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# THE QUARTERLY REVIEW of BIOLOGY



## THE ENVIRONMENTAL COMPLEX IN RELATION TO PLANT GROWTH AND DISTRIBUTION

By W. D. BILLINGS

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THE apparently innocuous question, "Why do plants grow where they do?" involves a number of fundamental problems in plant ecology. In this relatively young and complex science, however, this question has often been neglected in the multiplicity of problems presented to an ecologist in any region. In fairly recent times many ecologists' energies have been devoted, partially of necessity, to investigating the structure and dynamics of vegetation which is rapidly being changed or eradicated by modern civilization. This work is of great importance, but the solving of the principal problems in the relations between plant growth, distribution, and physical environments is fundamental to any understanding of plant aggregations and their changes.

In recent years, increased interest in these problems of why plants grow where they do has resulted in at least two large symposia devoted to the subject (A.A.A.S., Vancouver, B. C., June, 1949; A.I.B.S., Minneapolis, Minn., September, 1951). These symposia are but surface evidence of current attempts to solve complex ecological problems by understanding the environmental relationships of the various species of importance in particular vegetations. These large problems are far from solution. However, it is the purpose of the present paper to bring together some of the recent ideas and work in the widely scattered fields of plant ecology and its underlying sciences, with the hope

that such a synthesis will help to show in what directions future research in ecology is needed. It is patently impossible to cover such a large subject in small space, therefore the emphasis will be on certain ideas and concepts basic to an understanding of the complex plant-environment relations and the significance of these relations in the structure and interpretation of vegetation.

### STRUCTURE OF THE ENVIRONMENT

It is not the purpose of this short review to detail thoroughly the nature of environmental responses in plants and vegetation. This has been done far more completely in recent textbooks by Cain (1944), Daubenmire (1947), Oosting (1948), and in particular detail by Lundegårdh (1949). However, it is necessary to give in a general way the structure of a plant environment so that its complexity can be better understood.

### *Factoring the Environment*

The environment of a plant may be defined as the sum of all external forces and substances affecting the growth, structure, and reproduction of that plant. The environment provides the organism with its heat, light, water, elements, and compounds. If these are available in sufficient amounts and at the right time to satisfy the growth and reproduction requirements of any of the ecotypes or biotypes of a species, that species can grow

there provided its seeds and propagules can get there.

Since the environment is a complex, it has been customary for ecologists and plant physiologists to break it up arbitrarily into factors and to study the effect of such single factors on the plant. This is a somewhat artificial, but probably necessary, method of attack, since in nature it is almost impossible for one factor to change without affecting others. Yet if such an analytical approach is followed, each factor must be evaluated in relation to all of the other factors, and the analysis must be followed by a synthesis of the total results.

In an analytical approach, it is perhaps best to subdivide the environment first into large groups of factors and then to subdivide these to show the great ramification which a thorough investigation of the environment entails. Table 1 presents a more or less arbitrary subdivision of the environment into the principal groups of factors and shows how they may be subdivided into individual factors, factor subdivisions, and various aspects. Many things make up an environment, and an almost infinite degree of analytical breakdown is possible. However, this table can be considered as a guide to the types of growth and distribution factors which are at present being investigated by plant scientists. Unfortunately, papers dealing with the interrelations of two or more factors with the plant are few, and even fewer are the attempts to analyze and synthesize complete plant or biotic environments. Outstanding among these are the works of Lindeman (1941a, 1941b, 1942) on aquatic ecosystems using energy relationships during succession as a basis. For terrestrial communities, one of the best is the recent paper by Platt (1951) on the environmental relations of the Pennsylvania shale-barren communities.

#### *Principle of the Holocoenotic Environment*

Even though it is possible to analyze a plant environment and to study the effects of single factors on the plant, it has long been recognized by some ecologists, but not by all, that the environment-plant system is a dynamic unit in itself and reacts as a whole. Cooper (1926) viewed the vegetation of the earth as a flowing, braided stream governed and directed by all environmental factors at all times. Billings (1938) emphasized that successional changes in vegetation cannot be interpreted in terms of one factor, but only by considering the environmental complex as a whole. This

principle has been termed that of the holocoenotic environment by Allee and Park (1939), and has been restated and emphasized by Cain (1944). The holocoenotic principle is fundamental to any understanding of environment-plant relationships. Complete explanations of ecological phenomena are not possible without it.

The complexity of the interrelationships between the plant and its environment and between the various factors of the environment is almost enough to discourage any attempts at complete analysis and synthesis. In fact, Cain (1944) has stated that such ecological problems not only may be difficult to solve but may really be insoluble in a mathematical sense. However, attempts by ecologists should be and are being made (Lindeman, 1942; Major, 1951).

It would be of some help in understanding the holocoenotic principle to be able to visualize the principal interactions in the environment. Fig. 1 is a diagrammatic attempt to show such an environment and the interactions between the various factors themselves and between these factors and a plant. The factors in this diagram are large units and there has been some lumping of factors in order to simplify it. Furthermore, the fifteen factors are not of equal weight. Nevertheless, the relations in a complete environment are shown in the diagram. Some biologists would consider time as an environmental factor, but time might better be considered not as a factor in itself but as a dimension by which all other factors are qualified. Therefore, time is indicated around the edge of the diagram as affecting all of the reactions within the environment.

#### *Limiting Factors and Trigger Factors*

A second principle of environment which has been far more widely used than that of the holocoenotic environment is the principle of limiting factors. This stems from the work of Liebig (1843) working with agricultural plants and soils, and has been widely adapted and adopted by ecologists during the last half-century. The thesis of this principle is that plant growth and distribution are limited when any factor in the environment falls below the minimum required by that particular species. Actually, a plant may be limited not only when a factor goes below the minimum but when it goes over the maximum tolerance by the plant for that factor. In any case, a single factor can often limit the growth, reproduction, or distribu-

TABLE 1  
*Factors of a Terrestrial Plant Environment*

GROUPS	FACTORS	FACTOR SUBDIVISIONS	ASPECTS
Climatic	Radiation	Solar radiation	Wave-lengths Intensity Photoperiod and other cycles
		Cosmic radiation	Wave-lengths Intensity Cycles
		Terrestrial radiation	Wave-lengths Intensity Cycles
	Temperature	Air temperature	Degree Cycles Lateral variation Vertical variation
		Soil temperature	Degree Cycles Freezing and thawing Lateral variation Vertical variation
		Rock and parent material temperature	Degree Cycles Freezing and thawing Lateral variation Vertical variation (geothermal gradient)
	Water	Water vapor	Amounts Vapor pressure Vapor pressure deficit Evaporation Transpiration
		Condensed water	Cloud Fog
		Precipitation	Types Amounts Frequency Snow cover
		Soil water	Soil moisture Hygroscopic water Capillary water Water table
	Atmospheric gases	Composition	CO <sub>2</sub> content O <sub>2</sub> content Other gases

TABLE 1—Continued

GROUPS	FACTORS	FACTOR SUBDIVISIONS	ASPECTS
Climatic <i>(continued)</i>	Atmospheric gases <i>(continued)</i>	Pressure	Altitude Local pressure differences Cyclones
		Wind	Frequency Force Direction Abrasive agents
Edaphic	Parent material	Acid materials	Minerals present Structure Weathering susceptibility
		Basic materials	Minerals present Structure Weathering susceptibility
	Soil	Physical properties	Profile Structure Texture Soil moisture Soil air
		Chemical properties	Clay minerals Base exchange properties pH Anions Organic compounds
	Biotic properties	Soil flora Soil fauna Litter and humus Antibiotic effects	
Geographic	Gravity	Internal effects	Hormone effects Translocation
		External effects	Isostasy Fruit and seed dispersal Runoff Landslides
	Rotational effects	Coriolis force	Works through other factors
	Geographic position	Latitude Longitude Distance and direction from coast	Work through other factors
	Vulcanism	Thermal effects	See temperature
Mechanical effects		Ash cover Lava flows Gas explosions	

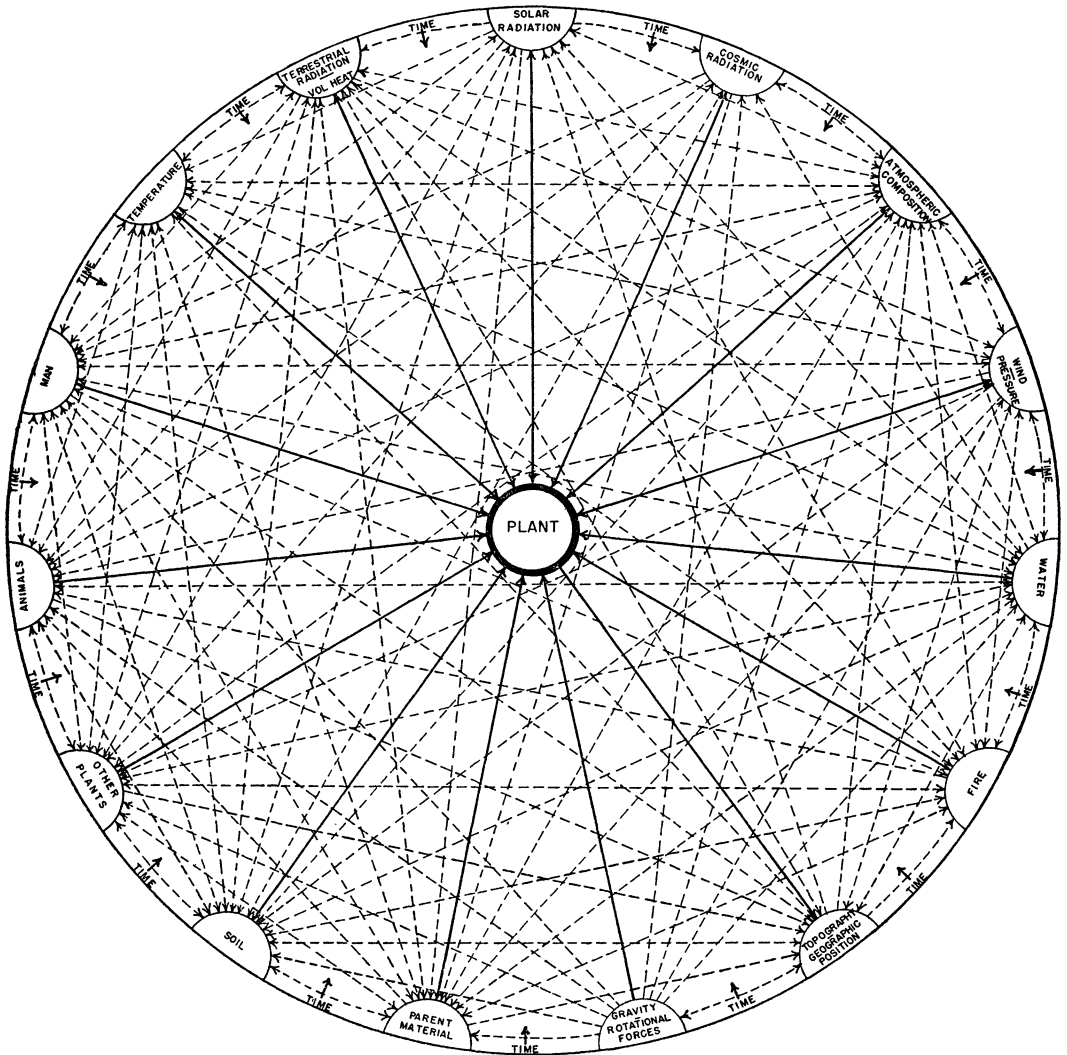
TABLE 1—Continued

GROUPS	FACTORS	FACTOR SUBDIVISIONS	ASPECTS
Geographic <i>(continued)</i>	Diastrophism	Folding } Faulting }	Work through other factors except very locally
	Erosion and deposition	Water } Snow (avalanches) } Ice (glaciation) } Wind }	May affect plants directly or through changing other factors
	Topography	Slope direction } Slope angle } Elevation }	Work through other factors
Pyric	Fire	Climatic effects	Temperature (air and soil) Intensity Post-burning microclimatic effects
		Edaphic effects	Organic matter destruction Soil structure changes Erosion
		Biotic effects	Community composition Animal populations after fire
Biotic	Other plants	Competition	Light competition Water competition Nutrient competition Antibiotic effects Autotoxic effects
		Dependence effects	Litter and humus Physical effects Chemical effects Cover
	Animals	Destructive effects	Use of plant as food, etc. Effects on soil
		Beneficial effects	Fruit and seed dispersal Nutrient effects
	Man	Can change almost any factor, at least locally	

tion of a single plant species. Cain (1944) has stated that physiological processes are multi-conditioned. He says that it is impossible to speak of a single condition of a factor as being the cause of an observed effect in an organism. In other words, since the environment is holocoenotic, Cain believes that it is erroneous to speak of a single condition of a single factor as being limiting. Major (1951) has indicated that his methods of environment-

vegetation analysis on the basis of factors as independent variables may appear to contradict Cain's statements. However, since Major is using the term "independent variable" in the mathematical sense, this is only an apparent contradiction.

Actually, it seems perfectly reasonable to assume that the principle of the holocoenotic environment and the principle of limiting factors are



A HOLOGENOTIC ENVIRONMENTAL COMPLEX

FIG. 1. DIAGRAMMATIC REPRESENTATION OF AN ENVIRONMENTAL COMPLEX

Solid lines show factor-plant relationships. Dashed lines show relations between factors. Arrows show the general direction of the effect. If the effect is reciprocal, arrows are placed at both ends of the line. Time is indicated by short inward-pointing arrows just inside the border of the diagram. The only group of factors not affecting the plant directly is that of topography and geographic position. These affect the plant only through other factors.

compatible. For example, water, or rather lack of water, is a principal limiting factor in semi-arid and arid regions. If water is added to desert adjoining cultivated land, the native desert plants are soon replaced by adventive weeds and other plants from nearby irrigated areas. These plants are kept out of the desert environments by lack of water even though their seeds arrive in the area

every year. As soon as the water content of the soil is brought above the adventives' minimum requirements, however, their seedlings survive, grow, and reproduce. Certainly the addition of water has far-reaching effects in the desert environment because this environment is holocoenotic, but lack of water is the *limiting* factor and no addition of any other factor to the desert environment will

result in the same change in vegetation. Of course, the amount of water available to the adventives might be increased by eliminating the competition provided by the native plants. If the water is added permanently, the whole desert environment goes through a change—a change which results in an entirely different vegetation. When a limiting factor, then, is changed in nature and sets off a chain reaction in the ecosystem, it might well be termed a “trigger” factor. The delicate balance of an ecosystem in dynamic equilibrium and the possible far-reaching effects of even small changes have been clearly stated by Cooper (1926) and Billings (1938). Allee et al. (1949) use drought as an example of a “trigger” factor in the emigration of muskrat populations based upon the work of Errington (1939).

Numerous examples can be found to illustrate the effects of “trigger” factors in vegetation. One of the best is provided by the change from bunchgrass-sagebrush to cheatgrass (*Bromus tectorum*) over great areas in the semi-arid portions of the Great Basin of western North America. This change, which has taken place in less than 100 years, was undoubtedly triggered by the introduction of domestic grazing animals. The probable course has been an initial weakening and elimination of the more palatable bunchgrasses, followed by an increase in density of the less palatable shrubs, particularly *Artemisia tridentata*, the big sagebrush. This open community of relatively deep-rooted shrubs was invaded late in the 19th century by *Bromus tectorum*, cheatgrass, introduced accidentally from Europe. This grass spread rapidly under and between the shrubs by utilizing the soil moisture in the upper part of the soil. Through most of the region it acts as a winter annual, germinating with the first heavy fall rains and going through the winter as a seedling. In the spring it grows rapidly, flowering in May, producing ripe seed in June, and then dying and becoming dry in most places by the end of that month. From then until fall it constitutes a critical fire hazard not present in the original vegetation. Range fires have become much more frequent and cover greater areas because of the inflammable character of this dry annual. By the time of burning most of the *Bromus* seeds are on the ground and those not near to the heat of the burning shrubs survive to allow the cheatgrass to pioneer in the newly burned area. Within two or three years the burn is practically a pure stand of annual grass

readily susceptible to further burning and deterioration. Recovery by shrubs is slow, the principal ones in the early stages being species of *Ephedra*, *Tetradymia*, and *Prunus* which can send up root sprouts. Sagebrush must reinvade by seed. One of the best browse shrubs, *Purshia tridentata*, is generally eradicated permanently by fire in the western Great Basin because it rarely root-sprouts in that region and its seeds are not particularly mobile. However, Blaisdell (1950) in eastern Idaho has reported that *Purshia* in that region is able to sprout and can survive unless the fire is too severe. As a result of the chain reaction started almost a century ago, the sagebrush-grass ecosystem is still out of equilibrium, and the end is not yet in sight. Perhaps man can take advantage of the situation and divert the chain back toward some sort of equilibrium by replanting perennial grasses on the burned areas, as the work of Robertson and Pearse (1945) has shown, and by proper ecological management of areas not yet in stages of extreme deterioration.

When change in a trigger factor upsets the delicate balance in an ecosystem, it is usually not possible to tell when and where the chain reaction will end. The accidental introduction of an aggressive adventive at an opportune time can greatly increase the speed and permanence of the change and thus affect the distribution of hundreds of species of native plants. This has happened in the case of the *Bromus* invasion in the intermountain region, as described above. Many of the native perennials are being killed out by the repeated fires, and some are probably doomed to extinction.

A good example of the impossibility of predicting the trend in an upset ecosystem is the present occupancy of much valuable winter range in north-eastern Nevada, southern Idaho, and northern Utah by *Halogeton glomeratus*. This very poisonous plant was accidentally introduced in the middle 1930's into areas already in a disturbed state, probably due to the trigger of overgrazing. No one could have predicted the present state of these winter ranges even as late as 1935, because the biotic potential of *Halogeton* was not recognized. Now thousands of acres of valuable winter range are not only useless but a very real danger to stock because of the pure stands of *Halogeton* now occupying them. Where this destructive change will end cannot be predicted with certainty at present, but applied ecological methods can help to divert



it in the direction of proper use and some type of recovery.

#### *Environmental Variation in Time and Space*

The environment of any individual plant or local population varies not only in space but also in time. Taylor (1934) has emphasized the importance of environmental extremes in determining not only plant distributional limits but also certain geologic and edaphic features in the environment itself. He has restated Liebig's Law of the Minimum in the following terms: "The growth and functioning of an organism is dependent upon the amount of the essential environmental factor presented to it in minimal quantity during the most critical season of the year, or during the most critical year or years of a climatic cycle." Time, like space, is then seen to be a dimension of an environment allowing or limiting the growth of individuals and local populations depending on the values of critical factors at critical times.

The environment of an individual is continually changing throughout its lifetime. Some of this change is cumulative and some is cyclic. If a factor becomes critical simultaneously with a critical stage in the life cycle of the plant, death of the individual or of many individuals in the local population may result. This may occur, of course, at any period of the life cycle, but at certain times the impact of a critical environmental extreme has greater effect. Germination, the young seedling stage, flowering, and fruiting are the stages most likely to affect plant distribution if they are disturbed or stopped by an extreme or unusual condition in the environment.

Normal growth and reproduction of a plant is genetically adapted to the changes of the environment usually encountered by the plant during its life from germination to fruiting and seed dispersal. Some degree of aberrancy in the environmental cycles and totals is to be expected. A species of wide tolerance range can survive these either in space or time. There are limits, however, beyond which even widely distributed species cannot go. These occur principally near the limits of distribution, and if they occur often enough they will keep the species from spreading farther. Endemic species have relatively narrow tolerance ranges in both space and time, and are limited to areas where the total environment and its cycles are just exactly what its gene-operated physiological processes need for successful growth and reproduction.

Boyko (1949), recognizing the importance of environmental extremes in plant distribution, has introduced a useful concept which he calls the *IF* threshold of a species in which *I* indicates the intensity of a limiting factor and *F* the time-frequency of its occurrence.

Fig. 2 diagrammatically illustrates how an environment could change during the life span of a hypothetical annual plant. Starting at time zero (zygote), this plant's environment would show certain combinations and rhythms of factors *A, B, C, D, E, F*, and *G*. These would probably not in most cases make up the best environment for seed germination for the species but by time *X* the environment has changed enough (and perhaps affected the seed enough as, for example, in low temperature after-ripening) to allow germination with combined values and rhythms of *A', B', C', D', E', F'*, and *G'*. This could be shown at any time during the life of the plant. The change in the environment and its effect on the plant could continue to successful production of seed provided no factor exceeded the tolerance limits determined by the gene structure of the plant. If this occurs, the individual might die or grow so slowly as to be out of phase with the environmental march and thus fail to reproduce.

#### ENVIRONMENT-PLANT COMPLEX

From the standpoint of ecology, no study of the environment alone can be very significant. The attempt must always be made to correlate or integrate the changes in the environment in time and space with the individual plants or vegetation with which it is intimately associated. The growth and distribution of plants are governed by this interaction of gene mechanism and environment.

#### *Tolerance Range Studies*

According to Good's (1931) Theory of Tolerance, a plant species is able to exist and reproduce successfully only within a definite range of climatic and edaphic conditions, such a range representing the tolerance of the species to these external conditions. The tolerance of a species is, according to Good, subject to the laws and processes of organic evolution in the same way as its morphological characters, but the two are not necessarily linked. In other words, Good correctly views the successful functioning of a plant in a particular type of environment to be the result of genetically determined tolerance limits. Mason (1936) has amplified

Good's theory in several ways, with particular emphasis on the limiting effects of narrower tolerance ranges during critical times in the life history of a plant. Cain (1944) and Good (1947) have further extended and expanded the Theory of Tolerance until it is now one of the foundations of modern plant geography.

Since individual plants of one or more species are the building blocks of vegetation, it is a serious handicap to ecologists and to other scien-

extent the ecology of certain species in certain regions. However, since the tolerance of a plant varies with time through its life-cycle, it was suggested as long ago as 1928 by Salisbury that the British Ecological Society should undertake to study and publish ecological life histories of the important plants of the British Isles. This suggestion led to the initiation of such a series in 1941; and within the last ten years a number of papers have been published in the *Journal of Ecology*

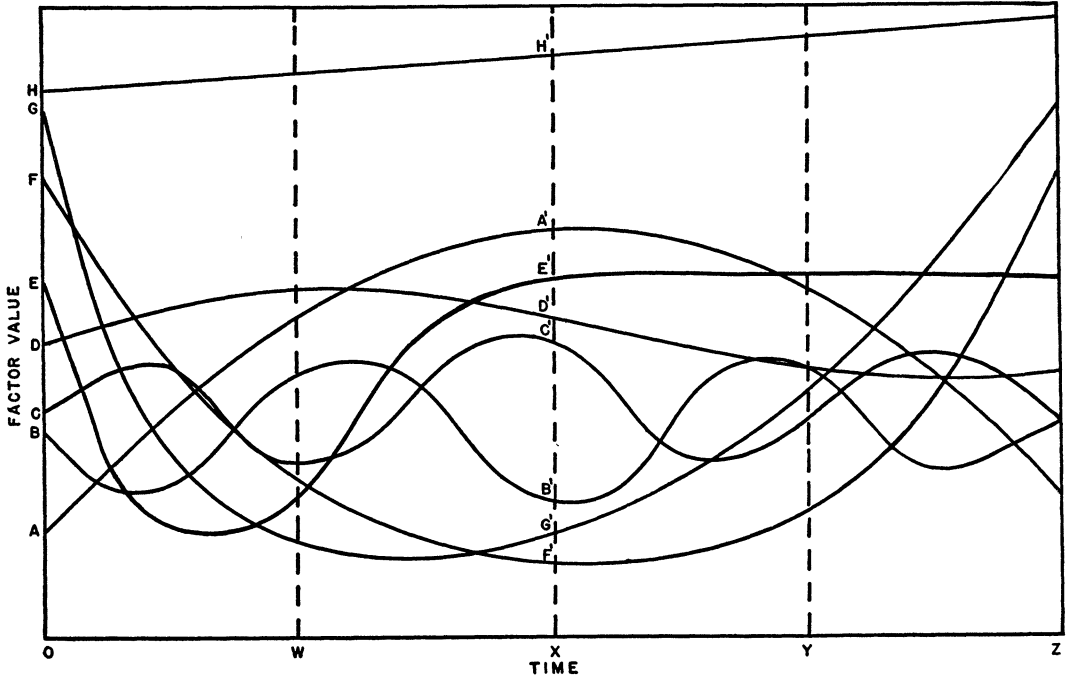


FIG. 2. DIAGRAM SHOWING HYPOTHETICAL CHANGES IN VALUES OF SEVERAL ENVIRONMENTAL FACTORS (A, B, C, D, E, F, G, H) THROUGH TIME IN THE LIFE OF AN ANNUAL PLANT

Time O (zygote), time W (dormancy), time X (germination), time Y (vegetative growth), and time Z (flowering) each show different combinations of values. Factor A would become A' at time X, factor B, B', etc. Some factor changes are cyclic, some cumulative.

tists concerned with pure and applied problems in plant distribution not to have available concrete data on the tolerance ranges of the more important plants of a region. The work of agronomists and plant physiologists has provided much of this type of information for cultivated plants. To a lesser extent, foresters have information of this kind for the principal forest trees. For the great majority of wild plants, however, few or no data on tolerance ranges exist. This lack of fundamental information on the ecology of individual species has long been recognized by some ecologists, and there exist a number of papers detailing to some

giving the ecological fundamentals for some of the important wild plants of the British Isles.

The need for this type of autecological work in North America was seen by several ecologists. Among them, D. B. Lawrence at the University of Minnesota, has used the ecological life history approach in his course in Experimental Ecology (Lawrence, 1947). In 1947, the Ecological Society of America established a committee on ecological life histories, with Lawrence as chairman. This committee has encouraged the publication of suggested outlines for intensive ecological studies of species belonging to various groups of plants

and animals. Among the outlines on plants are those by Pelton (1951) on trees, shrubs, and stem succulents, by Cooke (1951) on fungi, by Penfound (1952) on herbaceous vascular hydrophytes, and by Stevens and Rock (1952) on herbaceous angiosperms. Since these are so recent, no studies on the ecological requirements and tolerances of a species and based on the outlines have yet appeared. However, in recent years there have been some rather intensive studies on the ecology of certain wild plants. Among the best of these are those by Hall and Penfound (1944) on the American lotus (*Nelumbo lutea*), Jacobs (1947) on the greater duckweed (*Spirodela polyrhiza*), and Penfound and Earle (1948) on the water hyacinth (*Piaropus crassipes*).

In carrying out and interpreting ecological studies of wide-ranging species, it must be remembered that such species may consist of several to many biotypes, each with a slightly different tolerance range. Lawrence (1950) has stressed that the local population of a species should be the basis of work on ecological life histories. These local populations, as Clausen (1951) has pointed out, may consist, depending on pollination factors of a few or many biotypes at any one time. A thorough study of a widely tolerant species, then, would involve working with a number of local strains. This probably would not be necessary with narrow endemics which may consist of only one or a very few biotypes.

#### Compensation

Among the most interesting plant-environment relations which ecologists have noted is the apparent compensation of one environmental factor for another. This usually occurs near the boundaries of a species' range and allows the individuals of the species to grow in what at first glance does not appear to be a normal habitat. Rübél (1935) has discussed compensation and pointed out that an amount of a factor normally considered limiting for a species can be reduced even farther when compensated for by another factor.

The substitution of elevation for latitude, allowing plants of northern distribution to grow far southward on high mountain ranges, is a well-known example of compensation. A similar situation is brought about by the compensating effect of slope angle and direction for latitude upon northern species on the cooler and moister north-facing slopes, and upon southern species on the

warmer and dryer south-facing locations. Cantlon (1950), for example, has shown that north-facing slopes in north-central New Jersey have a vegetation more like that of level areas 300 miles farther north than like that of the south-facing slopes on the other side of the ridge.

Perhaps the most significant types of compensation, from the standpoint of disjunct plant distributions, are those in which parent material apparently compensates for climate. Such compensations are more striking and seemingly more common where certain climatic factors, particularly precipitation and temperature, are low, as for example in cold desert regions. The effects of limestones, serpentines, altered andesites, and other rocks of relatively narrow chemical composition are particularly marked in compensation and endemism.

Limestone often allows certain species to extend farther than normally into cold or wet climates. In Europe, for example, Thurmman (1849) long ago pointed out that certain plants restricted to chalk in northern France occur in the Cevennes to the south on gneiss, a siliceous rock. Shreve (1922) found that in southern Arizona, desert species such as ocotillo (*Fouquieria splendens*) and creosote-bush (*Larrea divaricata*) reach their upper limits from 900 to 1500 feet higher on limestones than on granite. In the Great Basin, there seems to be some tendency for pinyon (*Pinus monophylla*) to extend farther north and to higher elevations on limestones and other rocks rich in calcium. In the central White Mountains of eastern California, dolomites between 10,500 and 11,500 feet are covered with open pure stands of *Pinus aristata* while adjacent quartzite is occupied by a subalpine sagebrush-grass community.

On the other hand, some plants seem to be favored in disjunct distribution by acidic rocks. This seems to be particularly true with species which normally occupy moist montane situations, as a compensation for lesser precipitation when they occur in lower semi-arid regions. For example, several species of Sierran conifers and subalpine herbs extend into sagebrush steppe at some distance from the Sierra Nevada on islands of highly acid and infertile altered andesite (Billings, 1950). Since *Artemisia tridentata* and other desert shrubs and grasses cannot grow on the altered rocks, the soil moisture normally used by them can support the widely scattered conifers. The friable nature of the altered rock also allows deeper root pene-

tration of the trees than would be possible on the neighboring unaltered andesites. It would be interesting to know something of the mineral nutrition of the conifers, compared with the desert plants.

The more the question of parent material compensation is studied, the more it seems to become involved with that of endemism. Almost every rock type allowing compensation also has one or usually more endemic species characteristic of it. This is particularly true of limestones and serpentines, but endemics are present on almost all other chemically unusual rocks also. Mason (1946a, b) has discussed thoroughly and well the relationships between endemism and the highly mineralized nature of the substrates of many endemic plants.

One begins to wonder whether compensation is always an exact compensation or whether it ever is. Perhaps the individuals occupying the unique rock-climate environments belong to unique physiological biotypes. They may in a sense be endemics themselves: "biotypic endemics."

The solution of these complex problems of compensation and endemism lies principally in the use of the methods of experimental ecology, experimental taxonomy, and genetics. An outstanding example of the integrated use of these techniques is that by Clausen, Keck, and Hiesey (1948), who have shown that *Achillea lanulosa* and *Achillea borealis* are each made up of a number of climatic ecological races which react differently when grown in identical environments. Using one of these climatic ecotypes, the Inner Coast Range-Sierran foothill race of *Achillea borealis* (*A. borealis* subsp. *californica* of the Clayton-Knight's Ferry type), Kruckeberg (1951) found that it contained both serpentine-tolerant and serpentine-intolerant edaphic races. Kruckeberg correctly argues that since the environment of any particular place is a complex, no single uniform ecotypic response is possible. With this in mind, he has suggested that it might be better to think of natural populations as consisting of continuous or discontinuous arrays of ecotypic variation in response to the sum total of the environmental factors in an area.

#### *Biotic Potential*

As Mason (1946a) has pointed out, environment occupies area independently of whether or not a species can grow in that particular environment

or be restricted to it. Some species occupy all of the environment which is suited to their ecological tolerances. Other species, because of lack of sufficient time or because of barriers to the ready migration of their seeds or propagules, have not yet occupied all of the environments open to them. Of course, since environments are dynamic and continually changing, some species find their environmental areas getting smaller before they can be filled, while environments open to other species may be expanding.

Man has had a profound effect in altering the biotic potentials of many areas. Where once only the species and genera native to an area had ready access to its various environments, now exotic species from distant but similar environments may be transported and become established there. In some cases, such as that of *Bromus tectorum*, a species seems to be more successful in its new environment than in its native home. Some of this success may be due to gene exchange and evolution among the various ecotypes of the species, since Clausen (1951) has indicated that new ecological races can probably evolve in only a few generations to fit new environmental conditions. According to Stebbins (1950), the biological requirements for such rapid evolution are: (1) a high degree of heterozygosity, (2) a favorable population structure, (3) the degree of potentially preadaptive gene combinations, particularly those related to seeds, and (4) the intrinsic mutation rate. Since many widely distributed weeds are annuals, possibly there has been sufficient time for such genetic change and adaptation to occur simultaneously with their increase in range.

#### *Vegetation Influences*

In any discussion of the environment-plant complex, the reciprocal effect of vegetation upon its environment must not be overlooked. Microclimate, soil, and biota are all greatly affected by the structure and changes in the plant cover of an area. The local distributions of many species are greatly influenced by the microenvironments created and maintained by the vegetation itself. Most short-term natural succession is due to the cumulative influence of the principal dominants on the environment. Some of these effects are physical (Billings, 1938) while many are chemical (Went, 1942; Gray and Bonner, 1948). One of the most promising fields in plant ecology is the study of the effects of vegetational types upon the en-

environment and local plant distribution. Vegetational influences have been given more attention in forestry and range management than elsewhere, as indicated in the excellent compilation and discussion of such effects by Kittredge (1948).

*Solution of Complex Environment-Vegetation Problems*

As Cain (1944) has said, the exact mathematical solution of complete environmental complex-vegetation problems is extremely difficult, if not impossible. However, with some arbitrary simplification of terms it may be possible to arrive at approximate mathematical answers of great value in the solution of some problems in both applied and pure ecology. Major (1951) has attempted to solve complex vegetation-environment problems by simplifying the environment into five large factors: climate, parent material, organisms, relief, and time. Using these five factors in differential equations in a manner similar to that used with problems in soil formation by Jenny (1941), he has shown how it might be possible to put environment-vegetation relations on a functional, factorial basis.

Major's basic equation, adapted from Jenny, is:

$$v = f(cl, p, r, o, t)$$

where  $v$  represents any property of vegetation that can be expressed in quantitative terms, and  $cl$ ,  $p$ ,  $r$ ,  $o$ , and  $t$  represent respectively climate, parent material, relief, organisms, and time. Further adapting the equation to whole plant communities, it becomes:

$$V = f(cl, p, r, o, t)$$

where  $V$  represents an entire plant community or stand. Since in an assemblage of several species, it is almost impossible to reduce the community quantitatively to a single number, it is not yet possible to use quantitative terms in this last equation. Major follows Jenny in assuming  $cl$ ,  $p$ ,  $r$ ,  $o$ , and  $t$  to be mathematically independent variables, although he realizes that in nature this is only approximately so. By totally differentiating the first equation, he shows how it is possible to set up quantitative functions of a single variable with all others held approximately constant. For example, a lithofunction would be:

$$v = f(p)_{cl,r,o,t}$$

where parent material varies sharply, with other factors remaining constant. This would be the situation where serpentine adjoins sandstone on the same slope of a hill and the same species occurs in different quantities on the two rock types. Similarly, vegetation could be expressed qualitatively as parent material varies by a litho-sequence:

$$V = f(p)_{cl,r,o,t}$$

Similar equations for functions and sequences of other factors can also be set up.

Major's work is a forward step in the direction of logical expression of vegetational functions and their relations to environment. However, the method should be used with certain concepts borne clearly in mind. The premise that these factors are all independent variables might well cause confusion if the principle of the holocoenotic environment is accepted. Major realizes that these factors are not *ecologically* independent, but makes them *mathematically* independent so that they can be held constant in an equation while a single factor is varied mathematically. This is necessary to evaluate the effect of that one factor on the vegetation or local population. Among the many combinations of environmental factors in nature, examples of different rock types in the same climate can allow an evaluation of the parent material effect. This is only approximate because of the possible effect of parent material on microclimate and other factors, but it is probably close enough for practical results. Also, Major has deliberately restricted his problem to causation between vegetation and environmental factors and has purposely omitted the complex relations between the factors themselves. This, of course, greatly simplifies the problem but creates a more or less unreal situation, since in nature all of these interrelationships ultimately affect plant distribution and vegetation. Some disagreement is to be expected from the choice of only five factors (or groups of factors) to represent the whole environment. This is not too serious, since it would be very easy to add others, such as pyric (i.e., fire), and to set up a pyrofunction for *Bromus tectorum*, for example, in the equation:

$$v = f(py)_{cl,p,r,o,t}$$

Time is very definitely a part of any function or sequence involving vegetation, but whether it is truly an environmental factor is open to ques-

tion. Major concluded, since similar equations can be set up for both vegetation and soil, that they develop concomitantly and that soil formation cannot be separated from vegetative succession. This concomitant development has been clearly shown by the work of Braun-Blanquet and Jenny (1926) and of Pallman, Richard, and Bach (1948), among others.

While most ecological work is still far from the ideal mathematical design proposed above, there is now an increased realization that plant distribution and vegetation are almost always the result of the interaction of several environmental factors. Much careful work, experimentation, and statistical analysis have been done to show the relative effects of combinations of environmental factors upon the growth of certain plants in natural vegetation. Kozlowski (1949), for example, in a thorough study of the growth and competition of oak and pine seedlings, came to the conclusion that the ultimate failure of pine in Piedmont succession is due to *both* low light intensity and decrease in available soil moisture as parts of an environmental complex.

#### VEGETATION AS AN INDICATOR OF ENVIRONMENT

Since vegetation is the product of the interactions between the environment and the genetic tolerance limits of its component species, theoretically it can be the best indicator of conditions in natural environments. To this end it has long been put to practical use by foresters, range managers, soil conservationists, and farmers. However, certain precautions should be observed in any attempt to describe or to predict changes in an environment from the vegetation present in it.

In the first place, since environment occupies area independently of the plant species present and since many plant species have not yet occupied all of their potential environment, it would be a mistake to evaluate an environment on the basis of the *absence* of a given species. There are many reasons why it might not be present. Environments can better be judged on what species and vegetation are present.

Secondly, while there is some reason for using the physiognomy of vegetation as evidence of the physical environmental conditions, this must be done with great care. Many forests, particularly in western North America, are actually found in drier environments than the grasslands of the Mississippi Valley, but are maintained by a different

type of precipitation cycle. Beadle (1951) has pointed out the dangers of assuming that similar climates on different continents will exhibit vegetations of similar physiognomy. Semi-arid climates in New South Wales, for example, are not occupied by grasslands and shrub communities, as they are in North America, but by woodlands of *Eucalyptus*, *Acacia*, *Casuarina*, and other woody plants.

It should always be remembered that each species in a vegetation is distributed according to its own environmental tolerances. The resultant vegetation thus can be used as a delicate indicator of environmental conditions, provided it is analyzed floristically by adequate statistical methods and provided the environmental tolerances and indicator significance of its component species are known. These are difficult to determine on an exact basis and yet an experienced ecologist can, after a quantitative analysis of vegetation with which he is familiar, describe the environment and its cyclic and cumulative changes fairly well. Boyko (1947) has shown how quantitative climatic values can be deduced by using the geo-ecological shifts in environmental amplitudes of certain key species in the vegetation of Israel. However, much more research is needed before these evaluations can be put on an ideal quantitative basis.

As shown by Tüxen and Diemont (1937), Billings (1950), and others, floristic vegetation types within a large climatic type are not the result of climate alone but of the whole environmental complex, in which parent material is just as important as climate. Thus, it must be remembered that vegetation is an indicator of the whole environment and not just of climate, or parent material, or fire, or any other single factor.

#### CONCLUSIONS

1. The environment of a plant is holocoenotic.
2. Any study of plant growth and distribution in relation to environment must consider each factor in relation to the others of the complex.
3. Factors can be limiting or trigger factors in the dynamic complex. For a given species, these limiting factors may be different in different parts of its range.
4. Environment is dynamic and varies both in space and time.
5. Every plant species is distributed according to its own genetically determined tolerance limits, providing time has been sufficient to allow it to

occupy the whole potential environment open to it.

6. There is a definite need for much more autecological work on tolerance ranges under field or simulated field conditions. The effects of environmental shifts or environmental gradients should be worked out for groups of related species or for the important competing species in a community.

7. One environmental factor may compensate for another and allow a species to exist beyond its apparent tolerance range.

8. Genetic variation within a species, producing ecotypes and biotypes, is probably involved in the question of compensation.

9. It should be possible to put certain environment-vegetation relations on a quantitative functional basis if analyses are well-planned from the standpoint of both vegetation and environment

and if enough data are obtained. Some arbitrary simplification of the environment into factors may be necessary to do this.

10. Every plant species is distributed according to the tolerance ranges of its own ecotypes and biotypes. It is independent of other species except where individuals of other species constitute an integral part of its environment. It grows where it does because the *whole* environment in space and time fits its genetic requirements and time and the environment have allowed its seeds or propagules to reach that place. Communities result from such independent distribution and vary gradually or sharply as the whole environment varies.

11. Vegetation can be used as an indicator of total environment if the tolerances of its characteristic species are known and if the vegetation is adequately analyzed by statistical floristic methods

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