* on soil formed from decomposed rocks in the eastern states, a second on the loose glacial sands of northern Michigan, and a third on the sandstone cliffs of northern Illinois are certainly subject to different environmental conditions of soil. An association of prairie grass in Illinois and another in Nebraska undoubtedly have considerable differences in rainfall and available water. A cypress swamp in Indiana has a different temperature environment from one in Florida.

Two environments which are identical in regard to physiography and climate may be occupied by entirely different associations. It is perfectly possible to duplicate environments in the Andes of southern Chile and in the Cascade Mountains of Oregon, yet the plant life is entirely different. Duplicate environments may be found in the deserts of Australia and of Arizona, and again have an entirely different assemblage of species. Alpine summits have essentially the same environment at equal altitudes and latitudes throughout the world, apart from local variations in the component rock, and again have different floras. It seems apparent, then, that environment can not be used as a means of defining associations with any better success than the vegetation.

At the margin of an association, it comes in contact with another, and there is a transition line or belt between them. In many instances, particularly where there is an abrupt change in the environment, this transition line is very narrow and sharply defined, so that a single step may sometimes be sufficient to take the observer from one into the other. In other places, especially where there is a very gradual transition in the environment, there is a correspondingly wide transition in the vegetation. Examples of the latter condition are easily found in any arid mountain region. The oak forests of the southern Coast Range in California in many places descend upon the grass-covered foothills by a wide transition zone in which the trees become very gradually fewer and farther apart until they ultimately disappear completely. In Utah, it may be miles from the association of desert shrubs on the lower elevations across a mixture of shrubs and juniper before the pure stands of juniper are reached on the higher altitudes. It is obvious, therefore, that it is not always possible to define with accuracy the geographical boundaries of an association and that actual mixtures of associations occur.

Such transition zones, whether broad or narrow, are usually populated by species of the two associations concerned, but instances are not lacking of situations in which a number of species seem to colonize in the transition zone more freely than in either of the contiguous associations. Such is the case along the contact between prairie and forest, where many species of this type occur, probably because their optimum light requirements are better satisfied in the thin shade of the forest border than in the full sun of the prairie or the dense shade of the forest. Measured by component species such a transition zone rises almost to the dignity of an independent association.

Species of plants usually associated by an ecologist with a particular plant community are frequently found within many other types of vegetation. A single boulder, partly exposed above the ground at the foot of the Rocky Mountains in Colorado, in the short-grass prairie association, may be marked by a single plant of the mountain shrub *Cercocarpus*. In northern Michigan, scattered plants of the moisture-loving *Viburnum cassinoides* occur in the xerophytic upland thickets of birch and aspen. Every ecologist has seen these fragmentary associations, or instances of sporadic distribution, but they are generally passed by as negligible exceptions to what is considered a general rule.

There are always variations in vegetational structure from year to year within every plant association. This is exclusive of mere periodic variations from season to season, or aspects, caused by the periodicity of the component species. Slight differences in temperature or rainfall or other environmental factors may cause certain species to increase or decrease conspicuously in number of individuals, or others to vary in their vigor or luxuriance. Coville describes, in this connection, the remarkable variation in size of an *Amaranthus* in the Death Valley, which was three meters high in a year of abundant rainfall, and its progeny only a decimeter high in the following year of drought.

The duration of an association is in general limited. Sooner or later each plant community gives way to a different type of vegetation, constituting the phenomenon known as succession. The existence of an association may be short or long, just as its superficial extent may be great or small. And just as it is often difficult and sometimes impossible to locate satisfactorily the boundaries of an association in space, so is it frequently impossible to distinguish accurately the beginning or the end of an association in time. It is only at the center of the association, both geographical and historical, that its distinctive character is easily recognizable. Fortunately for ecology, it commonly happens that associations of long duration are also wide in extent. But there are others, mostly following fires or other unusual disturbances of the original vegetation, whose existence is so limited, whose disappearance follows so closely on their origin, that they scarcely seem to reach at any time a condition of stable equilibrium, and their treatment in any ecological study is difficult. The short-lived communities bear somewhat the same relation to time-distribution as the fragmentary associations bear to space-distribution. If our ecological terminology were not already nearly saturated, they might be termed ephemeral associations.

Now, when all these features of the plant community are considered, it seems that we are treading upon rather dangerous ground when we define an association as an area of uniform vegetation, or, in fact, when we attempt any definition of it. A community is frequently so heterogeneous as to lead observers to conflicting ideas as to its associational identity, its boundaries may be so poorly marked that they can not be located with any degree of accuracy, its origin and disappearance may be so gradual that its time-boundaries can not be located; small fragments of associations with only a small proportion of their normal components of species are often observed; the duration of a community may be so short that it fails to show a period of equilibrium in its structure.

A great deal has been said of the repetition of associations on different stations over a considerable area. This phenomenon is striking, indeed, and upon it depend our numerous attempts to classify associations into larger groups. In a region of numerous glacial lakes, as in parts of our northeastern states, we find lake after lake surrounded by apparently the same communities, each of them with essentially the same array of species in about the same numerical proportions. If an ecologist had crossed Illinois from east to west prior to civilization, he would have found each stream bordered by the same types of forest, various species of oaks and hickories on the upland, and ash, maple, and sycamore in the alluvial soil nearer the water. But even this idea, if carried too far afield, is found to be far from universal. If our study of glacial lakes is extended to a long series, stretching from Maine past the Great Lakes and far west into Saskatchewan, a very gradual but nevertheless apparent geographical diversity becomes evident, so that the westernmost and easternmost members of the series, while still containing some species in common, are so different floristically that they would scarcely be regarded as members of the same association. If one examines the forests of the alluvial floodplain of the Mississippi River in southeastern Minnesota, that of one mile seems to be precisely like that of the next. As the observer continues his studies farther down stream, additional species very gradually appear, and many of the original ones likewise very gradually disappear. In any short distance these differences are so minute as to be negligible, but they are cumulative and result in an almost complete change in the flora after several hundred miles.

No ecologist would refer the alluvial forests of the upper and lower Mississippi to the same associations, yet there is no place along their whole range where one can logically mark the boundary between them. One association merges gradually into the next without any apparent transition zone. Nor is it necessary to extend our observations over such a wide area to discover this spatial variation in ecological structure. I believe no one has ever doubted that the beech-maple forest of northern Michigan constitutes a single association-type. Yet every detached area of it exhibits easily discoverable floristic peculiarities, and even adjacent square miles of a single area differ notably among themselves, not in the broader features, to be sure, but in the details of floristic composition which a simple statistical analysis brings out. In other words, the local variation in structure of any association merges gradually into the broader geographical variation of the association-type.

This diversity in space is commonly overlooked by ecologists, most of whom of necessity limit their work to a comparatively small area, not extensive enough to indicate that the small observed floristic differences between associations may be of much significance or that this wide geographical variation is actually in operation. Yet it makes difficult the exact definition of any association-type, except as developed in a restricted locality, renders it almost impossible to select for study a typical or average example of a type, and in general introduces complexities into any attempt to classify plant associations.

What have we now as a basis for consideration in our attempts to define and classify associations? In the northeastern states, we can find many sharply marked communities, capable of fairly exact location on a map. But not all of that region can be thus divided into associations, and there are other regions where associations, if they exist at all in the ordinary sense of the word, are so vaguely defined that one does not know where their limits lie and can locate only arbitrary geographic boundaries. We know that associations vary internally from year to year, so that any definition we may make of a particular community, based on the most careful analysis of the vegetation, may be wrong next year. We know that the origin and disappearance of some are rapid, of others slow, but we do not always know whether a particular type of vegetation is really an association in itself or represents merely the slow transition stage between two others. We know that no two areas, supposed to represent the same association-type, are exactly the same, and we do not know which one to accept as typical and which to assume as showing the effects of geographical variation. We find fragmentary associations, and usually have no solid basis for deciding whether they are mere accidental intruders or embryonic stages in a developing association which may become typical after a lapse of years. We find variation of environment within the association, similar associations occupying different environments, and different associations in the same environment. It is small wonder that there is conflict and confusion in the definition and classification of plant communities. Surely our belief in the integrity of the association and the sanctity of the association-concept must be severely shaken. Are we not justified in coming to the general conclusion, far removed from the prevailing opinion, that an association is not an organism, scarcely even a vegetational unit, but merely a *coincidence?*

This question has been raised on what might well be termed negative evidence. It has been shown that the extraordinary variability of the areas termed associations interferes seriously with their description, their delimitation, and their classification. Can we find some more positive evidence to substantiate the same idea? To do this, we must revert to the individualistic concept of the development of plant communities, as suggested by me in an earlier paper.[3]

As a basis for the presentation of the individualistic concept of the plant association, the reader may assume for illustration any plant of his acquaintance, growing in any sort of environment or location. During its life it produces one or more crops of seeds, either unaided or with the assistance of another plant in pollination. These seeds are endowed with some means of migration by which they ultimately come to rest on the ground at a distance from the parent plant. Some seeds are poorly fitted for migration and normally travel but a short distance; others are better adapted and may cover a long distance before coming to rest. All species of plants occasionally profit by accidental means of dispersal, by means of which they traverse

[3] I may frankly admit that my earlier ideas of the plant association were by no means similar to the concept here discussed. Ideas are subject to modification and change as additional facts accumulate and the observer's geographical experience is broadened. An inkling of the effect of migration on the plant community appeared as early as 1903 and 1904 (Bull. Illinois State Lab. Nat. Hist. **7:** 189.) My field work of 1908 covered a single general type of environment over a wide area, and was responsible for still more of my present opinions (Bull. Illinois State Lab. Nat. Hist. **9:** 35–42). Thus we find such statements as the following: "No two areas of vegetation are exactly similar, either in species, the relative numbers of individuals of each, or their spatial arrangement" (l. c. 37), and again: "The more widely the different areas of an association are separated, the greater are the floral discrepancies. . . . Many of these are the results of selective migration from neighboring associations, so that a variation in the general nature of the vegetation of an area affects the specific structure of each association" (l. c. 41). Still further experience led to my summary of vegetational structure in 1917 (Bull. Torrey Club **44:** 463–481), and the careful quantitative study of certain associations from 1911 to 1923 produced the unexpected information that the distribution of species and individuals within a community followed the mathematical laws of probability and chance (Ecology **6:** 66–74).

distances far in excess of their average journey. Sometimes these longer trips may be of such a nature that the seed is rendered incapable of germination, as in dispersal by currents of salt water, but in many cases they will remain viable. A majority of the seeds reach their final stopping-point not far from the parent, comparatively speaking, and only progressively smaller numbers of them are distributed over a wider circle. The actual number of seeds produced is generally large, or a small number may be compensated by repeated crops in successive years. The actual methods of dispersal are too well known to demand attention at this place.

For the growth of these seeds a certain environment is necessary. They will germinate between folds of paper, if given the proper conditions of light, moisture, oxygen, and heat. They will germinate in the soil if they find a favorable environment, irrespective of its geographical location or the nature of the surrounding vegetation. Herein we find the *crux* of the question. The plant individual shows no physiological response to geographical location or to surrounding vegetation *per se*, but is limited to a particular complex of environmental conditions, which may be correlated with location, or controlled, modified, or supplied by vegetation. If a viable seed migrates to a suitable environment, it germinates. If the environment remains favorable, the young plants will come to maturity, bear seeds in their turn, and serve as further centers of distribution for the species. Seeds which fall in unfavorable environments do not germinate, eventually lose their viability and their history closes.

As a result of this constant seed-migration, every plant association is regularly sowed with seeds of numerous extra-limital species, as well as with seeds of its own normal plant population. The latter will be in the majority, since most seeds fall close to the parent plant. The seeds of extra-limital species will be most numerous near the margin of the association, where they have the advantage of proximity to their parent plants. Smaller numbers of fewer species will be scattered throughout the association, the actual number depending on the distance to be covered, and the species represented depending on their means of migration, including the various accidents of dispersal. This thesis needs no argument in its support. The practical universality of seed dispersal is known to every botanist as a matter of common experience.

An exact physiological analysis of the various species in a single association would certainly show that their optimal environments are not precisely identical, but cover a considerable range. At the same time, the available environment tends to fluctuate from year to year with the annual variations of climate and with the accumulated reactionary effects of the plant population. The average environment may be near the optimum for some species, near the physiological limit of others, and for a third group may occasionally lie completely outside the necessary requirements. In the latter case there will result a group of evanescent species, variable in number and kind, depending on the accidents of dispersal, which may occasionally be found in the association and then be missing for a period of years. This has already been suggested by the writer as a probable explanation of certain phenomena of plant life on mountains, and was also clearly demonstrated by Dodds, Ramaley, and Robbins in their studies of vegetation in Colorado. In the first and second cases, the effect of environmental variation toward or away from the optimum will be reflected in the number of individual plants and their general luxuriance. On the other hand, those species which are limited to a single type of plant association must find in that and in that only the environmental conditions necessary to their life, since they have certainly dispersed their seeds many times into other communities, or else be so far removed from other associations of similar environment that their migration thence is impossible.

Nor are plants in general, apart from these few restricted species, limited to a very narrow range of environmental demands. Probably those species which are parasitic or which require the presence of a certain soil-organism for their successful germination and growth are the most highly restricted, but for the same reason they are generally among the rarest and most localized in their range. Most plants can and do endure a considerable range in their environment.

With the continuance of this dispersal of seeds over a period of years, every plant association tends to contain every species of the vicinity which can grow in the available environment. Once a species is established, even by a single seed-bearing plant, its further spread through the association is hastened, since it no longer needs to depend on a long or accidental migration, and this spread is continued until the species is eventually distributed throughout the area of the association. In general, it may be considered that, other things being equal, those species of wide extent through an association are those of early introduction which have had ample t'me to complete their spread, while those of localized or sporadic distribution are the recent arrivals which have not yet become completely established.

This individualistic standpoint therefore furnishes us with an explanation of several of the difficulties which confront us in our attempts to diagnose or classify associations. Heterogeneity in the structure of an association may be explained by the accidents of seed dispersal and by the lack of time for complete establishment. Minor differences between neighboring associations of the same general type may be due to irregularities in immigration and minor variations in environment. Geographical variation in the floristics of an association depends not alone on the geographical variation of the environment, but also on differences in the surrounding floras, which furnish the immigrants into the association. Two widely distant but essentially similar environments have different plant associations because of the completely different plant population from which immigrants may be drawn.

But it must be noted that an appreciation of these conditions still leaves us unable to recognize any one example of an association-type as the normal or typical. Every association of the same general type has come into existence and had its structure determined by the same sort of causes; each is independent of the other, except as it has derived immigrants from the other; each is fully entitled to be recognized as an association and there is no more reason for regarding one as typical than another. Neither are we given any method for the classification of associations into any broader groups.

Similar conditions obtain for the development of vegetation in a new habitat. Let us assume a dozen miniature dunes, heaped up behind fragments of driftwood on the shore of Lake Michigan. Seeds are heaped up with the sand by the same propelling power of the wind, but they are never very numerous and usually of various species. Some of them germinate, and the dozen embryonic dunes may thenceforth be held by as many different species of plants. Originally the environment of the dunes was identical and their floristic difference is due solely to the chances of seed dispersal. As soon as the plants have developed, the environment is subject to the modifying action of the plant, and small differences between the different dunes appear. These are so slight that they are evidenced more by the size and shape of the dune than by its flora, but nevertheless they exist. Additional species gradually appear, but that is a slow process, involving not only the chance migration of the seed to the exact spot but also its covering upon arrival. It is not strange that individuals are few and that species vary from one dune to another, and it is not until much later in the history of each dune, when the ground cover has become so dense that it affects conditions of light and soil moisture, and when decaying vegetable matter is adding humus to the sand in appreciable quantities, that a true selective action of the environment becomes possible. After that time permanent differences in the vegetation may appear, but the early stages of dune communities are due to chance alone. Under such circumstances, how can an ecologist select character species or how can he define the boundaries of an association? As a matter of fact, in such a location the association, in the ordinary sense of the term, scarcely exists.

Assume again a series of artificial excavations in an agricultural region, deep enough to catch and retain water for most or all of the summer, but considerably removed from the nearest areas of natural aquatic vegetation. Annually the surrounding fields have been ineffectively planted with seeds of *Typha* and other wind-distributed hydrophytes, and in some of the new pools *Typha* seeds germinate at once. Water-loving birds bring various species to other pools. Various sorts of accidents conspire to the planting of all of them. The result is that certain pools soon have a vegetation of *Typha latifolia*, others of *Typha angustifolia*, others of *Scirpus validus;* plants of *Iris versicolor* appear in one, of *Sagittaria* in another, of *Alisma* in a third, of *Juncus effusus* in a fourth. Only the chances of seed dispersal have determined the allocation of species to different pools, but in the course of three or four years each pool has a different appearance, although the environment, aside from the reaction of the various species, is precisely the same for each. Are we dealing here with several different associations, or with a single association, or with merely embryonic stages of some future association? Under our view, these become merely academic questions, and any answer which may be suggested is equally academic.

But it must again be emphasized that these small areas of vegetation are component parts of the vegetative mantle of the land, and as such are fully worthy of description, of discussion, and of inquiry into the causes which have produced them and into their probable future. It must be emphasized that in citing the foregoing examples, the existence of associations or of successions is not denied, and that the purpose of the two paragraphs is to point out the fact that such communities introduce many difficulties into any attempt to define or classify association-types and successional series.

A plant association therefore, using the term in its ordinarily accepted meaning, represents the result of an environmental sorting of a population, but there are other communities which have existed such a short time that a reasonably large population has not yet been available for sorting.

Let us consider next the relation of migration and environmental selection to succession. We realize that all habitats are marked by continuous environmental fluctuation, accompanied or followed by a resulting vegetational fluctuation, but, in the common usage of the term, this is hardly to be regarded as an example of succession. But if the environmental change proceeds steadily and progressively in one direction, the vegetation ultimately shows a permanent change. Old species find it increasingly difficult or impossible to reproduce, as the environment approaches and finally passes their physiological demands. Some of the migrants find establishment progressively easier, as the environment passes the limit and approaches the optimum of their requirements. These are represented by more and more individuals, until they finally become the most conspicuous element of the association, and we say that a second stage of a successional series has been reached.

It has sometimes been assumed that the various stages in a successional series follow each other in a regular and fixed sequence, but that is frequently not the case. The next vegetation will depend entirely on the nature of the immigration which takes place in the particular period when environmental change reaches the critical stage. Who can predict the future for any one of the little ponds considered above? In one, as the bottom silts up, the chance migration of willow seeds will produce a willow thicket, in a second a thicket of *Cephalanthus* may develop, while a third, which happens to get no shrubby immigrants, may be converted into a miniature meadow of *Calamagrostis canadensis*. A glance at the diagram of observed successions in the Beach Area, Illinois, as published by Gates, will show at once how extraordinarily complicated the matter may become, and how far vegetation may fail to follow simple, pre-supposed successional series.

It is a fact, of course, that adjacent vegetation, because of its mere proximity, has the best chance in migration, and it is equally true that in many cases the tendency is for an environment, during its process of change, to approximate the conditions of adjacent areas. Such an environmental change becomes effective at the margin of an association, and we have as a result the apparent advance of one association upon another, so that their present distribution in space portrays their succession in time. The conspicuousness of this phenomenon has probably been the cause of the undue emphasis laid on the idea of successional series. But even here the individualistic nature of succession is often apparent. Commonly the vegetation of the advancing edge differs from that of the older established portion of the association in the numerical proportion of individuals of the component species due to the sorting of immigrants by an environment which has not yet reached the optimum, and, when the rate of succession is very rapid, the pioneer species are frequently limited to those of the greatest mobility. It also happens that the change in environment may become effective throughout the whole area of the association simultaneously, or may begin somewhere near the center. In such cases the pioneers of the succeeding association are dependent on their high mobility or on accidental dispersal, as well as environmental selection.

It is well known that the duration of the different stages in succession varies greatly. Some are superseded in a very short time, others persist for long or even indefinite periods. This again introduces difficulties into any scheme for defining and classifying associations.

A forest of beech and maple in northern Michigan is lumbered, and as a result of exposure to light and wind most of the usual herbaceous species also die. Brush fires sweep over the clearing and aid in the destruction of the original vegetation. Very soon the area grows up to a tangle of other herbaceous and shrubby species, notably *Epilobium angustifolium*, *Rubus strigosus*, and *Sambucus racemosa*. This persists but a few years before it is overtopped by saplings of the original hardwoods which eventually restore the forest. Is this early stage of fire-weeds and shrubs a distinct association or merely an embryonic phase of the forest? Since it has such a short duration, it is frequently regarded as the latter, but since it is caused by an entirely different type of environmental sorting and lacks most of the characteristic species of the forest, it might as well be called distinct. If it lasted for a long period of years it would certainly be called an association, and if all the forest near enough to provide seeds for immigration were lumbered, that might be the case. Again we are confronted with a purely arbitrary decision as to the associational identity of the vegetation.

Similarly, in the broad transition zone between the oak-covered mountains and the grass-covered foothills in the Coast Range of California, we are forced to deal arbitrarily in any matter of classification. Shall we call such a zone a mere transition, describe the forests above and the grasslands below and neglect the transition as a mere mixture? Or shall we regard it as a successional or time transition, evidencing the advance of the grasslands up the mountain or of the oaks down toward the foothills? If we choose the latter, we must decide whether the future trend of rainfall is to increase, thereby bringing the oaks to lower elevations, or to decrease, thereby encouraging the grasslands to grow at higher altitudes. If we adopt the former alternative, we either neglect or do a scientific injustice to a great strip of vegetation, in which numerous species are "associated" just as surely as in any recognized plant association.

The sole conclusion we can draw from all the foregoing considerations is that the vegetation of an area is merely the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment. As a result, there is no inherent reason why any two areas of the earth's surface should bear precisely the same vegetation, nor any reason for adhering to our old ideas of the definiteness and distinctness of plant associations. As a matter of fact, no two areas of the earth's surface do bear precisely the same vegetation, except as a matter of chance, and that chance may be broken in another year by a continuance of the same variable migration and fluctuating environment which produced it. Again, experience has shown that it is impossible for ecologists to agree on the scope of the plant association or on the method of classifying plant communities. Furthermore, it seems that the vegetation of a region is not capable of complete segregation into definite communities, but that there is a considerable development of vegetational mixtures.

Why then should there be any representation at all of these characteristic areas of relatively similar vegetation which are generally recognized by plant ecologists under the name of associations, the existence of which is indisputable as shown by our field studies in many parts of the world, and whose frequent repetition in similar areas of the same general region has led us to attempt their classification into vegetational groups of superior rank?

It has been shown that vegetation is the resultant of migration and environmental selection. In any general region there is a large flora and it has furnished migrating seeds for all parts of the region alike. Every environment has therefore had, in general, similar material of species for the sorting process. Environments are determined principally by climate and soil, and are altered by climatic changes, physiographic processes, and reaction of the plant population. Essentially the same environments are repeated in the same region, their selective action upon the plant immigrants leads to an essentially similar flora in each, and a similar flora produces similar reactions. These conditions produce the well known phenomena of plant associations of recognizable extent and their repetition with great fidelity in many areas of the same region, but they also produce the variable vegetation of our sand dunes and small pools, the fragmentary associations of areas of small size, and the broad transition zones where different types of vegetation are mixed. Climatic changes are always slow, physiographic processes frequently reach stages where further change is greatly retarded, and the accumulated effects of plant reaction often reach a condition beyond which they have relatively little effect on plant life. All of these conspire to give to certain areas a comparatively uniform environment for a considerable period of time, during which continued migration of plants leads to a smoothing out of original vegetational differences and to the establishment of a relatively uniform and static vegetational structure. But other physiographic processes are rapid and soon develop an entirely different environment, and some plant reactions are rapid in their operation and profound in their effects. These lead to the short duration of some plant communities, to the development, through the prevention of complete migration by lack of sufficient time, of associations of few species and of different species in the same environment, and to mixtures of vegetation which seem to baffle all attempts to resolve them into distinct associations.

Under the usual concept, the plant association is an area of vegetation in which spatial extent, describable structure, and distinctness from other areas are the essential features. Under extensions of this concept it has been regarded as a unit of vegetation, signifying or implying that vegetation in general is composed of a multiplicity of such units, as an individual representation of a general group, bearing a general similarity to the relation of an individual to a species, or even as an organism, which is merely a more striking manner of expressing its unit nature and uniformity of structure. In every case spatial extent is an indispensable part of the definition. Under the individualistic concept, the fundamental idea is neither extent, unit character, permanence, nor definiteness of structure. It is rather the visible expression, through the juxtaposition of individuals, of the same or different species and either with or without mutual influence, of the result of causes in continuous operation. These primary causes, migration and environmental selection, operate independently on each area, no matter how small, and have no relation to the process on any other area. Nor are they related to the vegetation of any other area, except as the latter may serve as a source of migrants or control the environment of the former. The effect of these primary causes is therefore not to produce large areas of similar vegetation, but to determine the plant life on every minimum area. The recurrence of a similar juxtaposition over tracts of measurable extent, producing an association in the ordinary use of the term, is due to a similarity in the contributing causes over the whole area involved.

Where one or both of the primary causes changes abruptly, sharply delimited areas of vegetation ensue. Since such a condition is of common occurrence, the distinctness of associations is in many regions obvious, and has led first to the recognition of communities and later to their common acceptance as vegetational units. Where the variation of the causes is gradual, the apparent distinctness of associations is lost. The continuation in time of these primary causes unchanged produces associational stability, and the alteration of either or both leads to succession. If the nature and sequence of these changes are identical for all the associations of one general type (although they need not be synchronous), similar successions ensue, producing successional series. Climax vegetation represents a stage at which effective changes have ceased, although their resumption at any future time may again initiate a new series of successions.

In conclusion, it may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favorable conditions. The species disappears from areas where the environment is no longer endurable. It grows in company with any other species of similar environmental requirements, irrespective of their normal associational affiliations. The behavior of the plant offers in itself no reason at all for the segregation of definite communities. Plant associations, the most conspicuous illustration of the space relation of plants, depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration. A rigid definition of the scope or extent of the association is impossible, and a logical classification of associations into larger groups, or into successional series, has not yet been achieved.

The writer expresses his thanks to Dr. W. S. Cooper, Dr. Frank C. Gates, Major Barrington Moore, Mr. Norman Taylor, and Dr. A. G. Vestal for kindly criticism and suggestion during the preparation of this paper.