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American Midland Naturalist, Vol. 21, No. 1 (Jan., 1939), 92-110.

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The Individualistic Concept of the Plant Association

H. A. Gleason

The units of vegetation, which form the subject of our discussions this week, were just as easily visible to primitive man as they are to us today. They were equally visible to the sages of Greece and Rome two thousand years ago, to our European ancestors a thousand years ago. Through all these long years they were neglected by scientists, whose thoughts were turned in different directions, but they were recognized by the laity. As a result the languages of Europe all contain a number of terms which refer, usually rather loosely, to vegetation.

Certainly every botanist who studied plants in their natural habitat during the eighteenth century was familiar with many types of vegetation, but to them he gave little thought, possibly considering that they were not proper subjects for scientific investigation. To see vegetation units is one thing; to take cognizance of their existence, to investigate their nature, to become aware that they have structure and behavior which may be analyzed, to formulate a philosophy in explanation of them, are entirely different matters.

For our purposes, and with the admission that many desultory references to vegetational units may be found in the works of earlier authors, we may say that the first definite, scientific discussion of the subject may be attributed to Grisebach, and we may repeat his often quoted words: *Ich möchte eine Gruppe von Pflanzen, die einen abgeschlossenen Charakter trägt, wie eine Wiese, ein Wald, u.s.w., eine pflanzengeographische Formation nennen.* This was in 1838, exactly a century ago, and we may congratulate ourselves that in this conference we are celebrating the centenary of the association-concept.

During the next sixty years, the study of vegetational units was sporadic, mostly superficial, and usually purely descriptive in nature. True, we can sometimes see in the literature of this period statements which may be interpreted as applying to the underlying philosophy of the association, but in most cases such statements are casual or accidental and do not indicate that the authors had given deep thought to the fundamental nature of the vegetation which they described.

Not until the advent of the twentieth century did botanists turn their minds seriously to the consideration of underlying questions. Since that time we have made great progress. We have developed methods for the exact observational study of the association. We have recognized conditions and processes in their development, their existence, and their disappearance, and these conditions and processes are quite unlike anything in the life-history of an individual plant or animal, so that our recognition of them has required the development of new habits of thought. We have described in modern terms vegetation from nearly all parts of the world. We have developed

systems of classification, by which the units of vegetation may be orderly arranged. We have invented and brought into accepted use a new terminology by which these conditions, processes, structures, and concepts may be described and discussed.

There is, however, one important question which has not yet been settled to the satisfaction of all concerned. This is the fundamental question, basic to all our work: What *is* a plant association?

Out of the thousands of pages of literature which have been used in expounding various views on the matter, three well marked theories may be chosen, and all others may be regarded as merely variants from them. These three are:

1. The association is an organism, or a quasi-organism, not composed of cells like an individual plant or animal, but rather made up of individual plants and animals held together by a close bond of interdependence; an organism, or a quasi-organism, with properties different from, but analogous to, the vital properties of an individual, including phenomena similar to birth, life, and death, as well as constant structural features comparable to the structures of the individual.

2. The association is not an organism, but is a series of separate similar units, variable in size but repeated in numerous examples. As such, it is comparable to a species, which is also composed of variable individuals. Under this view, the association is considered by some to be a concrete entity, merely divided into separate pieces, while by others the association as a whole is regarded as a mental concept, based on the common characters of all its separate pieces, and capable of typification by one or more of those pieces which most nearly approach the average or ideal condition.

3. The vegetation-unit is a temporary and fluctuating phenomenon, dependent, in its origin, its structure, and its disappearance, on the selective action of the environment and on the nature of the surrounding vegetation. Under this view, the association has no similarity to an organism and is scarcely comparable to a species.

In the original paper, in which this idea was presented to the botanical public in 1926, it was called the individualistic concept, a term which may well be continued.¹

Whether fortunately or unfortunately, my own work during these twelve years has been wholly taxonomic. Nevertheless, observation of numerous plant associations during my field work in this period has merely intensified my own belief in the fundamental truth of the individualistic concept. The exposition of the concept which follows is merely a re-statement of the subject in different terms; it is in no way different in principles or conclusions from the first presentation in 1926.

The argument for the individualistic concept rests on a series of theses,

¹ Gleason, H. A. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53(1):7-26, 1926.

each of which is so obvious, so well known, so universally understood and accepted by all ecologists, that none of them requires prolonged discussion.

1. Every species of plant has reproductive powers in excess of its need.

The land surface of the world is already fully occupied by plants. Room for additional plants is made available only by the death of plants now existing. If seed germination were always perfect, if there was no mortality among plants before reaching their reproductive stage, it would be necessary for each existing plant to produce only one seed in order to perpetuate its species and to maintain the existing number of individuals. On the contrary, every species of plants produces a considerable number of seeds or other propagating bodies, often yielding an annual crop over a long period of years. Since the world is full of plants, it is a fact that, on the average, only one of them comes to a state of full maturity, but huge numbers of seeds or other propagules are capable of growth and ready to grow if favorable conditions are offered. A well kept lawn, for example, may produce very few weeds during the course of the summer, but if the lawn is plowed, the same expanse will promptly develop an astonishing crop of weeds of many species. The bottoms of drained ponds, the first season after drainage, produce many plants of terrestrial species. These and other examples of the same sort are so well known and so conspicuous that we may safely state that the surface of the world is heavily planted with an excess of seeds, most of which never develop, but many of which will develop if a favorable opportunity is offered.

2. Every species of plant has some method of migration.

The means of migration are well understood and require no discussion. The effectiveness of migration is often not appreciated. The distance to which some seeds may be carried by currents of water, by wind, or by birds is known to some degree, but the migration of other less favorably adapted species is also remarkable. Such seeds may be carried by rodents or ants or washed away by heavy rains. It is a demonstrable fact for all plants, without regard to their methods of migration, that more seeds are finally deposited near the parent plant than are carried to a great distance, the number decreasing, roughly speaking, inversely as the square of the distance. But effectiveness of migration is increased by various kinds of accidents and also by the known longevity of seeds in many species. We may therefore conclude, and our conclusion is supported by direct evidence familiar to all of us by personal experience, not only that the world is heavily planted with seeds, as stated under our first thesis, but also that these seeds come not only from the existing plants of the immediate vicinity, but also from plants at some distance. In any unit of vegetation the potentiality of plant production includes not only the natural species of this unit, but numerous species not now found in it and derived from other vegetational units of different character.

3. The environment in any particular station is variable.

Probably the simplest instance of variability which may be mentioned is light. Each day starts at midnight with light at or near zero. A little before

sunrise the light curve begins to rise, reaches a theoretical maximum at noon and drops to zero shortly after sunset. The length of the curve varies with the season, being longest in summer and shortest in winter; the amplitude of the curve varies in precisely the same way, reaching its maximum on June 22 and its minimum six months later. Any and all of the 365 curves which constitute a year's cycle may be subject to irregular reductions in amplitude by cloudy weather. Nor is the quality of the light constant, but varies somewhat with the altitude of the sun and the condition of the atmosphere. These are all relatively simple matters, but there are also variations due to sun-spots, and there may have been and in fact may still be variations due to changes in the inclination of the earth's axis or the eccentricity of its orbit, or to other causes even more remote and far slower in their action. Locally, for many plants the light is changed again by the shade of taller plants, and this shade varies in its effectiveness from hour to hour, from season to season, and as the shading trees grow taller, from year to year.

The variation in temperature of the surrounding air shows similar irregular variations superposed on cyclic progressions in a way quite similar to the variation in light. Soil moisture is more irregular, with abrupt rises followed by longer periods of decrease, and with great variability in the amplitude of the curves. Available soil moisture is another question, based primarily on the total soil moisture, but complicated by matters of temperature, acidity, and other abstruse conditions. Similar conditions hold for every other factor of the environment taken individually and with all of them taken collectively: they are complex and variable to the last degree.

A second class of environmental variations may be called fluctuations. They are illustrated by our irregular alternation of cold and warm, of dry and wet years, of late and early seasons.

Still a third class of variations is important in its effect on plant life, and includes cumulative environmental changes which progress over a period of years or centuries or ages. Such, for example, are the silting up of a pond, the deepening and widening of a ravine by erosion, the exhaustion of soil fertility by percolation of rain water, the accumulation of humus, the increase in temperature following the retreat of a glacier, or the decrease in rainfall in the rain-shadow of a mountain range during its elevation. Although excessively slow, the cumulative effect of these environmental changes is ultimately profound.

All three of these classes of environmental variation are in operation simultaneously in every situation. The first class is regular and predictable; the second class is irregular and unpredictable; the third class is slow and often immeasurable. The amplitude of the fluctuations in the second class is normally much greater than the steady progression of the third class. A single year of deficient rainfall may cause a greater change in the depth of water in a pond than fifty years of silting, or may have more effect on the crops of Montana than five thousand feet of additional elevation of the Rocky Mountains. If we assume that we are now approaching another advance of continental glaciers, the annual drop in temperature associated with it is far less

than the fluctuation from a warm to a cold year. Nevertheless, the only fundamental difference between the three classes is the factor of time.

4. The development of a vegetational unit depends on one or the other of two conditions, the appearance of new ground or the disappearance of an existing association.

The appearance of new ground is a matter of very little importance. More land may be added around the coasts of our continents by further elevation of the coastal plain or the building up of the shores by coastal deposits. More land may be added in supra-alpine regions by reduction of altitude through erosion. More land can not be added by increasing rainfall in deserts: our deserts are already fully occupied by plant life; some deserts merely support less plant life than others.

In the vast majority of cases, an association appears on the ground previously occupied by a different association. It makes no difference whether the earlier association is removed by the slow processes of ordinary succession or suddenly by some cataclysm. If the existing vegetation is destroyed by the axe, by fire, by a landslide or by hot lava, some plants go first and some go last. If the vegetation is changed by a slow process of succession, some of the original inhabitants still go first and some linger. In both cases, some plants of the next association, the pioneers, appear first and others are delayed. The only essential difference between them is the factor of time, greatly shortened in the first case, often greatly prolonged in the second.

The various factors which collectively constitute the environment of a plant may be separately measured and diagrammed, although often with much difficulty, but no one has ever succeeded in reducing to a single statement or a single equation the total environment of any plant. For practical purposes the only measure of the environment is its result, as expressed in plant life. An oak tree may easily live to be three hundred years old. Let us see what this implies concerning its relation to the environment. It means that through this whole period, in spite of its extraordinary variability, the environment has never once exceeded the limits tolerated by the living protoplasm of the tree. The weather has never been too hot or too cold, too wet or too dry; the soil has never been too acid or too alkaline; no environmental factor has ever been too much or too little, or if the limits have sometimes been surpassed, it was for a period too short to be fatal.

The clearest example of temporary excess is the annual cold winter, during which the activities of the oak sink so low that we call the tree dormant. The oak is not only able to adapt itself to the variations in environment, but is able to vary its own life processes enormously to meet such a critical condition as winter cold. Not every plant meets the emergency in the same way. Some herbs actually die, but are fortunate in producing a seed which is not killed by cold and which produces another generation the following summer. There are still other plants whose seeds are also killed by the cold. These plants do not live with the oak, or, of they do, they must be re-established every summer by fresh seeds from a more favorable climate. Such plants are familiar as

cultivated in our gardens. The canna and dahlia may flourish not far from the oak, but they disappear forever if not removed by us to a more favorable climate for the winter and replaced the following spring.

Now leaving these trite illustrations, which have been used merely to recall to our minds what we all know from common experience, let us consider the question from a broader standpoint. We at once arrive at the general theorem, that each plant seizes and uses the particular time-period during which the environment is in a condition suitable to it. When the environment passes these limits, the plant dies. For the old oak, this limit has not been reached for the three hundred years of its life and, so far as we can imagine, not for still longer periods in the past when preceding generations of oaks were growing on the same spot, nor will it be surpassed for many years in the future, during which the descendants of the present tree will be living there. For the dahlia, the limit is reached before the plant has completed a single generation: it is cut off in October while it still bears young leaves and unopened buds. During the same summer, the *Galinsoga* which infests our gardens in this vicinity may produce several generations. If our lives were measured by days instead of years, we can imagine an ecologist saying, "I have seen three generations of *Galinsoga* on this one spot of ground. Evidently we are dealing with a stable environment and *Galinsoga* will live here forever." He would be wrong. With our knowledge of vegetational conditions actually extending over about three centuries, we now say, "Oaks have occupied this spot of ground for three hundred years. Evidently we have here a stable environment and the oak will live here forever." If our lives were seventy centuries instead of seventy years, would we not see that we were again wrong? Like the short-lived *Galinsoga*, which utilizes the time period which we call summer, the long-lived oak is utilizing a longer time-period, and the time has been, and in the future will be again, when the race of oaks can no longer live on this particular spot.

During the time-period when a species may occupy a station, diverse effects are exerted upon the plants by the variable environment. Variations of the first type, which are regular, periodic, and uniform, such as night and day, winter and summer, act uniformly and unavoidably upon all plants. The physiological processes of every plant are adjusted to meet them. While their investigation forms an important part of plant physiology, their effect on plant distribution and their interest to the plant ecologist are negligible.

Variations or fluctuations of the second type, including such phenomena as cold and warm years, of dry and wet periods, of late and early seasons, have a pronounced ecological effect. This is evidenced in agriculture and horticulture by years of heavy or light yield, by the abundance or lack of pests and parasites, by the lateness or earliness of bloom or fruit, by the losses due to late frosts in spring or early frosts in autumn. If such fluctuation is maintained for even a few years, its results become so grave as to be of national importance, as shown recently by the effect of only four years of deficient rainfall in our Plains States.

The effect of these fluctuations on natural vegetation is precisely the same

qualitatively, but less pronounced quantitatively, since crop plants are deliberately introduced into a region, while natural vegetation has been adjusted to the fluctuations through previous experience. In natural vegetation, the effect of fluctuation in the environment is seen in phenological phenomena, in the amount of annual growth, in the vigor of individuals, in the number of seeds produced, in the number of seedlings produced, and therefore in the relative number of individuals. These fluctuations rarely last very long, seldom affecting more than a single year; they therefore rarely cause the disappearance of a species or the appearance of a new one.

That fluctuations of environment affect the relative number of individuals of a species is a fact which has rarely been demonstrated in research in pure ecology, since accurate quantitative studies of vegetation have seldom been repeated in the same area over a series of years. I have personal records from the same area taken at varying intervals over twenty years and can assure you that they show conspicuous variations in the number of individuals of some species, and scarcely none for other species. We may assume that the physiological processes and environmental demands of the latter are so broadly adjusted that no fluctuations have ensued of sufficient magnitude to affect the plants. In the former group we may also assume that their physiological processes are more strictly defined or that the normal environment is already off the optimum for the species, so that fluctuations do interfere demonstrably with the number of individuals. Abundant records of this phenomena are available through the careful observations on our grazing lands. Here the environmental fluctuation is largely in the number of animals feeding on the plants, but the effect is precisely the same. Differences in grazing lead immediately to the reduction of certain species and the multiplication of others.

The rare disappearance of a species because of environmental fluctuation is probably due to the fact that the fluctuations of any one year have been repeated at various times in the past, and species which would be exterminated by them have already been removed. Nevertheless, the long period of drought recently ended in the western states will probably have this effect in many instances, although I am not able to cite any single example at the present time.

The relatively rare appearance of a new species for the same cause, is due primarily to the time-factor involved in plant migration. Environmental fluctuations are of relatively short duration; migration of plants is slow and before additional species can reach the spot, migration has been stopped by the return of the environment to normal. If next winter were to be omitted and summer temperatures should continue for another twelve months without interruption, we still could not expect to find mangroves along the shores of the north Atlantic. Sufficient time must always be allowed for the reaction of plants to any environmental change.

The variations of the third type, the slow-moving, long-continuing environmental changes caused by physiographic processes, geological developments, or climatic changes, cause no directly observable or measurable effect on vegetation, at least in most cases. In these days the effect of erosion during a single

year can sometimes be measured or estimated but it has taken a century for it to make an impression on our minds. The silting of a pond with the resultant changes in plant life is also fairly rapid, so that it has sometimes been observed and recorded by a single person during his own lifetime. Even in these relatively rapid examples, and of course in the slower variations of climate, the effect of the change is always masked by the wider amplitude and quicker action of the fluctuations just discussed. Nevertheless, these fluctuations are based on a norm, and if the norm itself varies the amplitude of the fluctuations tend always to abate in one direction and to extend in another.

Suffice it then to repeat that on every spot of ground the environment is continually in a state of flux, and that the time-period in which a certain environmental complex is operative is seized on by the particular kinds of plants which can use it. The vegetation of every spot of ground is therefore also continually in a state of flux, showing constant variations in the kinds of species present, in the number of individuals of each, and in the vigor and reproductive capacity of the plants.

With this idea of the time-period in our minds, let us look back to the origin of some hypothetical association, which is now populated by three species, designated X, Y, and Z. This association originated in one of two ways, on new and denuded ground bare of plants, or in replacement of a preceding association.

In the former case, of denuded or new ground, species X, Y, and Z must have been derived from some neighboring area or areas, and these must have been within migrating distance. In this neighboring area species X, Y, and Z may or may not have been living together. In these original stations the environment was variable, their seed production was variable, and the migration of these seeds was controlled largely by those inexplicable factors which we call chance. Some times, possibly seldom or possibly frequently, their seeds were carried to this particular spot of ground which we are considering. On this spot of ground the environment was also variable, and in this variation a certain time-period began which permitted the growth of species X, Y, and Z. Their seeds happened to be available, as association of X, Y, and Z appeared, and the time-period during which it may continue has not yet ended.

If our hypothetical association appeared in succession to some preceding association, the circumstances are still similar. The plants of the earlier association, which we may designate A, B, and C, eventually reached the end of their time-period and disappeared. Their disappearance may or may not have been simultaneous. The particular environmental changes which facilitated the entrance of X, Y, and Z may not have been the changes which caused the loss of A, B, and C. The former may have entered first, so that at one time the association consisted of all six species, or entry and disappearance may have been more or less serial, so that the association passed through successive stages of A, B, C; X, B, C; X, Y, C; and finally X, Y, Z.

In either case, whether the association developed *de novo* or as a stage in succession, the variations of the environment may have been such that the

permanent entry of X, Y, and Z was preceded by shorter time-periods during which one or some of them was temporarily present. In short, any number of different sequences may be imagined, all based on variation in the environment and on the species then available through the chances of migration. As a further generalization we may also postulate that species J, K, and L, although adapted to the new environment, did not enter because their nearest stations were beyond the reach of migration; that M, N, and O did not enter because of the chance failure of migration, but may be expected to appear at any time; and that P, Q, and R actually migrated into the area but were unable to utilize the environment.

I have seen this variable result of the interaction of migration and environment beautifully illustrated along the shore of a lake, where winter storms and ice action keep the shore denuded of permanent vegetation. Each spring some storm washes on the beach a long strip of flotsam, twigs, fragments of bark, and dead leaves, and in it seedlings develop. Some years the strip of drift is marked by hundreds of seedlings of willow, at other times by seedlings of elm, and again by seedling red maples. In each case the environment is the same. The difference is caused by migration. If the flotsam is deposited at the particular time when maple seeds are falling in quantity, maple seedlings appear. A difference of a week or two in time results in willows, or in elms, or in no plant life at all.

Under ordinary circumstances, the annual fluctuations of environment are not sufficient to cause any profound or permanent change in the vegetation. Their effects are shown in the size and vigor of individuals or by changes in the relative number of individuals of different species. Only when the fluctuations reach a certain maximum or minimum do old species disappear or new species appear. But in the meantime the slow long-term variations in climate are still in operation and are cumulatively important in environmental selection.

An excellent example of these conditions became apparent during my early work in northern Michigan. Thousands of acres were then covered with a virgin forest of the so-called climax type, with beech, maple, and hemlock as the dominant trees. Of beech and maple there were millions of young trees, ranging from seedlings to tall specimens of the second story of the forest. But there were no seedling hemlocks, except in rare cases; all the hemlocks were mature trees, mostly 300-350 years old. About the beginning of the seventeenth century there had been some sort of an environmental change. Since that time the old hemlock trees had not died, but new hemlock trees had not been established. Another century or less would probably have caused the disappearance of the old trees, and the hemlock would have almost disappeared from the forest. Was that change of three centuries ago a mere fluctuation which has not yet returned to the normal, or was it the accretion of a climatic change to such a stage that it permanently passed the limit of tolerance of the hemlock?

In spite of this exception, I am quick to recognize that the effects of environmental change is less apparent in eastern America and western Europe, where most of our ideas on the association-concept have developed, than in

certain other parts of the world. Our vegetation is composed very largely of perennial species, and even the herbs are generally of long duration. That means that these species are already adjusted to all ordinary fluctuations of the environment, so that the vegetation persists with relatively little change through cycles of high or low temperature, or of excessive or deficient rainfall.

But in other parts of our country, where the vegetation is largely annual, fluctuations in environment are followed immediately by a reaction in the plant life. In the Mohave desert, rains at the proper season induce a great development of the desert annuals, which sometimes carpet large expanses of the land with a sheet of color. Species appear which have not been detected before and rare species become common. The next year, if it fails to receive rain at the critical time, may see the display replaced by mere bare areas of desert.

For ordinary plants, rooted to one place in the ground, environmental selection depends wholly on excess seed production and migration. But many animals, gifted with powers of voluntary locomotion, are continually selecting their environment or being selected by it. No such animal is restricted to any biotic association unless it alone affords him his necessary environment. The scarlet tanager, an inhabitant of the forest canopy, appears in my garden in town when cherries are ripe, and disappears when they are eaten. Migratory birds choose a new environment twice a year. The turkey buzzard of our southern states, except in its nesting, belongs to no biotic association, but enters any one in which it finds a temporary food supply.

The development of a new biota on any spot is therefore the result of environmental selection from the available population of adjacent areas. Similarly, the continuation on any spot of ground of what we have been pleased to call a biotic association is also due to the interaction of the same causes, available population and environmental selection.

While we may all admit the validity of this statement, one argument will immediately come to mind which will seem at first to minimize its importance, namely, that the changes in environment which I have mentioned are so slight that they produce relatively little effect. It is a fact that the majority of individuals of perennial plants continue through environmental fluctuation, because of the well known fact that a mature plant can successfully withstand conditions which would be fatal to seedlings or would prevent the germination of seeds. It is also a fact that plants are themselves a part of the environment, and their persistence always tends to reduce the effect of a variation in the physical environment. It is not until a reduction in their vigor or in their number has broken their environmental control that the full effect of an environmental change can be seen. The individualistic concept does not postulate annual changes of great magnitude, it merely emphasizes that a fixed and definite vegetational structure does not exist.

Another objection which may be brought forward is that the argument of a continuously fluctuating or steadily progressing environment, or both, can scarcely be reconciled with the sudden successional transitions from one associ-

ation to another. This has already been answered in part, when it was stated that mature plants can withstand conditions impossible for their seedlings. When finally, as the result of cumulative changes, the environmental control of the mature plants is broken, the consequent change in the total vegetation is rapid and profound. In this connection it must also be remembered that the theory of sudden steps in succession is largely based on the abrupt transitions in space between different associations. As a matter of fact, these narrow transition lines are more apt to indicate a high degree of stability of vegetation than a rapid rate of succession. . In each of the adjoining associations variation in vegetational structure is always active, along the lines stated by me already, but the absence of cumulative progressive changes in environment, together with a high degree of environmental control by the plants, leads to narrow and well-defined lines between them.

All the statements which have been made so far concerning environmental variability have purposely been restricted to variation in one spot during the course of time.

Variability of environment may also be correlated with space. In time-variability, the environment changes from one time to another on the same spot. In space-variability, environment differs from spot to spot at the same moment. The idea is so axiomatic, so familiar to all, that it scarcely needs any discussion, yet some generalizations may be desirable before we attempt to relate the condition to the individualistic concept.

Space variations are in many ways analogous to time-variations, both in their nature and in their effect. Analogous to the fluctuations of environment in time, which fluctuations are comparatively uniform over a reasonable amount of space, are the abrupt fluctuations in space. These, as is well known, are mostly correlated with the soil, in its chemical and physical properties, its elevation, slope and exposure. It must be repeated that these are fluctuations in space, and emphasized that they are relatively constant on any one spot through a reasonable period of time. Such fluctuations are often of extreme importance to plant life. In any region, they tend to show a wider amplitude of variability than do time-fluctuations.

There are also gradual variations in environment, so gradual, in fact, that their effect can not be observed by comparison of adjacent regions. Such are the variation in mean temperature, in average rainfall, in length of growing season, in length of day and night. Between two adjacent regions, the difference in these conditions is so slight that they are concealed by the far greater and locally more important fluctuations mentioned in the preceding paragraph. But they are cumulative, and it is probably impossible to draw a line 500 miles long anywhere in the United States, certainly in the north-south direction, along which these climatic variations do not cumulate to such an extent as to cause a marked difference in the vegetation at the two ends of the lines.

The selective effect of space-variation on plants is very similar to that of time-variation. To any spot of ground come seeds of various species of plants. Those seeds which find in the spot the environmental conditions which they

demand germinate and as adult plants become an integral part of the association. The population varies from place to place in a manner and to an extent determined by the variation in the environment. The population is chosen by environmental selection from the available immigrants.

There is nevertheless one important difference. In a time-series, the surrounding population remains relatively constant. From year to year it affords the same group of species from which immigrants may be drawn. In a space-series, the surrounding plant population may vary greatly from one end to the other. Not only is the environment different, but the immigrating species are also different and the resulting environmental selection is different.

Furthermore, time is always necessary for an environmental variation to exert its full effect on plant life. Fluctuations in time are often of short duration and have passed before their full effects can be realized. Fluctuations in space, on the contrary, are of relatively long duration, and on each spot the full effect of environmental selection can be reached.

In summary it may be stated that environment varies constantly in time and continuously in space; environment selects from all available immigrants those species which constitute the present vegetation, and as a result vegetation varies constantly in time and continuously in space.

Those who disagree with the individualistic concept will very properly raise at this time certain questions, based on facts which at first thought seem to invalidate the whole concept. Before these questions are stated here, so that their obvious implications may be refuted, two general statements may be introduced.

First, an association, or better one of those detached pieces of vegetation which we may call a community, is a visible phenomenon. As such it has dimensions and area, and consequently boundary. While its area may be large, the community is nevertheless a very tangible thing, which may be mapped, surveyed, photographed, and analyzed. Over this area it maintains a remarkable degree of structural uniformity in its plant life. Homogeneity of structure, over a considerable extent, terminated by definite limits, are the three fundamental features on which the community is based. Without these three features, Grisebach would never have published his statement of a century ago; without them, all our studies of synecology would never have been developed. Also, besides its extent in space, every community has a duration in time. Uniformity, area, boundary, and duration are the essentials of a plant community.

Second, every community occupies a position in two series of environmental variation. In the space-series, as the community exists *here*, in this spot, it is part of a space-variation, and its environment differs from the adjacent communities. In the time-series, as the community exists *now*, at this time, it is part of a time-variation and in its environment differs from the communities which preceded it or will follow it.

The individualistic concept postulates a continuous variation in space and

time. How can we reconcile this with the admitted uniformity in space and time?

In any community of reasonable extent, the variation of rainfall, temperature, length of day, and similar factors from one end to the other is extremely small. Not only is their effect proportionately small, but this effect is overshadowed by the much greater seasonal fluctuation. Soil, also is often uniform over the whole community, and when it is not uniform but varies significantly within small distances, we are prone to overlook its effects and to classify the variable vegetation in a single community. More important still, the dominant plants, which are distributed over the whole area of the community, exert such a uniform effect on the other species that discrepancies in the physical environment are more or less smoothed out or obliterated.

Nevertheless, it is difficult or impossible to find in any community two quadrats which are precisely similar. The community is a complex or mosaic of slight irregularities, all of which blend into an entirety of apparent homogeneity. We have all known of this lack of perfect uniformity, and have endeavored to evade it by developing the concept of a minimal area, but we have failed to realize its significance as indicating the general variability of vegetation.

Cumulative progressive changes in environment are generally so slow in their development that they make no pronounced effect from one year to the next, while the wider swings of fluctuating environment are so short in their duration that their full effect is not experienced. Also, comparatively few observers have kept careful records of vegetational change over a series of years. Furthermore, as in space variation, environment control by plants tends to overshadow environmental variation. Nevertheless, succession, which is merely vegetational change, is accepted by all as a fact; exact statistical records, when available, do show continuous variations in structure, and in many locations complete vegetational changes have occurred within the experience of a single observer.

The postulated uniformity of the community is therefore far from absolute. A community is uniform, either in space or in time, only to a reasonable degree. This uniformity is sufficient to enable us to recognize the community and to accept it as a unit of vegetation, while its variability, although slight, is sufficient to indicate the impossibility of considering any such area of vegetation as a definitely organized unit.

If vegetation varies continuously in space, how can we explain the abrupt transitions from one community to another, which are so conspicuous a feature of natural vegetation in many regions?

Abrupt transitions are in every case correlated with abrupt variations in the environment or with abrupt differences in the immigrating plant population. Some abrupt changes in environment are due to physical conditions, notably the soil, which may change notably within a short distance. The other changes are due to environmental control of the physical factors by the plant life itself. These account for most of the abrupt transitions in the eastern

states, or in any other region where a dense vegetation is possible. The sharp demarcation of zones around a pond or bog, for example, is caused almost entirely by vegetational control.

Abrupt differences in immigration exist only in areas which have recently been disturbed, such as an abandoned field, a lake shore recently worked over by waves, a ballast heap or a tract of newly filled ground. In such places the accidents of immigration often lead to the temporary establishment of distinct patches of vegetation, each characterized by one or a few species. Continued migration tends to smooth out these irregularities in a short time; environmental fluctuation favors certain species over others; denser growth leads to environmental control by certain species, and in the course of a few years such patchwork vegetation has blended to a relatively homogeneous community.

If vegetation varies continuously in space, how can we account for the repetition of the same vegetation in many separate communities?

The answer to this question is simple. There is no exact repetition of the same vegetation from one community to the next. There is an approximate repetition only.

It is a fact that in any region several to many examples of vegetation may be found in which the differences are so slight that they are not observed, or if observed are considered as unimportant and negligible. In any community absolute homogeneity is impossible, and the observed heterogeneity may well be due to chance. But in a single community, if it is large enough, differences between two ends may be discovered. Every ecologist who has undertaken quantitative analysis of vegetation will probably agree with this statement. I once examined two adjacent sections, each an exact mile square, of virgin hardwood forest. The soil was uniform and level and there was no surface drainage system, nor any indication of wetter and drier parts. Careful quantitative studies in each section showed conspicuous differences, not important differences, to be sure, which could not be explained by any visible feature. At the Biological Station of the University of Michigan, the aspen association, with a single continuous community some six miles long, exhibits demonstrable variation from one end to the other, with no visible reason.

Between two different communities, not too far removed from each other, the observable differences in structure are of essentially the same degree of magnitude as these fluctuations within the same community, and one may easily tend to credit them also to the effect of chance. But part of them, possibly only a small part, is due to the space-variation in the environment, and another part, again possibly small, is due to a difference in the available plant population upon which environmental selection operates. If a series of communities are observed at successively greater distances, these differences cumulate, so that those at the ends of the series may be strikingly different, although connected by imperceptible or apparently negligible intermediates.

One short-coming of our ecology has been that our field work has generally been confined to a small area. We have investigated and described all the associations in a small area, instead of trying to trace a single association

over its whole extent. In any small area, environmental variation, essentially repeated in many spots, produces several well-marked types of environment, each characterized by a similar vegetation. We justifiably draw the conclusion, from this limited evidence, that association-types are definite. But as soon as we extend our observations, we begin to realize that each separate community is merely one minute part of a vast and ever-changing kaleidoscope of vegetation, a part which is restricted in its size, limited in its duration, never duplicated except in its present immediate vicinity and there only as a coincidence, and rarely if ever repeated.

In other words, the similarities between adjacent communities, which have led to the views that the association is analogous to a species, or analogous to an organism, are not perfect similarities. They are caused by *nearly* similar environmental selection, intensified by *nearly* similar environmental control, from a nearly similar population. In addition to the imperfections of similarity caused by chance, and largely masked by them, are other variations of a cumulative nature. These, increasing in importance and in conspicuousness as more distant communities are considered, finally lead to vegetation of such unlike nature that they would never be classed in the same association-type.

In my original paper on this subject I mentioned as an example the alluvial forests along the Mississippi River and its tributaries over a stretch of about a thousand miles from its mouth to the northward. From mile to mile these forests show no considerable change; over a space of a hundred miles the changes may or may not be of ecological importance and the more important differences are apparently due to lack of time for sufficient migration to smooth out the variation. Yet these differences cumulate. One by one species disappear; one by one other species appear, and by the time one has reached, say, Indianapolis, there has been an almost complete change in the appearance and composition of the forest. Or, if the observer swings more to the west and travels up the Missouri and the Platte, he can see the disappearance of species one by one without corresponding replacement, until the forest is reduced to a fringe of willows and finally disappears completely in western Nebraska.

Within the state of Michigan, the beech-maple climax forest, always considered to be a definite, well distinguished association-type, exhibits profound changes from one end of the state to the other.

I also venture to say, without personal experience to verify the opinion, that even more remarkable transitions might be discovered elsewhere. For example, the forests of the foothills of the Rocky Mountains in Colorado, composed there largely of *Pinus ponderosa*, might be traced northward with similar gradual variation, thence eastward along the northern boundary of the grassland in Canada, and again southward to the forests of Illinois, and lead us to the extraordinary conclusion that the *Pinus ponderosa* forests of Colorado represent the same association as the *Quercus velutina* forests of Illinois and the aspen groves of Manitoba.

Over such distances as the three I have mentioned the flora from which

any area may be populated changes greatly. Such environmental factors as temperature, rainfall, and length of growing season also vary greatly and to an extent that completely surpasses the local fluctuation between any adjacent communities. With the vegetation determined by environmental selection from the available plant population, and with both of these underlying features altered, obviously the resultant vegetation must also be entirely changed.

It must be remembered that we admit the essential uniformity of vegetation within a single community, and the frequent striking uniformity between adjacent communities. But the fact that these small cumulative differences do exist is basically important in the consideration of the general concept of the plant-association. They indicate that each community, and for that matter each fraction of one, is the product of its own independent causative factors, that each community in what we now choose to call an association-type is independent of every other one, except as a possible source of immigrating species. With no genetic connection, with no dynamic connection, with only superficial or accidental similarity, how can we logically class such a series of communities into a definite association-type? Truly the plant community is an individualistic phenomenon.

Every species of plant and animal migrates, whether as a mature individual, as many species of animals, or as a reproductive body, as the vast majority of plants. Among animals, migration is sometimes selective in its direction and goal, as illustrated by birds which follow definite routes to definite established breeding grounds. With other animals and with all plants, migration is purely fortuitous. It progresses by various means, it brings the organisms into various places and to varying distances, but only those organisms which have reached a favorable environment are able to continue their life. Into this favorable environment other species also immigrate, and from all of the arrivals the environment selects those species which may live and dooms the others.

In this migration each migrating body acts for itself and moves by itself, almost always completely independent of other species. The idea of an association migrating *en masse* and later reproducing itself faithfully is entirely without foundation. Those cases in which there is a semblance of such a condition are caused by the proximity of the original association and the advantage which its species therefore have in migration. Even then, certain species always precede and certain others lag behind.

SUMMARY

1. The ordinary processes of migration bring the reproductive bodies of a single plant or a species of plant into many places.
2. The ordinary processes of migration bring the reproductive bodies of various plants into the same place.
3. Of the various species which reach one spot of ground, the local environ-

ment determines which may live, depending on the individual physiological demands of each species separately.

4. On every spot of ground, the environment varies in time, and consequently the vegetation varies in time.

5. At any given time, the environment varies in space, and consequently vegetation varies in space.

6. A piece of vegetation which maintains a reasonable degree of homogeneity over an appreciable area and a reasonable permanence over a considerable time may be designated as a unit community. Within such an area and during such a period similarity in environmental selection tends toward similarity in vegetation.

7. 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.

Although a summary is generally considered to close a discussion, it nevertheless seems desirable to indicate very briefly the relation of the individualistic concept to other current philosophies of the plant community.

The individualistic concept is totally at variance with the idea that the association is an organism, represented by many individuals, and also does not admit an analogy or homology between the species and the association. While affirming the existence of definite communities, characterized by reasonable uniformity over a considerable area terminated by a definite boundary, the concept denies that all vegetation is thus segregated into communities.

The concept is by no means opposed to the recognition of the synusia, or union, defining it as a group of plants whose physiological demands are so similar that they are regularly selected by the same environment and consequently regularly live together.

If classification of communities on the basis of floristic resemblance is rejected, and if broader areas of vegetation are searched for characters indicating genetic or dynamic similarity, these are first found in the broad floristic group now known as a biome. The plants of a biome, living together now as their ancestors have lived together and evolved together in the past, represent an environmental selection of a broad type, while lociation and faciation within the biome indicate the variability of the environment and the irregularity of migration.

DISCUSSION

Lippmaa: Though the theses of the speaker are acceptable the same can not be said of his conclusion that it is "impossible to choose any one phase of the vegetation as typical." The environment does not vary *continuously* in time and space. Abrupt changes caused by the differences in rock and soil composition, exposure, water supply, etc. are not uncommon. To such changes as well as those factors listed by the speaker effecting the development of vegetation must be added other eminently important ones such as the competition between the species composing the community and the time necessary for the stabilization of the community.

As regards "the exact repetition of similar vegetation" it is clear, that the units used in phytosociology are of a different kind than those of taxonomy. For the fundamental unit of taxonomy—the species—could hardly be considered "exact" by the chemist.

Gleason: Most of these remarks do not differ essentially from anything which I have said. The first topic regarding variation may require brief explanation. The curve, in which periods of slow and rapid variation alternate, still represents continuous variation.

In my early work I tried to read all the works on descriptive ecology dealing with American vegetation. I could scarcely find any two regions which contained the same associations. Conard's paper illustrated the same variability since he reported a *Brometum* in western Europe and England which has twenty-nine variants. These are almost certainly an expression of such cumulative differences in structure. In every small region, association-individuals may be found which are sufficiently alike to encourage us to classify them together, but extension of observation over greater areas shows that the small observed differences cumulate into important differences.

Emerson: It is useful to break down the larger categories into their units. It is also useful to build the units into larger wholes. I think by the same logic could be proven that the concept of the individual and of the species presents the same difficulties as the concept of the association. Is it not true that the biological integration of units is as real as the units?

Gleason: It was brought out in several places in my paper that the biological control by existing plants is an important feature of the environment.

Emerson: The speaker showed that each community is an individual, but I think it is also necessary to put them together again.

Gleason: The species are present, and these groupings of plants into communities exist. What I hoped to bring out here was that the particular grouping of plants is not found duplicated elsewhere. There are similarities among stands, or slight differences from stand to stand, and if you trace an association those little differences are cumulative.

Emerson: That is also true of the individual. A research taxonomist talks about species and races. Does the concept of a human race have meaning?

Gleason: I think the concept of race does have a meaning which is merely complicated by the intermediate forms, but we have no genetic relation or connection between these plant communities.

Emerson: One of the first principles of genetics is the reassortment of genes and chromosomes. I do not think the only reality is the individual and that the associations are not real integrated units.

Steiger: I agree with everything the speaker said about these variations in time and species, but all that is true of every living being. Plants are living beings and as such they do not possess the same degree of exactness, as NaCl for instance. Apparently we need a terminology.

Gleason: A classification of plant communities is certainly needed to enable us to talk about them conveniently.

Steiger: However, I would not compare an association with an individual. Even the comparison with the species is limited.

Spith: As a taxonomist I do not like to hear associations compared with species. Any herring caught is going to have 60-65 vertebrae but it can not be predicted how many it is going to have. I think that is a very fundamental difference between the two.

Conard: I certainly enjoyed the speaker's analysis very much and I do not see any way of opposing his logic. Comparison of the association with the species has been stoutly opposed, but I feel that the same logic rules out the use of such terms as "species" or "human being". We are too different to be classified. It seems to me both from my own personal feeling and from reading the results of the work of others where the association as understood in the international sense has been used that there has been nothing in ecological inquiry which has been so fertile and so productive of results as the idea of the association. It is therefore so useful that whether logical or not, I am for it.

Gleason, Jr.: One can not deny the objective reality in a stand of vegetation any more than the objective reality in the daisy. But if all the daisies in the world were brought to some one location, that collection would be something very different from the concept of *Chrysanthemum Leucanthemum*. The latter is conceptual and purely subjective and very different from the other which is a specific collection of all the individuals which we have classified. There is a difference between human beings and *Homo sapiens*. The former have an objective reality, but the latter does not exist except in the mind of man. The same is true of any classification of vegetation. The vegetation exists and each individual stand exists, but the classificatory category exists only in the mind of man.

Emerson: I can not allow these remarks to go unchallenged. I think that the species has objective reality as well as the individual. If you say that "*Homo sapiens*" is a figment of the mind, I think you will be forced by logic to say that we are all individually figments of the mind.

Gleason, Jr.: I am certainly an aggregation of cells and a reality but the category obtained by classifying those cells is different from that aggregation, and is purely subjective. Modern logic has recognized the great importance of differentiating between a class and its components. The two have an entirely different logical value, and must be treated differently. Other treatment brings about the confusion of terms on which many well known paradoxes rest.

Emerson: The individual is a population of cells.

Gleason, Jr.: There is a distinction between a population of cells and a class of cells. A class of cells is an abstraction characterized by a quality, which is held in common by all those cells. That I think is fundamental.

Gleason: One can combine things of different nature and still have a concrete reality. When one classifies things he arranges them according to similarities. Philosophers agree that the development of a classificatory group leads always to an abstract concept.

MacGinitie: It seems to me that the speaker will have some trouble in limiting his defense from the other side. Why did he stop where he did? I do not like it for that reason.