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Plant Communities

Recent research suggests that they form units in a vegetation continuum rather than discrete classes.

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One of man's early perceptions of nature was of the variety of the vegetational mantle which covers the earth's surface. Long and intimate contact with specific types of vegetation has colored the ways of life and attitudes of a people, influenced its art, and provided a backdrop for its legends and literature. Herb doctors of the past and present search for desired plants in familiar settings, and colonial farmers recognized, in some cases erroneously, some aggregations of plants as indicators of desirable farm land and others as indicators of barren land. Our languages contain many words which refer, more or less specifically, to familiar and distinctive groups of plants. *Marsh, moor, fen, bog, brake, steppe, prairie, llano, pampas, heath, chaparral, maquis*—all indicate the widespread recognition of distinctive vegetation types which are part of man's natural heritage.

Earlier Views of Plant Communities

Prior to the 19th century, botanists, in much the same way as laymen, recognized and were familiar with diverse types of vegetation. It was not, however, until the middle of the 19th century that plant communities were consciously made objects of study. Extensive explorations of areas of the world then little known to Europeans had centered attention on the wonderful diversity of plants, and the vast primeval areas of vegetation newly viewed by naturalists stimulated attempts to describe and name them. A branch of botany called plant physiognomy arose, based upon the recognition of plant communities by their general appearance.

One of its early proponents was Anton Kerner, whose book *The Plant Life of the Danube Basin* explicitly voices the concept of plants as members of distinct communities. "Every plant has its place, its time, its function and its meaning. In every zone, plant life has been developing through an inconceivably long time according to the same pattern to build up its green structure over the naked earth. In every zone the plants are gathered into definite groups, which appear either as developing or as finished communities, but never transgress the orderly structure and correct composition of their kind" (*1*). Kerner's book was a subjective and esthetically appreciative description of the vegetation of the Danube Basin, interpreting the distribution of several physiognomically distinct "plant formations" as related to the environment. In North America such comprehensive study of vegetation lagged, although descriptions of vegetation by travelers and early botanists are numerous, and the insights of naturalists, such as Thoreau, into some aspects of the plant communities of their native areas, foreshadow the work of early plant ecologists (*2*).

Problems of Classification

It was not until the early years of the present century that intensive studies were made of the composition, distribution, development, and biological interrelations of plant communities. These studies brought to light many units of vegetation not previously recognized or dignified by name, and the list of plant communities grew rapidly. Description and naming are but the first steps in classification. As the number of described communities proliferated, systems of classification were erected analogous to those used by taxonomists. These classifications sought a basic unit or community, comparable to the taxonomic species, which would serve as a basis for a hierarchical classification of vegetation. The communities were commonly called "associations," the concept resting upon the mutual occurrence or association of species populations in recognizable communities defined by their floristic composition.

Unfortunately, there was little agreement among botanists about the nature and extent of the association or the precise basis upon which it should be defined. In some systems the association was recognized by specific combinations of the largest and most conspicuous plants, known as dominants. Trees are the obvious dominants of forest communities while grasses are the prairie dominants. In other instances the total species composition was used, certain character species, which occurred in a given proportion of the examples studied, serving to define the association.

The earlier work, based largely upon the subjective judgments of individual botanists familiar with the vegetation of an area, was soon supplemented by quantitative studies based on objective sampling techniques which described more precisely the characteristics and composition of communities. These studies served to multiply the difficulties of classification, for instead of having only combinations of species to consider, it became necessary to consider the relative frequency with which the species occurred. A community with the composition 75 percent species A, 20 percent species B, and 5 percent species C may not be in the same category as one with the composition 75 percent species C, 20 percent species B, and 5 percent

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species A. A multiplicity of communities of various degrees of complexity and size were described as associations, presumably all fairly distinct, one from another. Still, there was no unanimity of opinion about how much variation was permissible within an association, and the question was posed by Stanley Cain, "How many species must remain to preserve the identity of the association?" (*3*).

Great diversity existed in the associations described by botanists applying the precepts of various schools of thought. According to some schools, particularly in Europe, an association was a small-scale, homogeneous community which in some cases might be hidden under a Stetson hat (for example, a community of mosses). In America (notably as developed in the work of the pioneer ecologist Frederick E. Clements, whose views dominated American ecology for many years), an association was a large-scale unit including great variation (*4*). Moreover, according to Clements' concepts the association was comparable to an organism and was held to possess an overall unity and stability under the control of climate. As a consequence of these divergent viewpoints it was possible for Conard (*5*) to recognize 71 associations on central Long Island, while Clements recognized only three in the entire eastern deciduous forest formation of North America. These differences, aggravated by semantic difficulties, resulted in near chaos, and some ecologists advocated abandoning the term *association,* if not the concept.

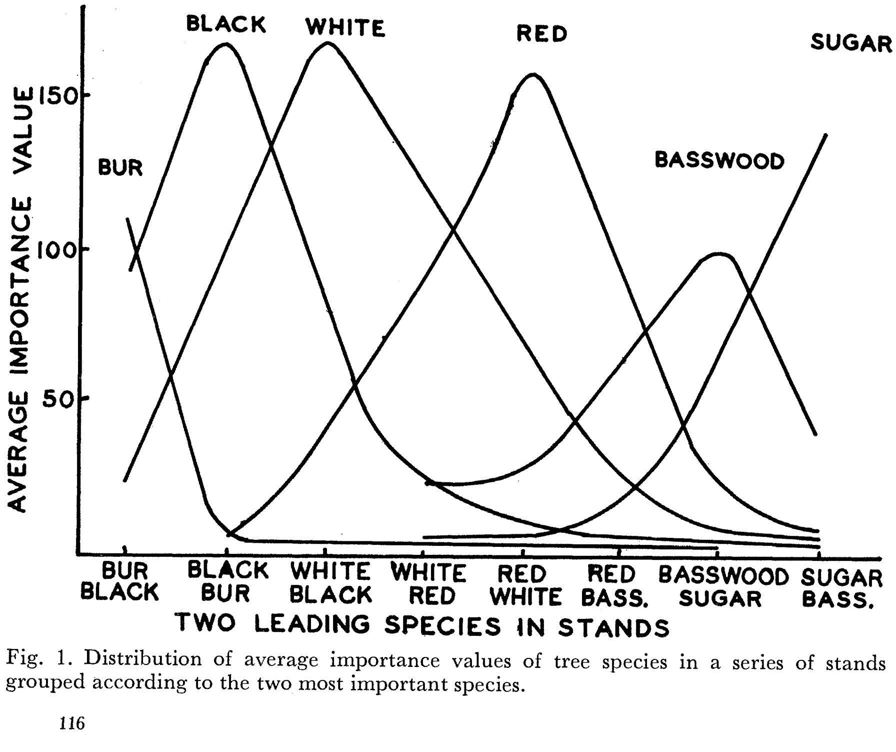


Fig. 1. Distribution of average importance values of tree species in a series of stands grouped according to the two most important species.

In spite of these difficulties, an almost unanimous opinion existed in Europe and America that, however nebulous the thinking or however great the differences of opinion, describable aggregations of plants occur, possess boundaries in nature, and can be recognized as rather discrete entities which are repeated in numerous individual instances in the vegetation of an area. This view of vegetation as composed of discontinuous assemblages of plants or unit communities is one of the cornerstones of classical plant ecology. Associations have been variously defined, usually in the following vein: "An association is a plant community of definite floristic composition, presenting a uniform physiognomy, and growing in uniform habitat conditions" (*6*); or, "Associations of plants on land are definable entities susceptible of naming and classifying" (*7*).

The Individualistic Hypothesis

Diametrically opposed to this consensus was the hypothesis advanced by Henry A. Gleason, tentatively in 1917 and more explicitly in 1926, which he referred to as "the individualistic concept of the plant association" (*8*). Gleason maintained that plant species were distributed according to their individual biological potentialities and that the aggregation of plants on any area was the fortuitous result of the local environment and the available plants. He stated that the environment varies continuously in space and time and that vegetation also varies continuously in space and time. Therefore, similarity of individual examples is approximate only, and a precisely logical classification is impossible. Although Gleason recognized the existence of large-scale areas of vegetation, such as grassland and deciduous or coniferous forest, he emphasized that within the matrix of such physiognomically distinct areas the differences between individual communities were cumulative, so that the variation increased with the distance separating them. He cited the forests along the Mississippi River basin and noted how small changes from mile to mile, as species drop out or appear, cumulate, so that over many miles an almost complete change in composition results. His thinking was not unique, for similar ideas were expressed by various European botanists.

Thus, two apparently antithetical concepts of plant communities were in the field. The first maintained that "the juxtaposition of plants in communities is not only an empirical generalization. The association of individuals and species is much more than a chance meeting. It is a part of the order of nature" (*7*). The second held 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" (*9*).

In America the individualistic concept of plant communities was nearly dormant for 20 years. Within the past decade new evidence from varied sources has revived and added credence to the individualistic concept. Studies of vegetation types as varied as the shad scale of Nevada and California (*10*), the forests and prairies of Wisconsin (*11, 12*), and the forests of the Great Smoky Mountains (*13*) lead to conclusions substantiating the individualistic concept. Concomitant with this has been an increased interest in order or pattern among units as against a system of classification of discrete entities.

The basic question is whether or not species populations occur as groups which are discontinuous with other groups and recognizable as a series of discrete classes. Quantitative and objective methods have been applied to varied vegetation types in a reexamination of this question. Two general approaches have been used. One, "gradient analysis"

(*13*), examines samples of vegetation along an environmental gradient such as altitude or moisture. This gradient serves as the basis for aligning and analyzing the vegetational data. The second approach is based upon the mass collection of large numbers of samples of vegetation without reference to environmental gradients or apparent aggregations of species. The data are analyzed to ascertain species relationships which might serve as a basis for classification or the construction of gradients based upon species composition. Such compositional analysis serves to orient the individual community sample to other samples, and, conversely to the method of gradient analysis, environmental data may be aligned on a vegetational gradient.

The gradient analysis approach is the basis of forest studies in the Great Smoky Mountains by Whittaker (*13*), who collected samples spaced along gradients of altitude and moisture and also random samples throughout the area. When plant populations are analyzed according to their quantitative distribution along an environmental gradient, he finds that each species forms a bell-shaped curve. The curves are distributed along the gradient as a series with overlapping ranges, but no two curves have identical ranges or optima. No clusters of species curves are found, indicative of similar species behavior relative to the gradient and leading therefore to recognition of a series of discrete units. This, Whittaker points out, suggests that species populations form a shifting series of combinations along environmental gradients and leads to the interpretation of vegetation as a "complex and largely continuous population pattern" (*13*).

The second approach, based on the analysis of proportionate composition with respect to the dominant plants in a large number of samples, is exemplified by studies in Wisconsin forests. The relative importance of each tree species in a forest stand is denoted by its "importance value." This value is the sum of measures of density, size, and distribution derived from a series of standard samples in each stand. Density is the number of individuals of a species in the total sample. Size is measured by the cross-sectional area of the trunk of each individual tree at a standard height. The measure of distribution of the species is based on the frequency with which the species is encountered in the samples. By expressing each measure as a percentage, three relative values are obtained for each species, the sum being the importance value of the species. The magnitude of the importance value serves as an indication of the sociological importance of the species in the community. The importance values for all species in a stand add up to a constant total of 300. In a pure stand of a single species, the importance value of that species would be 300, while in the more usual stand, in which there is a mixture of species, each would have an importance value constituting some portion of 300.

In the upland forest of southern Wisconsin only four tree species—black, white, and red oaks (*Quercus velutina, Quercus alba,* and *Quercus rubra*) and sugar maple (*Acer saccharum*)—commonly attain high importance values. When stands are classified according to their most important tree species, those stands in which black oak is dominant contain decreasing quantities of white oak, red oak, and sugar maple, in that order, while, conversely, those stands in which sugar maple is the leading species contain decreasing amounts of red oak, white oak, and black oak. This suggested a preliminary order of stands, from those dominated by black oak to those dominated by sugar maple, white and red oaks being intermediate. More detailed analysis was made by classifying the stands into groups based on the two most important species. These groups were arranged in the order suggested above, additional species being placed in sequence according to the relation of the stands in which they reached optimum importance to other groups of stands (Fig. 1). This empirical ordering of groups served to demonstrate a pattern of species distribution but did not suggest anything which could be interpreted as discrete communities. It soon became apparent that the number of classes is determined by the method of selection. If the order of the four most important species of trees in a stand is used as a basis of selection, each class includes a single stand. In other words, for the data at hand, no two stands had the same arrangement of the four most important tree species, and no natural groups of species combinations were apparent.

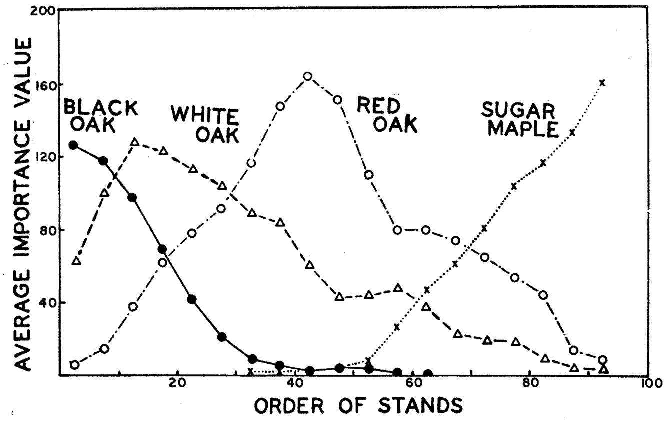
Since the groups of Fig. 1 are artificial classes, a simple method was devised for visually examining data with respect to the individual stands. The importance value of each species in a stand was marked to scale on a narrow strip of white Celluloid ten inches long. These strips could be placed side by side in any desired order, and the distribution of species among many stands could be seen at a glance. If natural groups exist, such a technique might reveal them. When the strips were placed in order of decreasing importance values for black oak and of increasing importance values for sugar maple, it was found that the species distributions of red and white oaks form approximately normal curves (Fig. 2). Species distribution of trees, shrubs, and herbs not involved in the original empirical ordering of stands also forms a continuous series of bell-shaped curves. The positions of the curves for each species are purely relative, but each occupies a characteristic position in an ordered sequence, no grouping of curves being evident. The entire order or sequence is called a vegetational continuum, for at no point can it be divided except on the basis of arbitrary criteria. The vegetational continuum represents a shifting series of species combinations in a linear pattern or gradient. Any stand is similar to, but slightly different from, its neighbors in the continuum, the difference between the stands increasing roughly as the distance between them.

Similar vegetational continua have been arrived at by using data for herbaceous plants rather than trees and by ordering the stands according to statistical measures of similarity of the species composition (*12, 14, 15*).

The concept of correlated change of species composition on a continuous gradient has its counterpart in the catena concept of the soils scientist, in which properties of soils are similarly conceived of as varying continuously. It has been compared to the spectrum of visible light. The extremes of red, yellow, green, or blue are readily apparent, but the intergradations are not so easily distinguished. The visible extremes are analogous to the conspicuously different areas of vegetation, such as prairie, oak forest, or maple forest, while the many intergradations between these extremes of vegetation suggest the continuous variation of the spectrum. The physicist designates a point or range on the spectrum not by color but by a number indicating its wavelength. Analogously, scales or index numbers have been developed to locate a given stand more precisely in a continuum.

Continuum Index

Various devices have been used to establish numerical scales to place individual stands in a vegetational con-



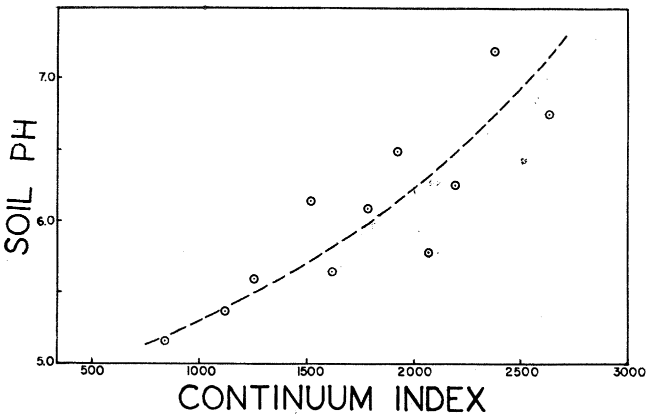


Fig. 2 (left). Distribution curves for four important tree species when individual stands are arranged in order of decreasing occurrence of black oak and increasing occurrence of sugar maple. The importance values are averaged by successive groups of five stands, and the curves are smoothed according to the formula $(a + 2b + c)/4$. Fig. 3 (right). Distribution of soil *p*H in southern Wisconsin forest stands according to the continuum index.

tinuum. In the case of the continuum described above, the tree species illustrated in Fig. 2 were rated; sugar maple was used as a standard and given the arbitrary value of ten. Other species received values ranging from one to nine, according to the position of their optimum occurrence relative to sugar maple. Black oak, for example, was assigned a value of two; white oak, four; and red oak, six. The importance value of each species in a stand was multiplied by the assigned value, and the products were added. The weighted total served to place the stand in relation to other stands on a numerical scale ranging from 300 to 3000. A stand composed entirely of bur oak, which was assigned a value of one, would have a rating of 300; a stand composed solely of sugar maple, with its assigned value of ten, would have a rating of 3000. All of the species in a mixed stand would affect the total for that stand, but the species having high importance values would naturally exert the greatest influence. This scale of weighted numbers is called the vegetational continuum index. The stands originally arbitrarily classified into groups or arranged in an order of individual stands may now be arranged on the basis of index values. The order and relative position of species curves remains the same, indicating that the linear sequence is preserved in the index order.

A vegetational continuum index is a new and useful tool in ecological studies of many kinds. Distribution of environmental factors may be related to the index, as illustrated in Fig. 3, which indicates interrelations of the community complex and factors of the physical environment. The vegetation can serve as a basis for analysis of the environment. Ecological studies of individual species in stands representative of various ranges of the index serve to illustrate variation in physiological and morphological characteristics as they are related to the index (*16*). Studies of soil microfungi (*17*) indicate that species and genera are preferentially distributed in given ranges of the continuum. The penicillia, for example, increased in percentage of total species toward the higher values of the index, while the Mucorales showed a reverse trend. Like the trees, forest soil microfungi form a series of changing species combinations along the continuum gradient. Hale (*18*) found that the most satisfactory method of analyzing the distribution of mosses and lichens growing on the bark of trees was on the basis of the vegetational continuum. Although host specificity resulted in a high degree of interspecific correlation, this was found to be relative and to be modified by position on the continuum index. Populations of breeding birds in stands spaced along the continuum index demonstrate, in many cases, graded responses of individual bird species and a continuous shift of species combinations (*19*). In short, the continuum index can provide a background for studies of varied kinds of organisms, particularly studies of characteristics which may be influenced by variation in community composition.

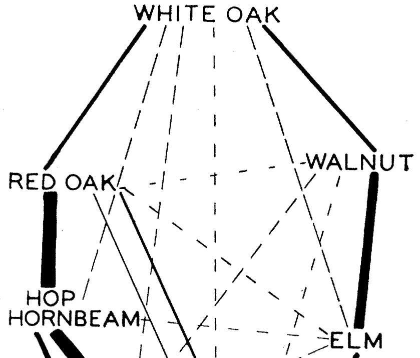


Fig. 4. Diagram illustrating interrelations among several tree species, constructed on the basis of Cole's index of interspecific association (*21*).

Community Pattern

In the development of the continuum concept it became apparent that this concept is not limited to a linear order but is multidimensional. One suggestion of this comes from a study of an area including species usually recognized as members of different forest associations (oak–hickory and maple–basswood). The composition of this stand was sampled intensively by means of a grid of quadrat (square area) samples (*20*). The mutual occurrences among the species were measured by means of an "index of interspecific association," developed by Cole (*21*). The index was computed for each of the possible species combinations. The index values range from + 100 percent for species which always occur together to − 100 percent for species which never occur together. If there is only chance association the index is zero. In the resulting matrix of indices of association between tree species it was notable that two species which are significantly associated with each other do not necessarily have similar association values with a third species. This is graphically shown in Fig. 4. In the figure, species pairs which have a positive index of association are connected by a line whose width is proportionate to the measure of association. Those pairs which have a negative value are connected by a dashed line in which the length of the spaces relative to the length of the dashes indicates the degree of negative value. Thus, walnut (*Juglans nigra*) and hop hornbeam (*Ostrya virginiana*), which had an index value of – 100, are not connected at all. Sugar maple and white oak, having an index value of – 62, are connected by a line that is 38 percent dash and 62 percent intervening space.

Red oak and walnut are both associated with white oak and in similar degree, as measured by the index, but are significantly disassociated themselves. White oak, walnut, and perhaps red oak might be suggested as a possible community, but the fact that red oak and walnut are significantly disassociated would suggest two communities. Or, sugar maple, basswood (*Tilia americana*) and hop hornbeam might be regarded as a community, but the significant association of red oak and hop hornbean would suggest that red oak also be included. Elm (*Ulmus rubra*) occurs with sugar maple and might be added to such a community, but elm and red oak and elm and hop hornbeam are significantly disassociated. It seems reasonable to view such a diagram as representing an arrangement of species combinations which are connected in a continuous two-dimensional pattern. It does not seem possible to reduce the pattern to discrete communities except by introducing arbitrary lines. The pattern emphasizes the fact that a continuous relationship between species is not a linear one, as the earlier figures might suggest, but is more complex and multidimensional. Species which occupy related positions in a linear order from white oak to sugar maple may occupy quite unrelated positions on other possible axes.

Grassland and Transition

The concept of continuously varying species combinations, as postulated by Gleason's individualistic hypothesis and borne out in the forest studies described above, has proved valid in studies of grassland and transition between forest and prairie.

Dyksterhuis (*22*) has shown a continuously varying composition in Western range land. Curtis (*12*) has constructed a prairie continuum index for Wisconsin prairies, based on five groups of indicator species ranging from species with optimum development in wet sites to those showing optimum development in dry sites. An index value for each prairie stand was calculated by multiplying the relative amount of each indicator group present by a weighting value for each group and adding the weighted products. When the stands were arranged in the order of index values, for all species, including nonindicator species, there were smooth curves of occurrence in a continuous series. Identical results were obtained in a direct gradient-analysis approach when species distributions were plotted on a gradient of capacity for retention of soil water.

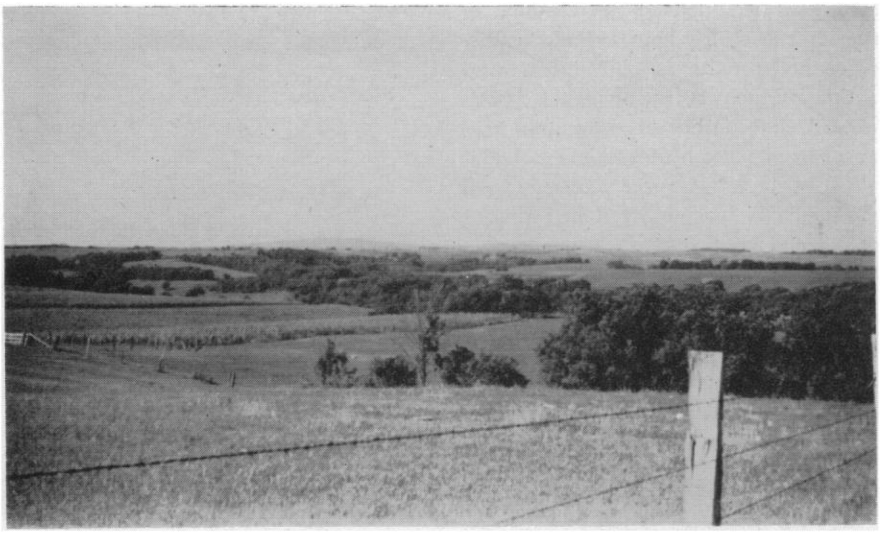


Fig. 5. Transition between prairie and forest. Here in the prairie-forest border region, forests appear in the draws; the upland, which is now cultivated, was originally largely prairie.

The work of Bray (*14*) is of particular interest. Working in the prairie-forest border region of Wisconsin, a broad intermediate belt between grassland and forest, he finds evidence of continuous transition between forest and prairie. In this region prairie and forest were originally intermingled in a mosaic of vegetation now almost universally disrupted by cultural activities (Fig. 5). Although prairies are found on various land forms, they commonly occur on rolling uplands and steep hills, and it is on the latter that many of the remnants are found in the prairie-forest border. Bray established a transect of samples extending from prairie into forest. He describes his findings as follows: "Here is the vegetation of two formations coming together within the oak opening transition of the prairie-forest border and interlocking so smoothly that of those species which reach their greatest frequency within the oak opening . . . it is difficult to state whether they are primarily forest plants or prairie plants."

The concept of continuity in vegetation is not at odds with any but the most fundamentalist views of the integrity of the associational unit. Practically all ecologists recognize the existence of intergrading areas of composition and characteristics between stands which may be described as representative of different associations. J. Braun-Blaunquet (*23*), whose work is commonly regarded as the archetype of classification of vegetation into associations, states: "The possible combinations of species are indeed endless." The essence of the continuum approach as an outgrowth of the individualistic concept is to switch the emphasis from the study of more or less similar units of vegetation with admitted intergrades to the study of the gradient itself. As Goodall (*24*) has pointed out, nothing will be lost, for any cluster of species which responded as a unit would still appear, and information about the reaction of species in zones now regarded as transitional would also be available. The logic of proceeding on an assumption of continuity of vegetation unless discontinuity is clearly demonstrated seems clear, in view of the confusion of opinions on association concepts.

The concept of plants as members of communities stated by Kerner and many others is substantiated in the work of modern plant ecology. The order inherent in nature is not, however, one of clear-cut cause and effect relationships resulting in well-defined aggregations of species into clearly bounded and readily pigeonholed units as objective natural entities. Much recent evidence points toward the concept of communities as an ordered pattern of species, individually distributed in space and time and most effectively considered in terms of orders and gradients.

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Folic Acid Coenzymes

Metabolic reactions involving "active formate" and "active formaldehyde" are surveyed.

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For a great variety of cells of animal, plant, and microbial origin, the vitamin, folic acid, serves as a growth factor by controlling the metabolism of the one-carbon (C_1) compounds, formate and formaldehyde. These C_1 compounds serve as building blocks in the biosynthesis of purines, certain pyrimidines, and certain amino acids. An increased capacity to incorporate formate into cellular nucleic acids (*1*), and also an elevated level of folic acid (*2*) and its coenzyme forms (*3*), has been found to characterize at least one type of abnormal growth, namely that of the leukemic white cell.

A description of C_1 metabolism is provided by the following generalized equations for the mobilization of *X*, the formaldehyde or formate group,

$$D{-}X + C \rightleftharpoons C{-}X + D \qquad (1a)$$

$$C{-}X + A \rightleftharpoons A{-}X + C \qquad (1b)$$

In these equations, *C* is the folic acid coenzyme, *D* is a donor molecule containing a potential C_1 unit (serine, purine, histidine, and so on), and *A* is an acceptor molecule (glycine, carboxamide ribotide, and so on). When the C_1 unit is bound to the folic acid coenzyme (*C—X*), the complex may be considered as "active formate" or "active formaldehyde," respectively; the latter complex is more frequently referred to as "active hydroxymethyl." The analogy between these complexes and the well-known "active acetate" (acetyl coenzyme A) is apparent.

Although the early recognition of various metabolites as donors and acceptors of formyl and hydroxymethyl units was achieved by tracer and nutritional studies (*4, 5*), recent work has been directed toward studies with isolated enzyme systems, which permit a greater degree of understanding of reaction mechanisms. Study of the detailed mechanisms of the various reactions, represented by Eqs. 1a and 1b, has been hampered by the multiplicity of the C_1 fragments (formyl, hydroxymethyl, and in some instances, methyl) and by uncertainty concerning the chemical structure of the intermediates, *C—X*, since, as is discussed in subsequent paragraphs, folic acid has several potential sites of attachment for a C_1 group.

In this article (*6*) we shall attempt to summarize the current information regarding the nature of "active formyl" and "active hydroxymethyl" complexes and to survey the various metabolic reactions in which these compounds participate (*7*).

Reactions Involving "Active Formaldehyde"

Serine hydroxymethylase. Numerous investigators (summarized in reference *8*) have studied the enzymatic interconversion of serine and glycine. In early work (*9*), in which tissue slices or intact animals were used, sensitive tracer techniques were required to detect the small conversions. More recently, larger conversions have been achieved by use of purified enzymes from avian and mammalian livers (*8; 10–13*).

The over-all reaction (Eq. 2) for the biosynthesis of serine from glycine and HCHO

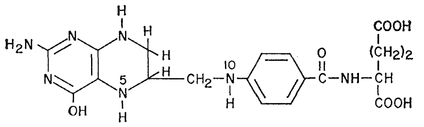
$$\mathrm{HCHO} + \text{glycine} \rightleftharpoons \text{serine} \qquad (2)$$

is actually the sum of two separate reactions

$$\mathrm{HCHO} + \mathrm{FH_4} \rightleftharpoons \mathrm{hFH_4} \qquad (2a)$$

$$\mathrm{hFH_4} + \text{glycine} \rightleftharpoons \text{serine} + \mathrm{FH_4} \qquad (2b)$$

where FH_4 is the abbreviation (*14*) for 5,6,7,8-tetrahydrofolic acid (I)



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the coenzyme form of folic acid, and hFH_4 symbolizes hydroxymethyl FH_4, without specifying the position of the C_1 group on the folic acid coenzyme.

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