

# AN UPLAND FOREST CONTINUUM IN THE PRAIRIE- FOREST BORDER REGION OF WISCONSIN<sup>1</sup>

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## INTRODUCTION

It has been said that the desirable order of ecological research in a given region is first, the study of communities, second, the study of the individual species, and last, the study of the habitat (Yapp 1922). Sociological investigations of constituent species and their numerical relations should precede autecological studies if the latter are to have maximum meaning. This sequence should lead to a greater efficiency in research, in that an initial knowledge of any natural groupings of species may enable the autecology of the groups to be studied simultaneously, with a resultant saving in time and travel expenses. The grossly inadequate state of autecological knowledge of even our most common species indicates that the current haphazard method of attack is faulty; if aggregations of species occur together under similar environmental conditions in nature, they could be studied in a systematic program. A long-term investigation of the communities of Wisconsin has been underway since 1946 with a view to determining the existence and the floristic nature of such aggregations (Curtis and Greene 1949). The present paper deals with the upland hardwood forests of the prairie-forest border region of the state and their interrelations with each other and with certain physical factors of the environment. Deep appreciation is expressed to Professor P. B. Whitford, who

generously placed his files on forest composition at our disposal; to Professors Grant Cottam, H. C. Greene, N. C. Fassett, R. S. Muckenhirn, M. L. Partch, and S. A. Wilde for valued advice and consultation; to Messrs. Orlin Anderson, and R. S. Brown for indispensable aid in the collection of field data; to Miss Margaret Gilbert for aid in the computation; to Messrs. A. M. Fuller, Neil Harrington and Fred Wilson for help in the location of stands; and to the many members of the Soil Conservation Service, the Regional Foresters of the Wisconsin Conservation Department and the advisers of the Junior Wisconsin Academy of Sciences, who so willingly imparted their knowledge of local conditions in their regions. The authors are also indebted to Professor K. J. Arnold, of the University Computing Service, for aid in the statistical phases of the work.

The taxonomic nomenclature used in this paper follows that of Gray's *Manual of Botany*, 8th edition, 1950.

## LITERATURE REVIEW

The earliest references to the vegetation of southwestern Wisconsin were made by the explorers and pioneer travelers in the years following 1698. For the most part, they contained only general descriptions, with remarks about unusual species. The first account by a competent botanist was that of Increase A. Lapham in 1852, but he dealt primarily with the distribution of individual species. The first description of plant communities as such was given by T. C. Chamberlain in 1877. This eminent geologist, who was later to exert such great

<sup>1</sup>This work was supported in part by the Research Committee of the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation.

influence on H. C. Cowles at the University of Chicago, was at that time the State Geologist of Wisconsin. He distinguished three forest communities in southern Wisconsin, but made clear that no abrupt line of demarcation existed between them, with repeated statements illustrating "a gradual transition from one to the other" and "an almost imperceptible merging of one into the other." His three communities were the "oak group" including *Quercus alba* (white oak), *Q. macrocarpa* (bur oak), *Q. rubra* (red oak), and *Q. velutina* (black oak), with *Populus tremuloides* (aspen), *Carya ovata* (shagbark hickory), *Prunus serotina* (black cherry) and *Pyrus ioensis* (wild crab apple) as lesser members; the "oak and maple group" in which *Acer saccharum* (sugar maple) was most conspicuous but *Quercus alba* and *Q. rubra* were still common, with *Acer rubrum* (red maple), *Ulmus rubra* (slippery elm), and *Tilia americana* (basswood) in small numbers; and the "maple group" with *A. saccharum* dominant, but with *Tilia americana*, *Ulmus rubra*, and *Ostrya virginiana* (ironwood) as characteristic and abundant associates. He comments about the "oak and maple group" as follows: "This group is not characterized by the exclusive presence of any prominent plant but by a distinctive association of plants common to several groups."

Bruncken (1900) also described three forest associations, but only two were found on uplands—the "hemi-xerophytic oak-hickory" and the "mesophytic basswood-maple." Additional observational studies on the forests of the region were reported by Pammel (1904), Marks (1942) and Stout (1944), but the first account in which quantitative data on actual composition were presented was that of Wagner (1947), who studied a stand in Jefferson County which fits into Chamberlain's oak and maple group. Cottam (1949) investigated an oak woods in Dane County by quantitative methods and reported in detail on the historical development of oak openings

and the changes which have taken place in them since settlement. He attributed major importance to fire in the maintenance of oak openings and to cessation of fire as the cause of the subsequent development of the present closed canopied stands.

The most comprehensive paper on the forests of southern Wisconsin was by Whitford (1951). Although this study was primarily concerned with the relation between the clone size of herbs and the age of the forest stands, considerable attention was devoted to the establishment of a method for classifying the stands. In the course of the investigation, Whitford studied a considerable number of stands and presented detailed data on tree, shrub, and herb composition. He arranged his series of 28 stands into three groups on the basis of shade tolerance of the tree species. He assigned each species to one of three tolerance classes, and then determined the relative fraction of all trees in a stand which belonged to each of these classes, on a summation basis. This method resulted in a sequence of stands from those composed entirely of intolerant species to those made up mostly of tolerant species. Whitford divided his stands into three groups—"oak-hickory, intermediate, and maple-basswood," but the division was made for pragmatic reasons and was not based on any internally apparent separation of the data into three groups.

Studies in Illinois, Iowa and Minnesota indicate that a series of forests similar to those in Wisconsin are found in at least portions of these states. No quantitative investigations in northern Illinois have come to our attention, but the general descriptions of Fuller and Strasbaugh (1919), and DeForest (1921) indicate a series of forest types from those dominated by *Quercus* and *Carya* to those dominated by *Acer saccharum*. In Iowa, the studies of Clark (1926) and of Aikman and Smelser (1938) show a succession from *Quercus macrocarpa* and *Q. velutina* in the initial stages through

*Quercus rubra-Tilia americana* stands to the terminal forests of *Acer saccharum* and *Tilia americana*. Daubenmire (1936) reported on the structure of the *Acer-Tilia* community and on its relation to the surrounding *Quercus* forests in the "Big Woods" of Minnesota.

While the results of the various investigations in these four states are by no means in complete agreement, there does appear to be a general uniformity of opinion as to the topographic distribution of the forests, with some type of *Quercus* forest on the most xeric forested sites and an *Acer* forest in the most mesic habitats. The disagreement seems to lie in the determination of the number of discrete communities that may be recognized, in the floristic nature of the boundaries between them, and in their exact composition. Many of the early workers emphasized the lack of sharp lines of demarcation, while later workers, who could study only the more completely dissected and isolated stands resulting from the highly agricultural land use of the present time, were more inclined to describe discrete communities of several types.

Although the flora of Wisconsin has many diverse floral elements, it was early pointed out that there are two major floristic provinces, separated by a diagonal line from northwest to southeast (Cheney 1894). The southwestern portion of the state contains the prairies and hardwood forests, while the northeastern part contains both hardwood and coniferous forests. The boundary line between them, actually a zone or band, is comparable to the tension zone proposed by Griggs (1914). Its position can be determined within fairly narrow limits by the method proposed by Clements (1905: 187) "The limiting line or ecotone of a . . . province is a composite obtained from the limits of principal species and checked by the limits of species typical of the contiguous vegetations."

Applying this to Wisconsin, a number of trees including *Quercus velutina*,

*Carya ovata*, and *Juglans nigra* reach their northern boundaries in a zone which also includes the southern limits of such trees as *Betula lutea*, *Abies balsamea*, and *Populus balsamifera*. This same zone marks the northward or southward extent of a great many herbaceous species, both native and exotic; it also separates closely related varieties of single species, as in the case of *Acer saccharum saccharum* and its subspecies *A. s. nigrum* (Desmarais 1948) and *Brachyelytrum erectum erectum* and *B. e. septentrionale* (Salamun 1950). The floristic province southwest of the zone is here termed the prairie-forest province, while that to the northeast is the northern hardwoods province (roughly equivalent to the Lake Forest of Weaver and Clements 1938). It is recognized that these names may be of local descriptive value only and are considered to be tentative. Perhaps the most characteristic feature of the floristic provinces from the standpoint of vegetation is the occurrence of oak woods in the early forest succession south of the zone in contrast to pine woods in the same successional position north of the zone. The terminal forests in both provinces are dominated by sugar maple. Within the narrow zone itself various elements of the two provinces occur in puzzling mixtures. Their elucidation must await completion of studies on both sides of the zone.

These floristic provinces are similar to the natural areas of Cain (1947) and the floristic areas of Raup (1947) and Egler (1948). They are characterized by the presence of a uniform flora such that "all stands have equal chances of containing all the same species" (Cain 1947). It is only within such limitations that plant associations can possibly achieve objective reality. One of the aims of the present paper is to determine whether discrete communities with definite structure and definable boundaries actually exist within such a natural floristic province, or whether plant associations are "metaphysical approximations

in a field where there are unlimited variables, combinations and permutations" (Cain 1947) even within the narrow limits set by the province.

#### DESCRIPTION OF AREA

##### *Physiography*

The south and west borders of the area included in this study (the Wisconsin-Illinois boundary and the Mississippi River) were prescribed by various non-ecological but nevertheless compelling reasons. The remaining boundary was based on the biologically more valid presence of the tension zone discussed above which extends across Wisconsin from northwest to southeast (Fig. 1). The major physiographic differentiation of the region is its separation into glaciated and non-glaciated areas. The Driftless Area in the western portion of the study area is a region of mature drainage patterns and rugged, almost mountainous, topography as contrasted with the glaciated eastern portion which possesses immature drainage and a more or less rolling topography. The glaciated areas consisted primarily of Wisconsin drift with lesser areas of older (Illinoian)

drift. The underlying bedrock is composed predominantly of old sedimentary rocks—Cambrian sandstones and Lower Magnesian, Ordovician and Silurian limestones.

##### *Climate*

The area under consideration lies almost wholly in the transition zone between climatic regions I and IV of Borchert (1950). As such, its climate is intermediate between that of the Northeastern forest region of snowy winters and reliable summer rains and that of the central Prairie region with relatively dry winters and frequent summer droughts. Partaking of both forest and grassland climates, it supports both prairie and forest and their intermediate expression, the oak savanna. Excellent summaries of the ecologically significant climatic variables for the general region are mapped by Borchert (1950).

##### *Soil*

The forest soils of the area belong to the grey-brown podzolic soil group and are largely of the Fayette-Dubuque series in the Driftless Area and the Miami-Bellefontaine series in the eastern glaciated area. The topsoils in both series are usually composed of loess or a mixture of loess and residual soil. Profile characteristics are similar throughout the study area. In genera, there is a well-marked dark  $A_1$  layer varying from one-half inch to as many as ten inches in depth, although one to four inches is more typical. The  $A_2$  is not well defined in terms of color but may be detected by textural differences; it is usually one-half to two inches in depth. The brownish B layer generally shows a well-defined nut structure.

##### *General vegetation*

The southwestern half of Wisconsin lies in the broad ecotonal belt between grassland and summergreen forest. In presettlement times its vegetation consisted of scattered prairies, oak openings

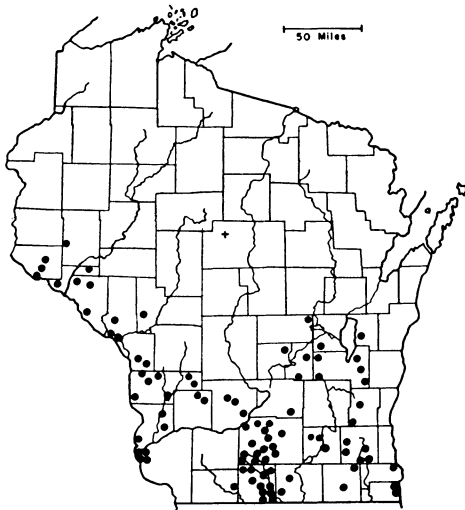


FIG. 1. Map of Wisconsin showing location of stands studied. The cross near the center of the map indicates 90° W. Long., 45° N. Lat.

of savanna-like aspect, and broadleaf deciduous forests of varying density and composition. The present-day stands of natural vegetation are mostly derived from these three communities, although other vegetation types are also present in the form of relics (McIntosh 1950). The deciduous forests occur on a range of topographic sites, from very dry through mesic to very wet. The driest sites, on cliffs, sandy soils and southwest slopes are characteristically covered with scattered stands of small oaks (*Quercus velutina*, *Q. macrocarpa*) or with red cedar (*Juniperus virginiana*) glades. As the moisture conditions improve, the forests become more dense, with a greater number of important tree species. The most mesic conditions commonly support sugar maple, basswood or other species of similar requirements. Wet soil forests are largely restricted to the flood plains of streams and rivers but are found to a limited extent also on the shores of glacial lakes in the eastern portion of the area. Their most characteristic trees are *Ulmus americana*, *Acer saccharinum*, *Fraxinus pensylvanica lanceolata* and *Quercus bicolor*.

Most of the original prairie has been placed under cultivation but small remnants still occur along railroads and highways and occasionally elsewhere. Prairies of several sorts occurred on the same range of topographic types as the deciduous forests (Curtis and Greene 1949). Prairies formed a part of the presettlement vegetation of all counties included in the present study, although the area covered varied from less than one per cent in Richland County to over 50 per cent in LaFayette County. It is estimated that 20 per cent of the total area was in prairie when the first settlement by Europeans began in the 1830's.

#### METHODS

The plan of the investigation used in this work is an adaptation of the mass collection method used by taxonomists (Anderson 1941; Fassett 1941). It is

our conviction that variation in floristic composition is one of the most important characteristics that may be determined in the study of any vegetation, and this may be understood only after a great many examples of the type have been analyzed. It is important that the initial ideas of the type limits be sufficiently broad to preclude the dangers of subjective selection of only those stands which fit a preconceived notion as to what a particular community should be. The only criteria used for the selection of stands in the present study were: (1) that they be natural forests (*i.e.*, not artificially planted) of adequate size, fifteen acres being the minimum, with forty acres or more preferred; (2) that they be free from disturbances in the forms of fire, grazing or excessive cutting; (3) that they be on upland land forms on which run-off waters never accumulate. If a stand fulfilled these conditions, it was studied, regardless of what species of trees might be present. It might be expected that homogeneity would have been a required characteristic, but, as will be shown below, it was found that this could be determined statistically from the data at a later time. If a stand was then found not to be homogeneous, its data were eliminated from the compilations.

A few of the stands were known to us before the study was begun, but the majority were found in response to a circular letter sent out to state and federal forestry agencies, county agents, Soil Conservation Service personnel, and others whose work brings them into contact with woodlands. All of the stands discovered in this way were checked in the field, and, if they met the criteria of selection, they were incorporated in the study. In this way, an essentially random selection of 95 stands in 29 counties was obtained without prejudice as to kind. The geographical distribution of the samples (Fig. 1) was believed adequate to give an accurate picture of the forests of the area.

*Field methods*

Each stand was sampled by use of the random pairs method (Cottam and Curtis 1949). Forty pairs of trees were used for the determination of frequency, density and dominance. Presence was recorded for all vascular species on specially prepared forms which contained the names of the 200 plants most commonly found in upland forests of the region. Frequency of herbs, shrubs and tree seedlings was obtained by 20 quadrats, each  $\frac{1}{4}$  milacre in size. Density was not determined for these forms.

Saplings over 1" DBH were counted in a transect between the two trees of each pair. Since the distance between the trees was variable, the transects resulted in different total areas in each stand and thus prevented the use of frequency as a measure. Density, therefore, is the only type of information available for the saplings. It appears desirable to devise some other methods of sampling saplings in future studies, for in many cases the sample derived by the method described above was inadequate.

As will be shown in detail elsewhere, the random pairs method, using 40 pairs of trees per stand, gives results whose accuracy compares very well with that obtained by the quadrat method. For example, a composite vegetational index (see below) by random pairs for three stands on which adequate quadrat data were also available showed an average deviation of only 2.9% from the index calculated from the quadrat figures. Duplicate analyses by the random pairs method made in three stands in two consecutive years by two sets of investigators showed an average trial to trial variation in the index of only 1.34%. This compares with an average deviation of 2.11% in five sets of quadrats made in as many years in one of the same stands. The random pairs method may therefore be assumed to give reproducible results of sufficient precision for the purposes at hand.

We knew of no way by which the homogeneity of stands could be determined objectively in the field, so it became necessary to devise a method of checking this after the data were collected. Since 40 separate pairs of trees are measured and recorded in sequence in the field, it is possible to segregate the data from successive groups of 10 pairs, each representing a different areal portion of the stand. Using these four groups as separate samples, the Chi-square test for homogeneity (Snedecor 1946) may be used to determine whether the actual occurrences of the major trees in any group deviate significantly from the occurrences expected on the basis of uniform distribution. The requirement of an expected value of at least five individuals in each sample makes this test applicable only to those tree species represented by at least 20 trees in 40 points. These species are the ones which determine the character of the stand in any case and if they are uniformly distributed, deviations on the part of lesser tree species are not likely to be significant. When this technique was applied to the current data it was found that in 95 cases only five Chi-square values exceeded the expected value at the five per cent level. In other words, five of 95 differed significantly from a homogeneous distribution. This approximates very closely the expected number (5 out of 100) of Chi-square figures which would exceed the expected by chance. On this basis it seemed reasonable to accept these as results of chance and reason for not rejecting the stands. This technique may be applied in the field in the future; if a stand is found not to be homogeneous further study will be in order.

Soil samples were collected separately from the A<sub>0</sub>, A<sub>1</sub>, and B horizons in most stands. This was accomplished by the use of three small pits located in representative portions of the wood, with the three subsamples pooled for later analysis.

### *Treatment of data*

The data were tabulated and recorded on standard data sheets. Measures of number, size, and distribution for each tree species were calculated from the figures provided by the random pairs method for each stand. Relative (per cent) density and relative (per cent) dominance were determined in the ordinary manner, but frequency was calculated as percentage sum of frequency or relative frequency (Raunkiaer 1934, Curtis and McIntosh 1950), rather than the more usual simple frequency. The purpose of this change was to place frequency on the same mathematical basis as density and dominance, so that a summation index (density plus frequency plus dominance), with a constant value of 300 for all species in a stand could be prepared. The relative importance of a tree species is more clearly expressed by this method than by the DFD (density-frequency-dominance) index in its original form (Cottam 1948; Whitford 1949, Stearns 1951) where the sum was indeterminate. The index is calculated by adding the separate values of relative density, frequency and dominance for each species. Its magnitude is an excellent indication of the vegetational importance of a species within a stand, since it is sensitive to such variables as apparent contagion or exceptional basal area. This summation index of a particular species within a stand will be referred to herein as its *importance value* in order to differentiate it from the DFD index used by earlier workers. Not only does it differ because of its use of relative frequency, but because frequency as determined by the random pairs method is not strictly comparable to frequency measured by quadrat sampling. Quadrat frequency values bear a mathematical relationship to density values, with a fixed minimum ratio and a variable maximum depending chiefly on the degree of randomness or contagion exhibited by the species (Curtis and Mc-

Intosh 1950). Random pair frequency numbers, however, are more limited, in that they may range from equal to the density, down to one half the density, but they never can be smaller than one half the density values. As a result, frequency numbers usually are close to densities in absolute magnitude. The importance value, therefore, is weighted toward density, in that the number of trees present exerts a greater effect on the index than does their size. This seems proper in a floristic index.

Soil acidity and water-retaining capacity were determined in the laboratory on air-dried samples which were ground with a mortar and pestle and sieved through a 2 mm screen. Acidity was determined by the Helige-Truog method, while water-retaining capacity was measured by the Hilgard method. Analyses for available phosphorus, potassium, magnesium, and for organic matter were made by the Helige-Truog and Wilde methods at the State Soils Laboratory on the University campus. Exchangeable calcium was determined by volumetric analysis, also at the State Soils Laboratory. Nutrient ion concentrations are expressed as pounds per acre for the measured depth and weight of the particular horizon sampled. In the interests of brevity, only the data for the A<sub>1</sub> horizon are presented in this paper.

### RESULTS

One of the difficulties inherent in the "mass collection" method of ecological study is the problem of handling the large quantities of diverse data that accumulate during the course of the investigation. It soon became apparent in the current work that the first requirement was a scheme for organizing or arranging the stands so that suitable comparisons of data could be made. To this end, an attempt was made to classify the stands into groups which had similar structure on the basis of tree composition. However, detailed examination of the data revealed no clear cut distinctions which

would readily separate the stands into such groups without the exercise of a considerable amount of subjective judgment.

It is possible to classify the stands objectively on the basis of the leading dominant trees in each. If the single leading dominant is used for this purpose it would be necessary to recognize 9 types in the 95 stands. The use of the first two tree species in order would necessitate recognizing 30 types; of the first three species, 75 types; of the first four, 95 types. In other words, no two stands of the 95 examined had the same arrangement of their first four most important tree species. The number of units recognized is thus determined entirely by the basis of selection and in no way represents an approximation of any natural groups. Accordingly, we attempted to devise a method whereby each species present in the stand might be taken into account in the classification of the stand. In this way, any tendency of the stands to fall into distinct groups would have maximum opportunity for expression.

A study of the importance values for all species soon showed that only a few species ever achieved high levels of importance. The majority of tree species never occurred as important elements in any of the stands. The ability of a tree species to achieve a given importance value, or what may be termed its importance potential, is the result of various hereditary physiological attributes whose nature is but poorly defined at present. Some species, like *Quercus alba*, reach major dominance in many forest stands covering a wide geographic area. Others, like *Gymnocladus dioica*, apparently never are important members of the forest community in any part of their range. Four tree species—*Quercus velutina*, *Q. alba*, *Q. rubra* and *Acer saccharum*—have an importance potential markedly greater than that of any other trees of southern Wisconsin (Table I). Since they are the major tree components

TABLE I. List of major tree species found in 95 upland hardwood stands of southern Wisconsin with data illustrating importance potential

Species	No. of stands of occurrence	Average importance value	Maximum importance value
<i>Quercus rubra</i>	80	90.4	228
<i>Acer saccharum</i>	45	82.8	201
<i>Quercus alba</i>	86	64.1	202
<i>Quercus velutina</i>	40	62.8	206
<i>Tilia americana</i>	63	39.6	179
<i>Ulmus rubra</i>	53	33.4	140
<i>Quercus macrocarpa</i>	25	24.8	170
<i>Fraxinus americana</i>	28	20.0	94
<i>Prunus serotina</i>	56	17.3	114
<i>Ostrya virginiana</i>	48	16.2	42
<i>Carya ovala</i>	39	15.7	61
<i>Acer rubrum</i>	18	13.3	58
<i>Juglans nigra</i>	21	12.5	30
<i>Carya cordiformis</i>	43	12.2	44
<i>Juglans cinerea</i>	23	12.1	53

of the upland forests of the region, it was decided to study their interrelations as a possible initial basis for community delimitation.

These four species were the leading dominants in 80 of the 95 stands studied. When these stands were placed in groups with the same leading dominant, it was found that seven stands had *Quercus velutina* as the major tree, 18 had *Q. alba*, 34 had *Q. rubra*, and 21 had *Acer saccharum*. The percentage occurrence (constancy, based on a sample of 80 trees in 40 random pairs) of each of the four species and their average importance values were calculated for each of these groups. The results are shown in Table II. The stands in which *Q. velutina* was the leading dominant had a greater average amount of *Q. alba* than of either of the other two tree species, and *Q. alba* was present in a much greater fraction of the stands. In stands dominated by *Acer saccharum*, *Q. rubra* was characteristically second in importance. On the other hand, stands dominated by either *Q. alba* or *Q. rubra* each had two species of about equal rank in second place. Under these circumstances, the most logical arrangement of stands is that indicated in the table, which shows a decreasing order of *Q. velutina* and an increasing order of *A. saccharum*, with *Q. alba* and *Q. rubra* in intermediate positions.



TABLE II. Average importance value (IV) and constancy % of trees in stands with given species as the leading dominant

(For species with highest importance potential only—80 stands)

Species	Leading dominant in stand			
	<i>Q. velutina</i>	<i>Q. alba</i>	<i>Q. rubra</i>	<i>A. saccharum</i>
<i>Q. velutina</i>				
Average IV	165.1	39.6	13.6	0
Constancy %	100.0	72.3	38.3	0
<i>Q. alba</i>				
Average IV	69.9	126.8	52.7	13.7
Constancy %	100.0	100.0	97.1	66.7
<i>Q. rubra</i>				
Average IV	3.6	39.2	152.3	37.2
Constancy %	25.0	94.5	100.0	76.3
<i>A. saccharum</i>				
Average IV	0	0.8	11.7	127.0
Constancy %	0	5.6	29.4	100.0

TABLE III. Average importance value (IV) and constancy % of trees in stands with given species as the leading dominant

(Eleven species of intermediate importance potential—80 stands)

Species		Leading dominant in stand			
		<i>Q. velutina</i>	<i>Q. alba</i>	<i>Q. rubra</i>	<i>A. saccharum</i>
<i>Q. macrocarpa</i>	IV	15.6	3.5	4.2	0.1
	C %	50.0	38.9	20.6	4.8
<i>Prunus serotina</i>	IV	21.4	21.8	5.9	1.4
	C %	87.5	89.0	64.8	19.0
<i>Carya ovata</i>	IV	0.3	8.8	5.2	5.9
	C %	12.5	61.2	38.3	33.3
<i>Juglans nigra</i>	IV	1.5	1.2	2.2	1.9
	C %	12.5	11.1	20.6	23.8
<i>Acer rubrum</i>	IV	3.9	2.3	2.4	1.0
	C %	12.5	33.3	23.5	4.8
<i>Juglans cinerea</i>	IV	0	2.7	1.7	4.8
	C %	0	11.1	20.6	47.6
<i>Fraxinus americana</i>	IV	0	1.9	5.1	7.6
	C %	0	11.1	20.6	42.8
<i>Ulmus rubra</i>	IV	4.6	7.7	8.3	32.5
	C %	25.0	27.8	53.3	85.7
<i>Tilia americana</i>	IV	0.3	5.9	19.0	33.0
	C %	12.5	16.7	73.5	100.0
<i>Carya cordiformis</i>	IV	2.5	5.8	4.1	8.2
	C %	12.5	33.3	41.2	66.7
<i>Ostrya virginiana</i>	IV	0	2.4	5.5	16.2
	C %	0	22.2	41.2	95.3

TABLE IV. Average frequency and constancy % of understory species in stands with given tree species as the leading dominant (80 stands)

Species	Leading dominant in stand			
	<i>Q. velutina</i>	<i>Q. alba</i>	<i>Q. rubra</i>	<i>A. saccharum</i>
<i>Cornus foemina</i>				
Average frequency %	20.0	23.9	16.2	0.0
Constancy %	66.6	100.0	67.8	12.5
<i>Sanguinaria canadensis</i>				
Average frequency %	0	7.5	7.8	14.0
Constancy %	0	35.7	46.5	50.0
<i>Laportea canadensis</i>				
Average frequency %	0	0	0.2	9.4
Constancy %	0	0	3.6	37.5

This ranking of the stands seemed to be in agreement with the general descriptions of the forest series reported for the region and thus gave promise of further fruitful investigation. Accordingly, the same method (based on groups with *Q. velutina*, *Q. alba*, *Q. rubra* and *A. saccharum* as leading dominants) was used to calculate average constancy percentages and importance values for a series of other tree species of intermediate importance potential. The results as shown in Table III have been arranged in a natural order in that those first in the list (*Q. macrocarpa*, *Prunus serotina*, *Carya ovata*) seem to be allied to *Q. velutina* and *Q. alba*, while those placed last (*Carya cordiformis*, *Tilia americana*, *Ostrya virginiana*) are clearly associated with *Acer saccharum*.

Average frequency and constancy

values for several herbs and shrubs were determined for the same groups of stands (Table IV); they showed the same types of distribution, with optimum values in a particular group for each species. Measurements of certain soil characters were also averaged by these groups (Fig. 2) and they too showed similar trends.

The alignment of lesser species with the four major dominant trees shown in Tables III and IV is not very precise, since it does not separate those species which may be associated with the same major dominant. To make further separation possible, the stands were classed into eight groups, based on the two leading dominants in order of their importance values. Thus the stands which had *Q. alba* as the main dominant were split into two subgroups—those with *Q. velutina* as the second most important tree and those with *Q. rubra* as the second tree. Constancy percentages and average importance values were calculated for all species in each subgroup. Some of the results are given in Figure 3. They are arranged with the sequence of the groups based on the information in Table II and with the individual species arranged in order from those most closely associated with *Q. velutina* to those most allied to *Acer saccharum* as shown by the position of the stands in which they reach optimum importance. On the basis of this information, the

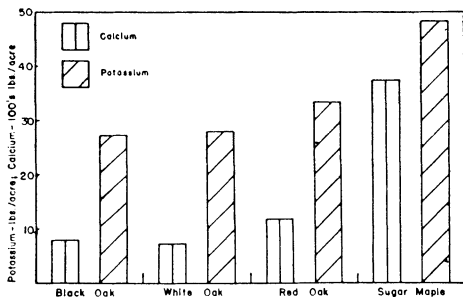


FIG. 2. Available potassium and calcium in the A<sub>1</sub> soil horizon of stands in which the indicated species are the leading dominants.

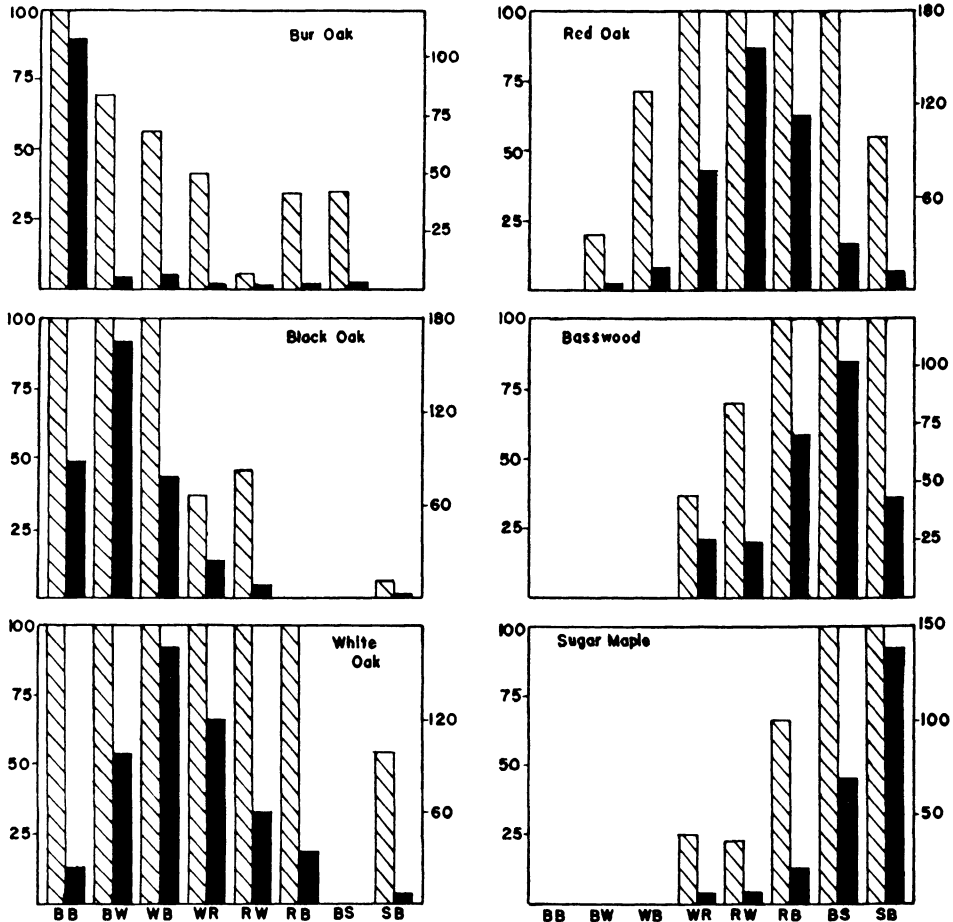


FIG. 3. Average importance value (solid bars) and constancy % (hatched bars) for major species in stands grouped according to the two leading dominants. The scales on the left ordinates are constancy percentages, those on the right ordinates are average importance values. The group of stands are indicated by the paired letters below the graphs, where BB represents the stands in which Bur Oak (*Q. macrocarpa*) is the leading dominant and Black Oak (*Q. velutina*) is the second leading dominant; BW represents stands with Black Oak as first dominant and White Oak (*Q. alba*) as second dominant; WB with White Oak leading and Black Oak second; WR with White Oak leading and Red Oak (*Q. rubra*) second; RW with Red Oak first and White Oak second; RB with Red Oak first and Basswood (*Tilia americana*) second; BS with Basswood first and Sugar Maple (*Acer saccharum*) second; and finally SB with Sugar Maple the leading dominant and Basswood second.

species can be arranged in the following order, from pioneer to climax species: *Quercus macrocarpa* → *Q. velutina* → *Prunus serotina* → *Q. alba* → *Carya ovata* → *Juglans nigra* → *Q. rubra* → *Acer rubrum* → *Fraxinus americana* → *Tilia americana* → *Juglans cinerea* → *Carya cordiformis* → *Ulmus rubra* → *Ostrya virginiana* → *Acer saccharum*.

The method of leading dominants thus served to arrange the stands into groups which showed a reasonable phytosociological pattern but it could not demonstrate the existence of discrete communities since it was based on an artificial, even though objective, choice of unifying species. In addition, it suffered from the vagaries resulting from the calculation

of averages from differing numbers of stands in each group or subgroup. It seemed desirable, therefore, to treat the stands individually, rather than to average them in groups.

To facilitate handling this large amount of data, the moveable strip method was devised. A strip of opaque white celluloid,  $\frac{1}{4}$  inch wide and 10 inches long, was prepared for each stand. The importance value of each tree species in the stand was shown on this strip by means of colored marks, located on the basis of the scale of importance values from 0 to 300. By this method the kinds and relative importance of the tree species in any stand could be determined at a glance, and by placing the strips side by side in a suitable frame, comparison of many stands could be accomplished by inspection. Natural groupings of tree species might be expected to become apparent, if any existed.

The most enlightening arrangement of stands was made on the basis of the information gained from the leading dominant method. The strips were placed so that the importance values of *Q. velutina*, *Q. alba*, *Q. rubra* and *A. saccharum* most nearly approached the order of these species which was indicated in Figure 3. This subjective procedure could not be very precise, but a good approximation was achieved (Fig. 4) as shown more clearly by Figure 5, where the same data are averaged by successive groups of

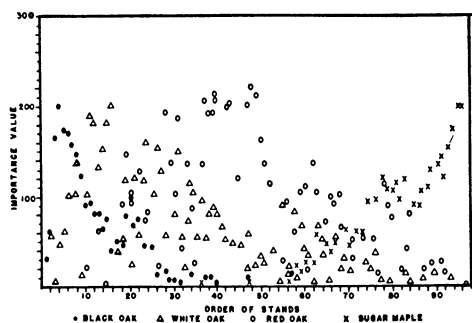


FIG. 4. Importance values of four major species in individual stands arranged in an order most closely approaching that shown in Fig. 3.

five stands, smoothed by the formula:  $(a + 2b + c)/4$ .

The other species were not used in establishing this original rank, but they were found to be distributed in characteristic positions when their importance values in each stand were arranged in the order established above. Figure 6 shows distributions of *Q. macrocarpa*, *Prunus serotina*, *Tilia americana* and *Ostrya virginiana*. *Quercus macrocarpa* and *Prunus serotina*, on the basis of their distribution relative to the major species, are seen to be more nearly akin to the pioneer species, while *Ostrya virginiana* and *Tilia americana* are seen to approach the climax species, thus substantiating the results of Figure 3. The remainder of the species are distributed similarly when plotted in this way.

The relative position in which each species approaches its optimum development can be fixed by means of diagrams similar to Figures 5 and 6 where sufficient data are available. The breadth of any of the figures and the absolute position of the mode would be changed if more stands were added to the series. However, the relative position remains essentially the same once a sufficient number of points is available. At the end of the first year's study, with data available for only 60 stands, the curves for the major species were well established in the same relative positions as given by the final data on 95 stands.

A study of all the figures shows that each species has a minimum, an optimum and a maximum point for development, with the points located by reference to similar states for other species. The only exceptions are *Q. macrocarpa* and *Acer saccharum*, which lack one of the cardinal points due to their location at opposite ends of the series within the limits of the study. It is to be emphasized that the optimum points for each species are purely relative. The strip method can show that *Juglans nigra* reaches its best development in forest stands which are intermediate between

stands dominated by *Q. alba* and others dominated by *Q. rubra* but it cannot give a precise measure of the difference. Nevertheless, the arrangement of stands provided by this method shows that the tree species found in the upland hardwoods of southern Wisconsin form a continuous series, with overlapping ranges but distinct conditions for optimum development of each species. No discrete groupings of species are apparent; rather, the entire assemblage forms a continuum.

*Climax adaptation numbers*

The above results indicate that each tree species reaches its optimum development in stands whose position is fixed in a definite relationship to the other tree species. The sequence of the species in this pattern is such that pioneer species are at one end and climax species at the other. Pioneer and climax are here used in their adjectival sense and refer to the entire syndrome of specific physiological attributes which enables the one to live in the high light, variable moisture and immature soil conditions of initial stands and the other in the low light, medium moisture and mature soil conditions of the terminal forests.

The results of this study, as well as those of other investigations in this area, indicate that *Acer saccharum* is the tree species best equipped to persist in the terminal forests of the area. All other species are less efficient in this respect, and their relative degree of "climaxness"

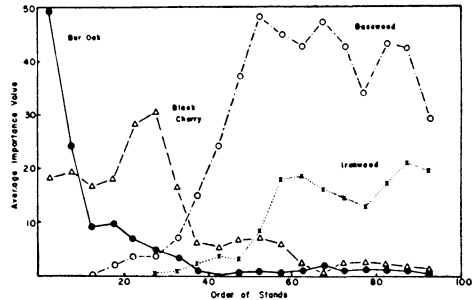


FIG. 6. Importance values of four lesser species, arranged in the order given in Fig. 4 and averaged by successive groups of 5 stands.

may be evaluated by the spatial relations of their optimum development curves as illustrated in Figures 5 and 6. Thus *Tilia americana*, whose highest importance values are reached in stands near the *A. saccharum* end of the pattern, is better adapted to terminal forest conditions than *Q. rubra*, with a peak closer to the middle of the series, while *Q. macrocarpa*, which is most important in stands remote from those dominated by *A. saccharum*, is the least well adapted.

Using *Acer saccharum* as a standard, all other species can be rated on the basis of the distance of their optimum stands from those dominated by *Acer*. The rating was accomplished by arbitrarily assigning a relative value of ten to *A. saccharum* and lesser numbers to the other species according to their position, as shown in Table V. Those species designated by an asterisk are tentatively placed with an approximate value inasmuch as they occur only rarely in the samples and thus their position is not clearly established by the few points available.

The choice of suitable words to designate the two ecologically distinct ends of the series is a troublesome one. The word "climax" for the terminal end is especially doubtful, since it already has a plethora of meanings and probably would not be defined the same by any two practicing ecologists. It has been suggested that the term "mesophily," as employed by Dansereau (1943), be used in the

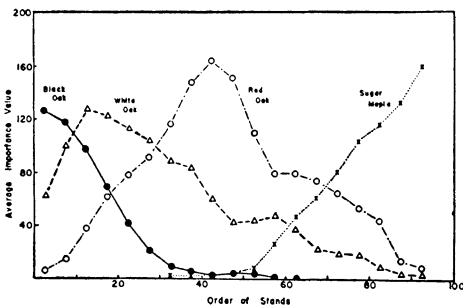


FIG. 5. Same data as in Fig. 4 averaged by successive groups of 5 stands.

TABLE V. *Scientific and common names of tree species found in stands studied, with the climax adaptation numbers of each*

Scientific name	Common name	Climax adaptation number
<i>Quercus macrocarpa</i> Michx.	Bur oak	1.0
<i>Populus tremuloides</i> Michx.	Trembling aspen	1.0
* <i>Acer negundo</i> L.	Boxelder	1.0
<i>Populus grandidentata</i> Michx.	Large-tooth aspen	1.5
<i>Quercus velutina</i> Lam.	Black oak	2.0
<i>Carya ovata</i> (Mill.) K. Koch	Shagbark hickory	3.5
<i>Prunus serotina</i> Ehrh.	Black cherry	3.5
<i>Quercus alba</i> L.	White oak	4.0
<i>Juglans nigra</i> L.	Black walnut	5.0
<i>Quercus rubra</i> L.	Red oak	6.0
<i>Juglans cinerea</i> L.	Butternut	7.0
* <i>Ulmus thomasi</i> Sarg.	Rock elm	7.0
* <i>Acer rubrum</i> L.	Red maple	7.0
<i>Fraxinus americana</i> L.	White ash	7.5
* <i>Gymnocladus dioica</i> (L.) Koch	Kentucky coffee tree	7.5
<i>Tilia americana</i> L.	Basswood	8.0
<i>Ulmus rubra</i> Muhl.	Slippery elm	8.0
* <i>Carpinus caroliniana</i> Walt.	Blue beech	8.0
* <i>Celtis occidentalis</i> L.	Hackberry	8.0
<i>Carya cordiformis</i> (Wang) K. Koch	Yellowbud hickory	8.5
<i>Ostrya virginiana</i> (Mill.) K. Koch.	Ironwood	9.0
<i>Acer saccharum</i> Marsh	Sugar maple	10.0

\* Climax adaptation number of these species is tentative, because of their low frequency of occurrence in this study.

present case instead of climax. It is true that the climax plants here discussed are extreme mesophytes, in the sense that they achieve optimum development only in habitats of medium and relatively constant conditions of both atmospheric and edaphic moisture. However, it is equally true and probably of greater significance that these climax plants are shade-loving plants (sciophytes) able to grow and reproduce in conditions of very low light intensity. For the most part they are also plants of high nutrient demands, with tendencies toward partial heterotrophism. They are therefore not median with respect to light or nutrition and the use of the word "mesophily" might carry unfortunate connotations. It would involve an extension of meaning as great as in the case of "climax." What is perhaps needed is a word to encompass all of those adaptive physiological and morphological characters that differentiate plants of initial stands from plants of terminal stands. In the absence of such a word, we have deemed it best here to use the phrase "climax adaptation" as a tentative description of these characters, and to call the relative values as-

signed to each species "climax adaptation numbers." High numbers indicate good adaptation to all of the environmental factors present in terminal stands while low numbers indicate adaptation to the conditions of initial stands. This admittedly unsatisfactory compromise at least has the merit that it does not unduly emphasize one factor in an obviously multiple factor situation even though it does further burden the already overworked word climax. "Succession number" has been suggested, but it is inadequate, since an intermediate stage in the series may be reached by retrogressive as well as by successional processes.

A comparison of these climax adaptation numbers with the shade tolerance ratings of foresters indicates that they are roughly parallel. This is not unexpected, since the characteristics that contribute to great shade tolerance are largely the same as those that make for persistence in terminal stands. The method used here in establishing the climax adaptation numbers may offer a supplement to the usual procedures for the subjective determination of

shade tolerance. It offers greater possibility of refinement than the coarse, qualitative estimates generally used. It must be recognized, however, that the application of this type of rating is only feasible within the bounds of a single floristic province, since shade tolerance as measured by the adaptation number of a species may vary in other areas with different component floras.

*Vegetational continuum index*

To establish a basis for evaluating forest stands in terms of their total tree composition it was decided to use the climax adaptation number of each tree species as a means of weighting its importance value as determined from the sampling data. The adaptation number of each species (as given in Table V) was multiplied by its importance value in a particular stand. The products were added and the resultant weighted total used as a basis of placing the stand in its proper relation to other stands. The maximum possible range of these weighted numbers is 2,700 units from 300 to 3,000. A stand composed entirely of *Q. macrocarpa* or a mixture of *Q. macrocarpa* and *Populus tremuloides* would have a sum of 300; a stand composed solely of *A. saccharum* would have a sum of 3,000. A stand consisting of mixtures of species whose climax adaptation numbers lie between one and ten would have a sum somewhere between these extremes. This range of

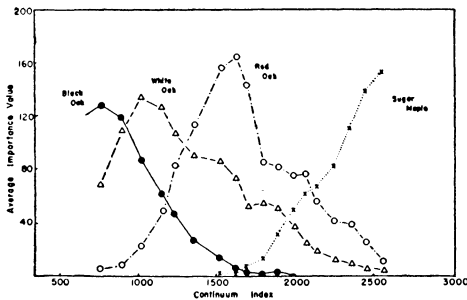


FIG. 7. Importance values of four major species arranged in numerical order of continuum index and averaged by successive groups of 5 stands.

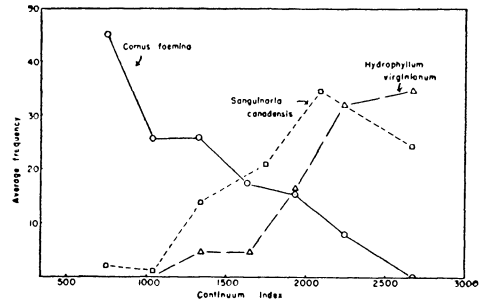


FIG. 8. Average frequency values of three herbs, arranged in order of continuum index.

weighted numbers is termed the *vegetational continuum index*. A continuum index value was calculated for each stand in the study. When the celluloid strips for each stand were arranged in the numerical sequence given by these index values (Fig. 7) it was found that the distributional pattern for each of the tree species retained the same relative position as before.

The vegetational continuum index is actually a means of utilizing all of the tree species in a stand to express the position of that stand on a gradient. Major importance in assessing the position of a stand falls upon those species which have a high importance value but each of the other tree species contributes in some degree.

Tree reproduction is distributed on the vegetational continuum index in a pattern similar to that of the mature trees. The reproduction should possibly be used to further weight the position of a stand in the vegetational continuum index, but, as indicated earlier, the sampling method used in this study gave inadequate data on saplings in most cases and therefore such weighting was not attempted.

Herb and shrub species which played no part in developing the vegetational continuum index were found to be distributed on it in patterns similar to those of the tree species. The distributions of certain shrub and herb species is illus-

trated in Figure 8. They are found to form curves with characteristic minimum, optimum and maximum points for development. These curves locate the lesser species relative to the tree species and to each other. Some herbaceous species, unlike most trees, are found to cover the entire range of stands, but it is nevertheless possible to predict with reasonable accuracy the important herb species to be found in stands in any given range of the vegetational continuum index.

Soil factors also may be related to the forest cover by means of the vegetational continuum index. The relation of exchangeable calcium and of soil reaction to the index is shown in Figures 9 and 10. The values in these graphs were

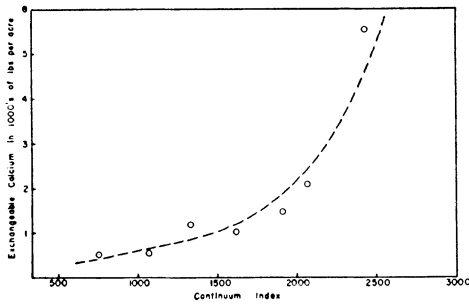


FIG. 9.

obtained by averaging successive groups of three stands for which data were available. Similar correlations were obtained with the water retaining capacity and the organic matter content.

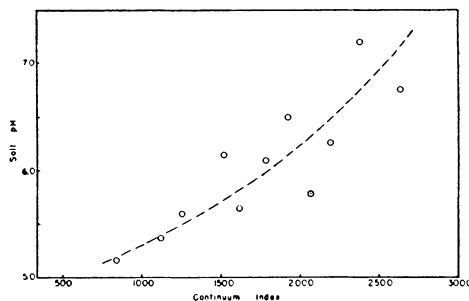


FIG. 10. Acidity of the A<sub>1</sub> layer in stands arranged on the continuum index.

## DISCUSSION

Three possibilities as to the nature of the upland hardwood forests of this area may be postulated. The first of these is that the forests represent an amorphous collection of plants in which no units or patterns are discernable. In other words, they are chance aggregates according to the viewpoint of Mason (1947) and are dependent solely on a "coincidence of tolerance" between plants and environment. The presence of a pattern definable in terms of tree composition and the demonstration that trees and other plants are not found together in chance mixtures but in a rather definite pattern would indicate that this interpretation is not tenable in the present case.

Secondly, one could maintain that these forests represent several discrete communities, distinguishable from each other by boundaries which are reasonably distinct in terms of the measurements available to the plant ecologist. If this were true, then determination of the relative sociological importance of the trees in each stand should show that certain groups of tree species reach their optimum development in the same stands, while other groups occur together in other stands. If the boundaries between communities are actually distinct, then the species of one group should never occur as important members of another group. The results of this study indicate that such a discrete grouping of species does not occur in Wisconsin. Rather, each species reaches a high level of importance in only a few stands, with no groups of two or more species showing optimum development in the same stands.

It is thus necessary to accept the third possibility, namely that the upland hardwoods of southwestern Wisconsin represent a continuum in which no clearly defined subdivisions are discernable but in which a definite gradient is exhibited. If this is truly the case then the entire physiognomic upland hardwood forest is to be interpreted as an entity (or por-



tion of an entity) without discrete subdivisions. The failure of any one or any group of the environmental factors measured to indicate any separation substantiates the conclusion of unity based on the tree data. The presence in certain of these environmental factors of some indication of a gradient or trend related to the tree gradient is further indication that these forests represent a continuous cline from initial stages composed of pioneer species to terminal stages composed of climax species.

This conclusion would appear to substantiate the individualistic association hypothesis of Gleason (1926) and its emendation by Cain (1947). It differs, however, in that "unlimited variables, combinations and permutations" (Cain) do not occur. All things are not possible, only some, and these possible permutations seem to follow a pathway prescribed by the physiological potentialities of the available flora within the limits of the existent physical environment as modifiable by that flora. Within a given floristic province, the amplitude of environmental tolerance of each species is more limited than the full range of environment in that province. Furthermore, although the tolerance range of each species may overlap that of many other species, the range for optimum development of each species is different from that of all other species. There are, therefore, no groups of tree species which regularly occur together and only together, except for accidental duplications of narrow environmental ranges. Rather, tree species occur in a continuously shifting series of combinations with a definite sequence or pattern, the resultant of a limited floristic complement acting on, and acted upon by, a limited range of physical environmental potentialities. Such a gradient of communities is here called a vegetational continuum, to differentiate it clearly from the controversial concept of a plant association. As applied to forests, it is similar in scope to the "sylvan continuum" of Darling (1949).

The geographical limits of this continuum outside of Wisconsin are not known at present, but it appears that southeastern Minnesota, northeastern Iowa and northern Illinois are definitely included. There are indications that the upland forests on the southern border of the prairie peninsula are similar also, especially those in Missouri, Nebraska (Aikman 1926), Arkansas (Arend and Julander 1948) and Kentucky. This is perhaps to be expected on the basis of climatic similarities (Borchert 1950). The continuum throughout is intimately associated with the prairie-forest border. Its major trees are better adapted to xeric conditions, particularly those associated with periodic severe summer droughts, than are most other species of the deciduous forest. It has borne the brunt of repeated prairie advances in post-Wisconsin time and possibly in earlier interglacial periods as well (Lane 1941, McComb and Loomis 1944). As a result, it is probably simpler in both floristic composition and developmental pattern than the forest aggregations farther east and south. It is recognized that this simplicity was an important factor in the recognition of the continuum pattern and that similar patterns may be more difficult to ascertain in other regions of greater floristic variety.

If the vegetation of a particular physiognomy on a particular topography in a particular floristic province (*i.e.*, deciduous hardwood forests on the uplands of southwestern Wisconsin) forms a continuum without identifiable individual segments, as is the contention of the present paper, then certain far-reaching implications are apparent. Without at this time entering the perennial argument concerning the relative scope of the word "association" as used by American and European workers, it is obvious that both groups usually apply it to discrete communities which are thought to be recognizable as distinct entities in the field. It is on this characteristic that the whole series of "synthetic" characters of

plant communities was erected by Rübél (1922), Braun-Blanquet (1927) and other European workers. Such well-established community measures as presence, constancy, and fidelity become of greatly restricted value when applied to stands which form a continuum. For example, in the present case, a number of herbs are known which may be found in almost every initial stand in which the leading dominant is *Quercus velutina* and thus would have a high degree of presence or constancy in those stands. All of them, however, also occur in lesser amounts and in a smaller percentage of the stands which are dominated by *Q. alba*. This diminution continues in the *Q. rubra* stands and most of the species become very rare or absent in the terminal *Acer saccharum* forest. A similar situation in reverse exists for a group of species most common in the *Acer* stands. The absolute value of presence or constancy, therefore, is determined almost solely by the amplitude allowed by the investigator in his choice of stands to be studied. If a large portion of the continuum is used, then all species except the most ubiquitous and least demanding have very low values of presence and constancy. These ubiquitous species are commonly found in nearby non-related assemblages and hence are of very low value as community indicators in any case. As the portion of the continuum used becomes restricted in scope, then the presence and constancy values increase in magnitude. As we have seen, however, scarcely any two stands exist which have precisely the same complement of tree species, to say nothing of the more numerous herbs, and hence, presence and constancy values rarely achieve truly high levels.

It appears probable from preliminary observations that the lowland forests (which receive at least temporary accumulations of run-off water) of this area will eventually prove to be part of the same continuum herein discussed. If this should indeed be the case, then the

synthetic characters would be still further reduced in usefulness, since their arithmetic values would be of very low magnitude. Presence and constancy may continue to maintain their useful roles in phytosociology if each investigator accompanies them with a detailed account of the limits set by him on the range of communities included within his study. When used in this way, the synthetic characters may be very valuable, particularly in comparative studies, as between grazed and non-grazed woodlots or the like.

It is hoped that the concept of a vegetational continuum and the methods for its analysis as developed in this paper will prove to be widely applicable to the forest stands of other regions. Whether or not all floristic provinces have similar continuous gradients rather than recognizably discrete communities is not known at present, although a few studies based on the analysis of many stands in a single region (Hanson and Whitman 1938; Whittaker 1948; Allen 1950; Potzger 1950) clearly indicate that similar continua are present. Dyksterhuis (1949) also shows a continuously varying composition of grassland under the impact of overgrazing which is essentially similar to the forest continuum here described.

In those areas in which its construction is possible, the vegetational continuum index offers a new approach to ecological studies of many types. It may be used to describe local deviations in tree composition such as occur when pioneer species enter spot openings in a mature forest resulting from a restricted fire or other disturbance and such other situations as are included in the "gap phase" concept of Watt (1947). Autecological studies of an herbaceous species may be conducted in stands which are known to be optimum for the development of that species and comparative life history studies of groups of species may be made readily in stands known to be similar on the basis of trees and soils. The index

provides a more detailed framework for the study of the relation of random and contagious distributions of herbaceous species in relation to age of occupancy as discussed by Whitford (1949). Mammal, bird, insect or other animal populations, their fluctuations and interrelationships, are all inseparably interwoven with plant communities. One of the major difficulties heretofore encountered in studies of natural animal populations has been the lack of an adequate means of delimitation of the nature of the plant segment of the habitat complex. The vegetational continuum index affords a more accurate means of describing this habitat factor and in addition immediately places a stand in its proper relation to other stands. As further information is collected on the correlations between the physical factors of the environment and the index and on the relations of the microbiota or other special groups of organisms to the index, it will be possible to summarize a very considerable amount of information by means of an index number. There is no thought here that the index will serve as the final touchstone of phytosociologists, nor that the complex of physical and biological agents of importance in a community can possibly be reduced to a single number. The index rather should serve as a framework upon which a great amount of independently derived information may be arranged and interrelated.

#### SUMMARY

1. The upland hardwood forests of the prairie-forest floristic province of southwestern Wisconsin were studied by means of a random sampling of undisturbed stands distributed through 29 counties covering an area 160 miles by 230 miles. Data on tree, shrub, and herb composition were obtained in 95 stands by the random pairs method of sampling. Soil acidity, nutrient concentration and moisture constants were also determined for these stands.

2. The relative ecological importance of each tree species in each stand was expressed by a summation index of the relative frequency, relative density and relative dominance herein called the *importance value*. This value has a constant total of 300 for each stand.

3. Four tree species (*Quercus velutina*, *Q. alba*, *Q. rubra* and *Acer saccharum*) attained an average importance value in all stands much higher than that of any other species. When the stands were arranged into groups each dominated by one of these four species, it was found that each of the lesser tree species was associated with one of the groups. Further breakdown of the stands into subgroups according to the second most important species, resulted in a more accurate alignment of all species into a series beginning with the pioneer species, *Quercus macrocarpa*, *Populus grandidentata*, and *Quercus velutina*, and ending with the climax species *Ostrya virginiana* and *Acer saccharum*. Each species reached optimum development at a given point along this series, but no groups of species were found which achieved their peak in the same stands. Thus no discrete communities could be detected on the basis of the leading dominants in the stands.

4. Use of a strip method for visual comparison of the importance values of all species in each stand resulted in a ranking or order of stands which agreed with the order obtained from the leading dominants. The initial stands in the rank were composed of shade-intolerant, non-mesic, pioneer species, while the terminal stands contained the very shade-tolerant, mesic climax species. Upon the assumption that *Acer saccharum* was the most successful species in the terminal forests, it was possible to arrange all other tree species in a descending order according to the position of the stands in which they reached optimum development, relative to the stands containing *Acer saccharum*. Arbitrary numbers from one to ten, called *climax adaptation*

numbers, were assigned to the species to indicate the degree to which they approach the climax *Acer* in autecological characteristics. For the more important trees of the region, the adaptation numbers are as follows: *Quercus macrocarpa*—1.0, *Quercus velutina*—2.0, *Carya ovata*—2.5, *Prunus serotina*—3.5, *Quercus alba*—4.0, *Quercus rubra*—6.0, *Ulmus rubra*—7.0, *Tilia americana*—7.5, *Ostrya virginiana*—8.0, and *Acer saccharum*—10.0.

5. The climax adaptation numbers were used as a means of weighting the importance values of each species in a stand, as determined by field sampling. The summation of these weighted numbers resulted in an index which served to locate the stand along a gradient. All species present contributed to the index, with the greatest effect exerted by the dominant species. On this basis, the 95 stands studied were distributed uniformly between an index value of 632 and a value of 2,650 (out of a possible range from 300 to 3,000). No distinct groups of stands were apparent—rather the entire series of communities formed a continuum in which a definite gradient was exhibited from initial stages composed of pioneer species to terminal stages composed of climax species. Such a gradient of communities is here called a *vegetational continuum*.

6. Herb and shrub species were found to be distributed in typical patterns when their frequencies were plotted against the continuum index. Each of these understory plants was restricted to a particular range on the index—each reached optimum developments only within a particular group of closely related stands. Various measurements of soil properties showed a good correlation with the index. This was especially true of the concentration of available calcium, the water retaining capacity and the organic matter content of the A<sub>1</sub> soil layer.

7. It is suggested that the vegetational continuum index may be a useful tool for the coordination of much independ-

ently derived information on animal populations, microbiota, and physical factors of the environment.

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