THE SAVANNA VEGETATION OF WISCONSIN AND
AN APPLICATION OF THE CONCEPTS ORDER
AND COMPLEXITY TO THE FIELD
OF ECOLOGY

A thesis submitted to the Graduate School of
the University of Wisconsin in partial fulfillment
of the requirements for the degree of Doctor of
Philosophy.

by

John Roger Bray

Date August 3, 1955
To Professors: Curtis Cottam Stauffer

This thesis having been approved in respect to form and mechanical execution is referred to you for judgment upon its substantial merit.

Approved as satisfying in substance the doctoral thesis requirement of the University of Wisconsin.

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CHAPTER I

INTRODUCTION

This thesis on the phytosociology of savanna is presented as a contribution to a continuing project which will eventually include all the plant communities of Wisconsin. The project, started in the late 1940's by Dr. J. T. Curtis and his students, has, as one of its goals, a statement of both the compositional structure and relationship of Wisconsin communities. Since savanna in Wisconsin is transitional to two major North American formations, prairie and deciduous forest, this present study will attempt to examine the nature of the transition as well as the structure of the various savanna communities.

The term "savanna" has today largely lost its tropical connotations and is defined as all grasslands in which there are scattered open grown trees. Savanna probably forms a part of all temperate and tropical grassland and usually exists as a broad ecotone region bordering on forest. The definition of savanna given above is an exact one -- a degraded forest where trees were closed grown is not a savanna, nor is the ecotone between taiga and tundra properly a savanna, for although the trees have a parkland aspect, the ground cover is not primarily grassy.

This section of the thesis is entitled the "Savanna Vegetation of Wisconsin" and includes all those natural areas
which fit the above definition, from the cedar glades through the oak openings to the elm-ash groves. In all these stands, prairie was or is the ground cover and all of the trees are open grown. There are several words which are descriptive of savanna types. Oak-opening is the term which was originally used by many Wisconsin settlers as they emerged into the more open canopies of the Middle Western oak woods. Oak or elm grove is a common word among farmers and means a clump of usually open grown trees which are without understory. Oak island is also used, especially in the counties which were primarily prairie and where the oak grove loomed as an island ahead of the settlers moving through the tall grasses. The word, "wood", is in its stricter ecologic sense, an open canopied stand of trees as contrasted to a closed canopy forest. This distinction was also made by settlers and is sometimes used by farmers today with the additional connotation that a woods is something one can see coming to an end whereas a forest stretches on interminably.

Areas which contained fire degraded forests with shrubby trees and grubs were called "barrens" since the early settlers assumed the skimpiness of the tree growth was due to the sterility of the soil. Many of the original barrens quickly grew into forests and the term barren later came to apply mostly to sand areas, usually with an acid soil, where there were scattered black or Hill's oaks, shrubby growth and the continued presence of fire.
Around many oak groves and at the buffer edges of oak woods where the trees were open grown, there was a fringe of one or more of the following woody shrubs: hazel, dogwood, wild plum, wild crab, and sumach. These fringes extended from ten feet to a fairly broad band (Gleason, 1954) and were called ruffs by the early settlers after their resemblance to the Elizabethan collar. (Vestal, 1954).

The cultural and scientific value of savanna is sufficiently great to justify the careful preservation and maintenance of scattered pieces of different savanna types throughout the Middle West. Culturally they represent a vegetation which once covered a large land surface and which sheltered both the original European settlers and their cattle, when they first entered the region. Almost every major Mid-Western university was built, at least in part, in savanna; and outside the windows of their biology buildings, it should always be possible to see the bur oak trees which now grow there.

From a recreational standpoint, savanna deserves special protection since it is the only place where one can sit and relax beneath the shade of a tree and enjoy the beauty of the colorful prairie flora.

The scientific value of savanna lies in its representation of a vegetation which developed an integrated community under a disturbance which was largely the result of man's
activities. It is also a place where critical studies can advantageously be made on the interrelations of environmental factors, especially those of light intensity, relative humidity and soil moisture.

It is with very sincere appreciation that the author acknowledges the aid of the many individuals who have helped in this study.

Dr. J. T. Curtis, who supervised the overall project and created the phytosociologic climate in which the work took place, provided stimulating advice and valuable criticism throughout the study.

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CHAPTER II

LITERATURE REVIEW

Historic

Much of the early history of savanna has been extensively reviewed by Gleason (1923), Stout (1944), and Anderson (1954), and the general history of the change from savanna to forest outlined by Cottam (1949). This section will review some specific aspects of these historic descriptions.

Every discussion of savanna should include the description of bur openings of Cooper (1893) from the notes of Boden which were made near Kalamazoo, Michigan, in 1812: "In places they stand with a regularity resembling that of an orchard; then, again, they are more scattered and less formal, while wide breadths of the land are occasionally seen in which they stand in copses, with vacant spaces, that bear no small affinity to artificial lawns, being covered with verdure." Bayley (1954) describes the oak openings in Wisconsin in the 1840's as "covered with trees about as far apart as in a common orchard", and Stout (1944), says of Albion Opening, "These oaks are all broad-topped and so spaced that seldom are the branches of two trees interlocked".
In 1766, Carver (1838) describes the lead hills which were visible to the southwest for a distance of 30 miles, from somewhere immediately above Sauk City on the Wisconsin River: "Only a few groves of hickory and stunted oaks covered some of the valleys. For many miles nothing was to be seen but lesser mountains which appeared at a distance like haycocks, they being free of trees". Keating (1834) on a trip between Chicago and Prairie du Chien in 1823 relates: "The only defect which we observed in the country between Chicago and the Mississippi is the scarcity of wood, which is more seriously felt on the west side of the Rock River, than to the east of it", and "The woods consisted of small oaks without undergrowth". The small size of bur oaks is noted by Cooper (1893), who describes the trees as "low oaks" of "very uniform size, being littler taller than pear trees". The evidence from Albion (Stout, 1944) is that the trees started growth around the 1740's. The early descriptions of small trees by Carver, Keating, and Cooper might, therefore, be some indication that the openings were young at that time.

The extent of savanna has been indicated by Cottam (1949) who reviewed studies of land survey records and concluded that within the southern upland forest, oak opening covered most of the land surface which was not true
prairie. Curtis (1950) shows the vegetation of the state around 1840 with over one-half of the land within the southern forest covered by oak. When the surveyor's records have been completely analyzed for trees per acre, the area of the oak woods, which was sufficiently open to be considered savanna, can be determined.

The descriptive records from county histories also provide evidence for the extent of savanna. Lapham (1846), states of Dane County: "there are no considerable portions that can be called timber land, it being almost entirely oak opening or prairie". Guernsey and Willard (1856) write of Rock County: "This county is about equally divided between prairie and oak openings." A good description is available of the early relationship between savanna and prairie. "On Rock River is a belt of timber and openings. Groves are interspersed through the prairies at intervals besides which, points of openings jut into the prairie at different places, thus rendering the outlines of the prairie unequal, and at the same time bringing wood and timber within a short distance to all its settlers; in fact, few men on the prairies live more than three miles from timber". (Guernsey and Willard, 1856).

Probably the earliest description of the shrubby growth of grubs is by Carver (1838) who describes what he considers a separate species of oak: "Like that it bears an acorn, but it never rises from the ground above four
or five feet, growing crooked and knotty." The town of Perry in Dane County is described by the Western Historical Society (1880) as being covered in its native state with brush and grubs. Muir (1913) states: "When an acorn or hickory nut had sent up its first season's sprout a few inches long, it was burned off in the autumn grass fires; but the root continued to hold on to life, formed a callus over the wound and sent up one or more shoots the next spring. Next autumn these new shoots were burned off, but the root and calloused head, about level with the surface of the ground, continued to grow and send up more shoots, and so on, almost every year until very old, probably for more than a century, while the tops, which would naturally have become tall broad-headed trees, were only mere sprouts seldom more than two years old. Thus the ground was kept open like a prairie, with only five or six trees to the acre, which had escaped the fire by having the good fortune to grow on a bare spot of the door of a fox or badger den, or between struggling grass-tufts wide apart on the poorest sandy soil."

The use of fire by man in burning vegetation has been reviewed by Stewart (1951) and Eisely (1954). Stewart discusses more than ten reasons for burning and remarks that he found, in preparing his article, over 200 anthropological references to burning by North American Indians. Anderson (1954) quotes extensive descriptions of fire in Wisconsin.
Almost all the historic references consulted in this review mentioned fire. Lapham (1846) states: "and besides this, the fires that have annually raged over the surface often kindled purposely by the Indians on their hunting excursions...." Bayley (1954) says the: "fires sweep over these [the openings] as over the prairies every year, but the thickness of the bark is such that the trees are rarely killed by it. Where the fire is kept off, these openings soon become covered with a vigorous growth of young timber". Sargent (quoted in Cheney, 1944) describes the stopping of fires as resulting in the openings "losing their open, park-like character by the appearance of a young growth which has sprung up among the old trees". Guernsey and Willard (1856) state: "...besides the openings are annually burnt over, like the prairies", and Muir (1913) says the oak openings of Wisconsin were swept by running fires almost every autumn after the grass became dry. If there were no autumn fires the openings would burn the next spring.

The appearance of European man and his agriculture largely stopped or localized fire. A description of farming in the early openings is given by Bayley (1954): "The roots of both these [bur and white oaks] strike down so that they are not in the way of the plough and it is no uncommon thing to see large fields of wheat with the trees all standing but girded to prevent the foliage shading the ground."
With the stopping of fire there was a rapid appearance and growth of timber. Bayley (1954), Warder (1881) and Sargent (cited in Stout, 1944) report this sudden appearance without offering any explanation other than the stopping of fire. Cheney (1894) considers rapid re-timbering to be the result of oak, elm, and cottonwood seeding, while Muir (1913) describes it in terms of the growth of grubs. Muir's description completes the history of the oak openings: "The uniformly rich soil of Illinois and Wisconsin prairies produced so close and tall a growth of grasses for fires that no tree could live on it. Had there been no fires, these fine prairies, so marked a feature of the country, would have been covered by the heaviest forests. As soon as the oak openings in our neighborhood were settled, and the farmers had prevented running grass-fires, the grubs grew up into trees, and formed tall thickets so dense that it was difficult to walk through them and every trace of the sunny "openings" vanished."

**Ecologic**

The many good descriptive and historic accounts of savanna contrast with the almost complete absence of quantitative phytosociologic studies. Only one reference was found to a stand of open grown bur or white oaks in which shrubs studied.
which the native shrubs and herbs were studied. The majority of ecologic references are to either the origin and general nature of savanna, or to the composition and environmental relations of the shrub and thicket borders between forest and prairie. There are also many references to sand barrens in which the tree cover is usually scattered oaks or pine.

A work on the savannas of the world, outside the tropics, has been published by Funk (1927) with especial emphasis on Russia and North America. Funk is a geographer who follows the "landscape" school of Passarge in a manner similar to that used by the historian, Malin, on the North American grasslands. Funk considers savanna to be a: "Raublandschaften"; that is, one which is despoiled, and regards fire as a major savanna factor. He believes, as does Clements, "The best indication of the fluctuating climate and soil relationships of savanna is the vegetation of the region".

Among references to European savanna, Funk lists Rudnyskyj (1916), who states the forest in the governmental district of Poltawa was reduced from 13 percent to 4.7 percent by burning from 1850 to 1900. Another reference is to Krylow (1915) who divides savanna into three sub-zones based on the percent coverage of the forest. Krylow apparently considers any area with 60 percent forest to
be no longer savanna since his first zone, Die Rasenwiesenunterzone, is covered with from 45 to 60 percent forest.

In discussing North American savanna, Funk closely follows Gleason (1923) and the early descriptive accounts of Russell (1904) and Baker (1911).

Gleason's discussion of vegetational history (1923) and his early papers on groves and prairie fires (1912, 1913), have been a basis for much subsequent work and will be discussed in Chapter XII.

The major importance of fire in savanna which was outlined in the historical section of this chapter has also been noted for other areas of the Mid-West outside Wisconsin.

Welch (1929) lists the woody plants of the groves in Benton County, Indiana, in an area which was once almost entirely covered with prairie and slough. The two bur oak opens in the county occurred at the heads of streams unprotected from the west by a pond or lake. The other groves, which contained a larger number of woody plants including intermediate tree species as red oak and basswood, were on the north or northeast side of a pond, lake, or spring. The only grove which contained sugar maple was on the southeast side of a morainal ridge.

Vestal (1914) states for an area west of Chicago, Illinois: "The forest is to the east of a line of sloughs, which may have served to protect it from the inroads of
prairie fires." Shimek (1915) found 26.5 percent forest to the west of streams in the Lake Okoboji region in Iowa and 73.5 percent on the east side.

While admitting the importance of fire in forest border regions, general studies of prairie in the Mid-West, in which savanna is considered, agree that fire is not the only agent which causes an absence of trees. Shimek (1915), for example, observes that even without fire, the bluffs and "exposed" surfaces of Iowa remain prairie. Both Transeau (1935) and Borchert (1950) consider the climate of the prairie peninsula to be favorable to grassland. Transeau concludes: "Fire as an ecologic factor seems to boil down to this: that in forest climates it retards development and may result in scrub, but it does not result in prairie. In a prairie climate it helps maintain and perhaps rarely enlarges the prairie."

Sampson (1921) favors the importance of the edaphic factors of deficient drainage and poor aeration for Illinois prairie. He describes early settlers, who: "swam their horses across them [prairies] in early spring and who skated for many miles across country in winter with but short walks between the swamps." Turner (1934) also describes the poor drainage and the ponds which stood into early summer, while Transeau (1935) notes the soil as under water part of the year and another part "desicated with cracks and fissures extending three feet or more into the subsoil."
The width of the shrub and brush transition into prairie was regarded by eastern workers as being fairly narrow while towards the west the width greatly increases. Thus, Chavannes (1940) and Anderson (1954) in Wisconsin describe the fairly sharp break between forest and high lime prairie; Irwin (1929) in Ohio describes a similar break around the periphery of a relic prairie; Vestal (1914, 1918) from both southern and northern Illinois reports narrow thicket, shrub and herb zones of less than 100 feet. Transeau (1935), writing of the eastern portion of the Prairie Peninsula in general, describes the transition as only a few rods in width.

Further west, in Iowa, Aikman (1928) lists the shrub buffer as from a few feet to a mile or more in width. Winchell (1875), Moyer (1910) and Ewing (1924) in Minnesota describe wide shrub borders. Winchell writes of the western boundary of Big Woods: "It is not well marked; the trees gradually becoming thinner and smaller, and more and more restricted to the valleys of the streams, till the country is changed to a treeless prairie. Around the outskirts of the woods small oaks and aspens contribute almost the only arboreal vegetation."

Lists of the plants of the shrub and thicket transition are available in all the preceding references. A good description of a boundary in southern Illinois is given by
Vestal (1918): "The boundary between prairie and forest vegetation is in places somewhat ragged and indefinite, partly because prairie and forest herbs intermingle along the border, where also occur the forest border sunflowers, *Helianthus strumosus* and *Helianthus divaricatus* and *... Baptisia leucantha* and *Ceanothus americanus.*"

Studies have been made along the forest border upon the interaction of the vegetation with features of climate, soil, and topography. Weaver and Thiel (1917) show the change from lower to higher humidity, from higher to lower temperature, and from high to low wind velocities from the prairie through shrub and into woodland. To confirm this work, extensive tests of soil moisture and evaporation were made by Pool, et. al. (1918). Again, the prairie was shown to have a lower soil moisture and a higher rate of evaporation than the thickets, which in turn were more xeric than the woodland. Within the woodland itself, a further gradient was noted which led from bur oak on the ridges through red oak on the medium north slopes to basswood on lower slopes and ravines.

As stated previously, only one reference was found to open savanna with native herb vegetation, that of Shimek (1911 and also 1915). The plants listed by Shimek for bur openings are very similar to those of the herb and shrub borders. The many studies of scattered black or Hill's oak on sand (Jennings, 1909; Gleason, 1910; Gates, 1911; Vestal, 1913; and Moseley, 1928) also give species lists with a
mixture of plants which are usually described as either prairie or woodland.

Weaver (1954) reviews many references to the prairie forest border in his work on the prairies.

The numbers of trees per acre in the early savannas can be calculated from several references. Thus, Beal (1902) in Michigan describes large old open grown white oaks, in a forest which has closed its canopy from grub sprouting and seedlings, as one white oak to 20 square rods which would make 8 trees to the acre. As previously mentioned, Muir (1913) stated there were 5 or 6 trees per acre in north-central Wisconsin. Wing (1937) in Michigan measured the spaces between yellowish-brown circles of soil, 60 feet in diameter which were scattered through a field in which the rest of the soil was a dark and heavy clay-loam. He found the circles, which he considered the former sites of large open grown oaks, to be an average of 100 feet apart, which would make 6.3 trees per acre. Cottam (1949) calculated from the surveyor's records of 1834 an original density of 14.3 trees per acre for Stewarts Woods in southwestern Wisconsin.

Finally the transformation of savanna into more closed canopy forest is described by Cottam (1949) for Wisconsin; Beal (1902) for Michigan; Schockel (1916) for northern Illinois; and by Loomis and McComb (1944) and McComb and Loomis (1944) for Iowa.
CHAPTER III

DESCRIPTION OF THE REGION

Savanna, as a part of the southern hardwood forest, gives a distribution of stands, in Figure C-1, similar to that plotted by McIntosh (1950) for the upland hardwoods. The pattern of southern hardwood distribution, as is evident from the maps in McIntosh, does not show any correlation with geographic or physiographic provinces, with underlying rock structure or glacial deposits or with soil type. To all these physical features the southern forest is indifferent in the sense that it is not limited to any one physical province nor does it completely fill the area of some provinces in which it occurs.

Climatically, however, there are a number of correlations which have been noted by Wisconsin ecologists. From the work of Borchert (1950), which outlines the movement of air masses across central North America, an explanation is available of the forest border in terms of fluctuating air mass strength. Mild to severe droughts are a cyclic feature of summers along the forest border and occur when the Gulf air mass weakens and the drying western air mass moves eastward. Periods of low rainfall and low relative humidity are also a seasonal phenomenon related to air mass movement.
and the latter part of July and August and September usually has lower rainfall than May and June. The eastward movements of the dry western air masses described above do not, however, prevent the development of climax forest vegetation anywhere in southern Wisconsin and can only be considered as aids in the establishment of savanna when other factors, as fire and grazing, are present.

A series of correlations of vegetation with climate have been given in Curtis (1950). Of the six factors presented by Curtis, one, that of a snowfall of less than 45 inches shows a boundary which almost exactly outlines the distribution of southern forest (neglecting the beech-woods near Lake Michigan). Another climatic factor, that of a mean summer temperature of 68 degrees Fahrenheit, or more, also gives a good correlation.

The zone within which these climatic factors interweave is called the tension zone and has been discussed by McIntosh (1950) and Lindsay (1951) as an ecotonal region between northern and southern forest.

Figure C-2 shows the two climatic boundaries mentioned above plus the northern limit of southern forest drawn around the stand locations in Figure C-1 and the map locations of McIntosh, and the southern limit of distribution of ten northern tree species drawn as an optical average by Culberson (1954).
Other climatic factors listed by Curtis which give fairly good correlations with tree distribution are number of days above 68 degrees Fahrenheit (60 or more) and a July evaporation of five inches or more.

**Physiography and Geology**

Within the area occupied by savanna in Wisconsin, the greatest physiographic differences occur between the western Driftless Area and the eastern glaciated region. In the west there is a dissected peneplain with level uplands, steep bluffs and hillsides and deep valleys. There is consequently a well-established drainage pattern with the only undrained, marshy areas occurring in the Wisconsin and Mississippi valleys behind natural terraces thrown up by the rivers.

In the eastern part of the state, within the area described by Martin (1932) as eastern ridges and lowlands, there are fewer extremes in altitude and in steepness of slope, with few real bluffs except along the Niagara escarpment. Whatever hilliness was present here has been rounded off by glacial action or deposited by the glaciers in the form of knolls and kettles. There are many poorly drained lowlands in the east, which originally accounted for perhaps more than one-third of the total land surface.

An important difference for savannas between east and west is the manner in which the lay of the land offered
resistance to fire. Fire in the west was apparently either a valley or an upland affair with the burning from valley to upland or vice versa taking quite a time because of the steep topography. Anderson (1954) gives a description of an early burning which moved up valleys near Maiden Rock, Wisconsin.

In the east, however, the fire apparently swept over the rolling hills and flats with little topographic resistance. The areas of maple forest survival in the east are usually to the lee side of lakes or marshy areas and only in the Kettle Moraine and the old drift parts of Green and Rock Counties did steep topography protect maple forests. This is in marked contrast to the west where there are no lakes and few marshes and where many northeast facing steep slopes have some maple if not a maple forest.

Soils

A good general soils description of the soils of the southern upland forest has been given by McIntosh (1950) with the concluding statement: "More knowledge concerning the forests as such and the reciprocal relations of forest and soil is sorely needed." A discussion of some possible reasons why the interpretation of plant community distribution in relation to soil type is difficult for an ecologist will be given in Chapter XI.
In addition to the discussion of McIntosh, it is interesting to note that regardless of the classification type of upland soils in southern Wisconsin there are no soils with the possible exception of some sandstone and granitic areas which are low in bases or which are markedly deficient in any essential nutrient. The ability of climax deciduous vegetation to develop throughout southern Wisconsin points out the relative unimportance of soil as a factor in the distribution of vegetation.

An interesting feature of soils of the prairie forest border is that they lie in an area, according to Transeau, in which precipitation barely exceeds evaporation. The plant cover, therefore, has the opportunity to provide a crucial influence both in the balance between pedocols and pedofers and in the tendency toward or away from podsolization.
FIGURE C - 1

Map Showing Location of Stands.
FIGURE C - 2

Map of Southern Forest Boundary within State with Climatic Correlations. Unmarked Line is Northern Limit of Southern Forest. Line with Triangles is Optical Average of Southern Limit of 10 Northern Tree Species. Line with Squares is Southern Limit of 45-inch Snowfall. Line with Circles is Northern Limit of Mean Summer Temperature of 68 degrees Fahrenheit.
CHAPTER IV

METHODS

Location and Selection of Stands

The location of several oak openings and cedar glades was already known from previous field work by members of the Ecology Section when the present study was initiated. Additional stands were found by driving along roads and walking railroad tracks in areas in which savannas were likely to occur. These areas included: (1) low meadows and prairies in eastern Wisconsin in which there was inadequate drainage for crops and in which, for some reason, there had never, or rarely, been grazing; (2) thin soil areas on the gravelly slopes of the Kettle Moraine which were only lightly grazed in the past and are at present protected by state ownership; (3) sand areas in southern and central Wisconsin which have never been used agriculturally, usually because of poor soil; and (4) steep hillsides and bluffs along the Wisconsin and Mississippi Rivers which are too steep to be cropped or grazed by cows. Several stands were also found which, because of either an original inclusion into a non-farming estate or an accident of ownership, had not been exploited.

The savannas on the slopes and bluffs in western Wisconsin were especially valuable to the study since they
often represented sites with mesic prairie flora which had not been grazed because of the tendency of cows, as related by several farmers in this region, to step off the bluffs. These mesic savannas filled in the gaps left by the agricultural use of all the mesic drained flatland and rolling land savannas, not one of which has, to this date, been found intact. The time spent in locating these bluff stands was great and many days were spent climbing into steep slopes which lay an hundred or more feet above the road and which were found to be grazed.

The criteria used in the selection of stands were very rigid. No stand was sampled in which there was any evidence of cutting or in which grazing was at all evident. A grazed stand could be easily recognized by the almost complete absence of prairie grasses, by the partial absence of prairie forbs and by the presence of weedy grasses and European pasture forbs. Many woods were rejected in which past grazing had removed the prairie grasses but in which many prairie forbs had survived grazing and were rapidly regaining their former importance. These stands usually contained fewer than 30 to 40 species and were often characterized by a matrix of Poa pratensis and Poa compressa with scattered prairie plants which often included Amorpha canescens, Baptisia leucophaea, Comandra richardsiana, Coreopsis palmata, Lithospermum canescens, Monarda fistulosa, Oenothera biennis and Physalis virginiana.
**General Survey Methods**

The random pairs technique of Cottam and Curtis (1949) was the basic method used to sample trees in the field. Saplings were measured by including the four closest saplings to each point. These saplings must have occurred, however, within a circle whose radius was half the distance to the next point. The size of stand was first required to be 20 acres or over in order that 40 tree points might be included. This size was later reduced when it became evident in the field that savannas of 20 acres or more were either grazed or limited to a single type -- that of black oak on sand. Consequently, stands of five or more acres were sampled and the number of tree points was reduced to 20. This reduction made little change in sampling accuracy since the number of species in a savanna stand was rarely more than four. A total of 59 stands were sampled by the point method in the field.

Herbs, shrubs, and seedlings were measured by 20 1x1 meter quadrats which were laid at random in each stand in which a point survey of trees was made, unless the stands were grazed. Presence of species was recorded for each quadrat.

**Special Survey Methods**

Several additional methods were used to study herbs and shrubs. These methods were applied when a more complete
analysis was needed or when a stand contained only a few
trees or was not sufficiently large to support a point
survey.

The first method used a transect of contiguous 1 x 1
meter quadrats which were laid at compass point from the
trunks of lone trees which grew surrounded by prairie. The
transects were laid directly north, south, east, and west
of each tree and usually covered a distance of 10 meters.
Stands sampled in this manner included Kenosha, Lake Lulu,
Nashota, Scuppernong and part of Garwin Heights.

The second method depended on a subjective division of
the area into homogeneous units, as prairie, brushland,
shrubland, savanna, and various degrees of closed canopy
forest. Within each unit, quadrats were scattered at ran-
dom. Stands sampled in this manner included Butte de le
Chien, Garwin Heights and Kettle Moraine.

The third method was based upon a random scattering
of herb quadrats within 10 x 10 meter tree quadrats, which
lay along a contiguous line transect. Trempealeau was
sampled in this fashion.

A total of 84 herb stands were sampled in the field
in 49 separate geographic locations. Within these stands
1,760 1 x 1 meter quadrats were examined for presence of
species.

In 18 stands, five of which contained the original herb
vegetation, the random pairs method of sampling was supplemented
by a measurement of individual tree heights, of the distance from the ground to the first limb, and of the diameter of the canopy.

Tree height was measured with an Abney level at a constant distance of 50 feet from the base of the tree. The angle measured by the level to the top of the tree, plus the constant distance to the base were thereby sufficient, using a trigonomic formula, to determine the height of the tree. In a few cases the tree was of such a height that an additional distance had to be measured from the tree base in order to include the top within the upper range of the Abney level.

The distance to the first limb which had a diameter of 1 inch or over was estimated if it were less than around 15 feet and was measured by an Abney level if the distance were greater than that amount.

The diameter of the canopy was measured with a tape along east-west and north-south directions. The mean average of these two measurements was considered to be the diameter of the canopy.

A total of 680 trees were measured for some aspect of their growth form.

**Environmental Sampling**

Soil samples from the $A_1$ layer were taken from three profiles in most stands. In Scuppernong Prairie, nine
cores of a constant volume were taken from each of 20 stand segments.

Light measurements with a Weston Photometer were made over the herb quadrats of many stands and along transects in some stands which were pastured. These measurements were made only between 10 A.M. and 2 P.M. when the sun was at an intensity in the open of 10,000-plus foot candles. This level of intensity is usual for a clear day in southern Wisconsin and if even a slight haze appears, a haze which is not perceptible to human vision, the intensity will drop below 10,000-plus foot candles. An attempt was made to measure light on days with a uniform cloudiness or haziness. It was found, however, that no layer of clouds or haze is ever stable and fluctuations of as much as 2,000 foot candles often takes place within less than one minute.

When light intensity was taken over an herb quadrat, the paddle of the light meter containing the photo-electric cell would be held at a distance of three feet above the quadrat and rotated in a small arc in the direction of the zenith until the maximum intensity was reached. The paddle cell was never exposed for longer than two to three seconds at the higher light intensities. When readings were made along a transect, the sensitive side of the paddle would be held toward the ground and flipped in the direction of the sun when a reading was to be made.
Usually, one reading was taken per quadrat but in some stands four readings were taken; one above each quarter of the quadrat.

Light readings were taken in 20 stands and a total of 4,000 readings were made. Two thousand of these readings were made, however, in Albion and Ant Woods. The total number of readings which were made above herb quadrats was 946.

**Recording and Compilation of Data**

The techniques used in the present study, both in the field and in the laboratory, to record data and to calculate the behavior of tree, herb, and environmental data are the same as described in McIntosh (1950). The same manner of field operation as was outlined by the above worker was followed except in the special studies already discussed.

In the laboratory, one tree stand was discarded because of lack of homogeneity. This lack was caused by an attempt in the field to separate a continuously varying black-red oak complex into two distinct entities. As a result, two of the blocks had red oak and the other two black oak and the stand was heterogeneous.
CHAPTER V

PHYTOSOCIOLOGY OF TREE STANDS

Tree Stand Composition and Gradient Location

Twenty-eight species of adult trees, two hybrids, two species which occurred only as saplings, four species of understory tree and four species which occurred only as seedlings were found in savanna for a total of 40 tree species. Of these 40 species only 15 were found to occur in more than ten percent of the stands and of these 15 species, there were six species -- those presented in Table E-1 -- which accounted for 90 percent of the sum of the Importance Indexes of the species in all the stands.

In spite of this strong domination by a small number of species, six additional species managed to reach dominance in one or more stands, while four other species were found to have importance values of above 50 in at least one stand in which they were secondary dominants. The six species of Table E-1 previously mentioned reached dominance or secondary dominance in all but seven of the 59 stands and it is the mutuality of their behavior which will be used as a primary guide to an ordered arrangement of the savanna stands.

The mean Importance Index value (DFD of Curtis and McIntosh, 1951) of each of these six species was calculated
for each set of stands in which each of the species was a dominant or secondary dominant with an IV of above 50. These calculations are shown in Table E-1 with the numbers of stands in each set shown in the second column and the name of the species which was dominant in the set listed in the first column. There were 59 stands with 39 of them containing secondary dominant as defined above, so that 59 stands could have been listed a total number of 98 times in the sets in column 1. The six species of Table E-1 accounted for 80 of these 98 listings, another indication of their major savanna importance.

The arrangement of sets in Table E-1 was based upon a trial and error ordering which attempted to place those sets which had the greatest similarity in specific quantitative behavior in greatest proximity to each other. Thus, set one, dominated by red cedar, is more nearly similar to set 2, dominated by black oak, than to set 6, dominated by white elm. The patterns of quantitative behavior despite the tendency of many savanna stands towards domination by a single species, show the characteristic intergrade suggestive of continuous variation in community composition. The manner of variation was, therefore, considered justification for the construction of a linear ordination with endpoints, represented by those stands which were dominated by red cedar or white elm.
The Assignment of Adaptation Values

The ordination technique adopted was that of the assignment of adaptation values (Curtis and McIntosh, 1951). In assigning adaptation values the influence of important historic factors on the relative mutualities of the species of Table E-1 was noted. Bur oak and white oak, though related to the other species in that table in a somewhat similar fashion, have a very low occurrence of 5.8 and 8.0 with each other. This lack of occurrence is considered to be evidence for the different historic happenings which produced the savannas in which these species are important.

Bur oak is not found in white oak savannas because the areas which today contain open grown white oaks were once more closed canopy forests from which bur oak had been excluded as the canopy closed, by seedling intolerance of low light intensity and an inability of the open grown trees to alter their growth forms and compete vigorously with younger, upward growing trees.

Present day white oak openings or white oak-black oak openings are the fire degraded remnants of intermediate stands in which white and black oak survived by stump sprouting and grub formation and as the canopy reopened by seedling production which led to grubs and shrubby thickets. Many of these white oak-black oak shrubberies or barrens,
especially those on the flats where fires could build up high velocities, were probably completely converted to prairie, with perhaps a few older trees surviving. Into these tree-demuded flat areas bur oak could then move by seeding. It was often noted in the field that in some bur oak opens there would be one to a few older, larger branch gnarled white oaks or black oaks. These trees were perhaps remnant members of an earlier closed canopy stand. The few other stands in which bur oak was found with white oak were often buffer savannas on the edges of bluffs behind which a more closed canopy forest was located. In these buffers, bur oak was often further out in the prairie and the white oak was nearer the woods so that by a different course of sampling, two distinct stands, one with bur, the other with white oak, might have been sampled.

On the other hand, white oak is not too likely to be found in bur oak savannas in an open where white oak was not previously present because white oak is in no way a pioneer species and its seedlings are not likely to compete successfully in the prairie soil and under a high light intensity.

A certain amount of subjective judgment was, therefore, used in assigning the adaptation values of species to bring in considerations of historic factors. White oak and bur oak were given intermediate values of 3.0
although it later became apparent from gradient position in Table E-3 that white oak should have a slightly lower value. Between the extremes of 1.0 for red cedar and 5.0 for white elm, the other species were then arranged on the basis of their relative phytosociologic nearness to the endpoints. This nearness was judged by an inspection of stand summaries and from field observation. It was unfortunate that bur oak with its very wide amplitude (from high dry prairies to swamp meadows) could not have been given a shifting scale of adaptation values, but no objective method could be found which would number the tree independent of its habitat location. The assigned adaptation values are listed in Table E-2.

**Ordination Construction**

A linear ordination was then constructed in which each of the 59 stands was given a position determined by the following formula:

\[
\text{O. I. equals} \quad \frac{\sum \text{(adaptation number of each species x its Importance Value)}}{\sum \text{(of the Importance Values)}}
\]

The resulting compositional gradient was divided into five equal sections and the mean importance behavior of the 40 savanna trees plotted for the stands within each of the five sectors. These importance distribution patterns are shown in the five columns of Table E-3. The species are
arranged in decreasing order of the sum of their tree
importance values. The meaning of the value in each row
is explained at the conclusion of the table.

In interpreting the importance behavior patterns of
Table E-3, it should be understood that if species are
together in the same area of the savanna gradient they are
not necessarily found together in the same stands. Nor is
any stand like the composite average of the sector of the
gradient in which it resides. For example, bur oak and
white oak show a large overlap and yet, as previously
discussed, they do not often occur with a high importance
in the same stand. If, however, two species, like red
cedar and swamp white oak do not overlap along the gradient,
they cannot be found together in a stand.

A series of stands selected at approximately equal in-
tervals along the savanna gradient are shown in Table E-4.
The tendency of savanna stands to be strongly dominated by
one species is evident from this table.

Although all savanna stands were defined by the same
criteria, there is still an increase in mean basal area and
in dominance per acre as site conditions improve from cedar
glades to elm groves. The increase is shown in Table E-5.
The number of species also increases although there are more
species in the cedar glades in interval one, than in the
black, white and bur oak openings of intervals two and three.
The major savanna species will now be discussed in relation to gradient position and adaptation to savanna conditions.

**Adaptation of Southern Forest Trees to Savanna Conditions**

Since resistance to fire is not a prerequisite for occurrence in some present day savannas, the only general requirement which must be met is that the tree be able to most grow under open conditions. The seedlings of a savanna tree must, therefore, be able to germinate and compete with whatever grassland or weedy herbs are present, and the saplings must grow to maturity under conditions of maximum light intensity and must endure the wide fluctuations in soil moisture and relative humidity which occur in areas unprotected by a tree canopy. It is not surprising that of the trees which occur as dominants in savanna, six are under certain conditions, pioneer species, and while the remaining six are intermediate species, none are climax. Of the six species which accounted for 90 percent of the total Importance Values within savanna, all but white oak are, at times, pioneer.

In reviewing the gradient positions and some autecological aspects of the major savanna trees, the species will be considered in two groups. The first group includes
all trees which were a major component of savanna 100 years ago, species which could survive the extreme burnings of those days or could regenerate after fire and maintain their savanna position. The second group includes those trees which have entered or matured within the savannas since the stopping of fire and the commencement of grazing.

**Bur Oak**

Of the six major savanna species, bur oak was originally and is still perhaps today the most common tree in the forest border area of southern Wisconsin. Although its sum total importance along the savanna gradient is not as great as black oak, the areas of the gradient in which it predominates cover a larger acreage in southern Wisconsin and it is, therefore, more abundant. The most interesting aspect of its gradient amplitude is its extreme width. Bur oak can grow from bottomlands and low meadows to thin soiled lime bluffs and reaches a maximum importance on rich flatlands and gently rolling hills.

Bur oak peaks in the third sector of Table E-3 and decreases evenly away from that point. It is nearly reproducing its relative importance in saplings although its seedling frequency is less than a third the level of mature tree frequency. Seedling abundance is greatest in open
groves, less so in prairie and non-existent in closed oak
woods. The seedlings found in prairies were often growing
near the edge or occasionally in the middle of sumach
clones and dogwood or hazel thickets. The advance into
prairie of bur oak behind brushy thickets is described by
Weaver and Kramer (1932) and by Ewing (1924). Prairies and
pastures with scattered bur oaks which were moderately
grazed often contained an abundance of seedlings, each of
which were many years old and showed the stub ends of
twigs which had been clipped off by grazing.

Bur oak is a tree which very probably developed many
of its distinctive features during a time when fire and
drought were an important factor on its landscape, and it
is the only major savanna tree which can successfully invade
undisturbed prairie. The morphologic and physiologic fea-
tures which enable bur oak to survive fire are well known
and will be briefly listed. (1) The bark of the Wisconsin
bur is extremely hard and dense, with a thickness of up to
two inches in older trees. This bark tightly encloses the
trunk, limbs and even small branchlets of the tree, does
not flake or slough off, and cannot be easily pried away
from the wood. As trunk expansion continues, the bark
divides into long twisting minuate ridges which are cleft
almost to the cambium. In a small proportion of Wisconsin
burs there are corky winged limbs and branchlets. The
thickness and density of the bark provide heat insulation for the cambium and the bark is very resistant to burning. The bur oaks in Kenosha prairie were swept by fire in the fall of 1950. Later in the summer of 1951, when the trees were examined, the thin layer of charred bark less than one mm. thick, had fallen off from most of the trunk and was visible only at the base where there was at the most two mm. of charcoal. In this same opening there were several fallen limbs without bark on the floor which were almost completely burned. An old bur is probably immune to even the hottest prairie fire unless it is diseased or split so that fire can reach the wood. Fire can also burn into the wood from unhealed scars left when the large lower limbs fall away.

(2) The buds of bur oak are enclosed by large numerous thick scales which are very hairy. While these scales cannot give much fire protection, they probably shield the meristem from scattered tongues of flame. In the spring of 1954, during the burning of the University of Wisconsin Arboretum prairie, an area of young bur oak saplings was also burned. The ground cover around the saplings was unfortunately weedy and didn't burn with the same intensity that a prairie vegetation would. Nevertheless, many of the buds of the limbs within three to four feet of the ground were burned and failed to develop later in the spring. A hot fire would probably have completely destroyed the lower
limbs of these saplings. A bur oak which develops in the open can send out horizontal branches of great strength which can grow outward and receive sufficient light to withstand the competition of higher branches of the tree. There seems to be no reason why the lower branches of all open burs should not be within a few feet of the ground as they are on occasional high lime bluffs unless the lower branches were killed by the burning of the buds. Figure E-1 shows a bur with a large low branch.

(3) Bur oak forms on all leaves a completely developed abscission layer early in autumn and leaf fall takes place immediately. There are never, therefore, any leaves left which might catch fire during the autumn prairie burning and heat the bud meristems or contribute heat to the burning of the branchlets.

(4) Bur oak can form if it is burned or grazed during its seedling or sapling days, a thick woody grub which is capable, if there is a period of several years without fire or animal damage, of sprouting and growing to a size where it can withstand further burnings. A bur oak grub is shown in Figure E-2. This grub was found and photographed by Mr. Ralph Dix near Mazomanie in an area along the Wisconsin River where burning is still frequent.

The ability of bur oak to invade prairies and to survive prairie drought is probably due to its vigorous tap
root. The rapid growth of bur oak seedlings in open stands is described by Holch (1931). An examination was made of bur seedlings in several stands and they all showed the deep thick tap root which Weaver and Kramer (1932) have described. The large amount of food stored in a bur oak seed is used to immediately develop a strong tap root; in all the seedlings examined there was a much greater weight in the underground parts.

It is interesting to speculate on the balanced configuration of factors which will allow a bur oak seedling to become established in a prairie and to grow to maturity.

First, the acorns must be formed during a good seed year which is also a year when the larvae which parasitize acorns are sufficiently under the control of their predators to allow even a small percentage of acorns to be larvae-free.

These acorns must then be transported away from the parent tree into prairie. This dissemination probably takes place mainly through prairie rodents which carry the acorns to their burrows or storage areas, or hide them haphazardly after the manner of squirrels. There is no reason to assume that bur oak acorns cannot be carried by the strong autumn and spring winds and tornados which are a cyclic feature of the Middle-West. Another equally feasible means of transport is by stream, the possibility even existing that the acorns could move upstream in the backwash of the yearly
spring floods. (Vestal, 1949). These spring floods also covered, sometimes for weeks, large areas of the flatter prairies and during flood time, acorns could have floated across these sheets of water to unsubmerged islands or ridges where no burs had previously grown. Blue jays or crows might carry a bur acorn in flight and accidently drop it over a prairie. The use of acorns for food by the Indians (Aller, 1954) especially acorns with a low tannin content as white oak, swamp white oak and bur oak, means that acorns collected at one place may have been carried elsewhere and accidently dropped en route. Bur oaks might have been planted by Indians and the high coincidence of oak openings with former camp grounds might be in part the result of deliberate planting.

After the acorn is moved away from the parent tree, it must escape being eaten and must germinate, presumably under optimum conditions of soil moisture and aeration. After germination would come a critical period when there must be sufficient photosynthesis and growth to develop a root system which can meet the autumn drought. Enough food must be stored in the tap root that grazing of leaves and stem by cattle or rabbits can be followed the next year by renewed upward growth.

Once the sapling stage is passed without destruction by fire or animals, the bur oak is extremely hardy. It has
no major leaf defoliating insect pests, it is immune to oak wilt and fairly immune to heart rot and because of its extensive root system, it is very drought tolerant.

**Black Oak---Hill's Oak**

The identification of the trees in this group is very difficult and a tree was usually labeled as black oak in the field unless it could very clearly be classified as Hill's oak. As a result, the amplitude of Hill's oak is squeezed more to the left of the gradient in Table E-3 than it should be and some of the high importance of black oak in column two of the table more properly belongs to the amplitude curve for Hill's oak.

These two species which shall be discussed as a single entity, reach a high importance towards the red cedar end of the gradient but drop off sharply within stands dominated by mesic to moist trees. Black oak occurs both in stands dominated by white oak and by bur oak.

Black oak, like bur oak, is reproducing a sapling importance almost as great as the relative importance of its mature trees but unlike bur oak, its seedling reproduction, within the less open canopied groves, is very vigorous.

Black oak shares many of the adaptive characters listed for bur oak. Its bark is hard and dense. The buds are
covered with thick hairy scales and the tree can form grubs. Black oak is also able to stump sprout. It does not, however, have either a complete or uniform abscission layer and many trees are partly covered until spring with dried leathery leaves. It is very subject to oak wilt and this factor combined with its apparently slightly lower fire resistance from a more sensitive cambium, probably accounts for its lesser importance in the original savannas.

Black oak is probably more highly mobile than bur since it has a lighter acorn which is more likely to be carried by birds or by the wind. Black oak seedlings were sometimes noted in undisturbed prairie which was somewhere in the vicinity of a mature tree. These seedlings do not seem to have the hardiness of those of bur oak and most of the seedlings found in prairie had chlorotic light green leaves.

**White Oak**

Although white oak peaks toward the left of the center interval of Table E-3, it is not necessarily a less mesic tree than bur oak; its strong savanna occurrence with black oak is probably due, as mentioned earlier, to manner of historic origin.

White oak is the only major savanna tree which never invades prairies or old fields. During four summers spent in field work, a white oak was rarely found isolated in the
center of a prairie or an area which had formerly been prairie, and in every savanna in which it occurred, that savanna was immediately contingent to a more closed canopied woods. It is very likely that given its inability to pioneer, every area where white oak trees are present today was formerly a closed canopy forest.

Those characters which are of adaptive advantage to white oak in savanna seem to be introgressed from bur oak. The bark of many white oaks in savanna is thicker and more tightly held than that of most forest grown whites. The white oaks in savanna don’t seem to be subject to the disease which causes white flaky bark and chlorosis in forest white oaks. The leaves of savanna white oaks are lost earlier and more uniformly than those of trees in forest areas, and the buds are thicker and more hairy. In addition, white oak can form grubs and can stump sprout which enable it to survive in fire degraded forest lands.

Since it is an intermediate species within the upland forest continuum, it does not seed in well under open canopy and its sapling and seedling percentage importance values are only a little over half that of the adult trees.

**Swamp White Oak**

Swamp white oak was a dominant tree in the original bottomland savannas; it is still very common in low meadows
and is in addition an important intermediate species in bottomland successions. In many ways, swamp white oak has the same behavior in lowland areas that white oak has on better drained sites. It is a shade tolerant species which usually enters bottomland forests following willow, poplar, or black birch on sand and its presence in most bottomland savannas might be the result of a previous occupancy of the area before fires were a consistent bottomland factor. Then, as with white oak, it may have survived the fires which cleared cut more susceptible species and managed to reach some kind of balance with the invading grassland.

It differs from white oak, however, in being a more aggressive species. It can invade abandoned bottomland pastures and disturbed terrace meadows. It cannot occupy newly laid silt or clay flats along rivers, but comes in sometimes after an herb stage has been established on sand terraces.

Swamp white oak, as will be shown in Chapter XII, has many introgressed characters from bur oak which are of adaptive advantage in savanna.

All of the stands in which swamp white oak was open grown were grazed and no data on reproduction is available.

**Shagbark Hickory**

Shagbark hickory has a wide symmetrical amplitude within the savanna gradient of Table E-3 and reaches greatest
importance in areas dominated by white oak, black oak or bur oak. It is never very common in any one woods although it reaches dominance in one stand.

Like black oak, which has an adaptation value of 2.0 in the upland hardwood continuum, shagbark hickory is an early intermediate species and has an adaptation value of 2.5. It is also, like black oak, reproducing in savanna a sapling and seedling population with a higher importance level than is possessed by its mature trees. Its seedlings were widely distributed and were often noted in prairies as well as in oak forests. The seedlings in prairies were usually chlorotic. Saplings were rarely noted out in prairie which also suggests the seedlings do not do well there. Shagbark has an amplitude which is fully as wide as that of bur oak and it sometimes occurs in bottomland forests in eastern Wisconsin. A notable feature of some grazed stands with shagbark is that the hickories are concentrated in one place, indicating they were planted and other trees were cut away to give them room to grow.

The bark of shagbark is fire resistant and the tree was found in several openings which were recently burned. There is a possibility, though, that its low importance in most savanna stands may be due to a slight fire susceptibility.

Its presence in the forest border, were it not the result of prior occupancy before fire, might be explained by
the planting activities of Indians. On the mounds along both sides of the Mississippi River and at Chief Oshkosh's old camp grounds near Lake Winnebago, there is a much larger proportion of hickory trees than in most woods where hickory is present. The hickory nut was gathered and dried by Indians just before it was ripe and squirrels and ground squirrels had carried it away. Then it was crushed and boiled in water and the oil which floated to the top was used like butter. (Kephart, 1917).

Fire Susceptible Trees

All of the following species are more or less fire susceptible although very large trees of some of the following species can withstand burning. They survived the periodic burnings by occupying niches which were fire protected by rivers, lakes, ponds, permanent sloughs, steep bluffs or very hilly terraces. Since burning has stopped they have moved into grasslands, usually to the accompaniment of grazing and trampling.

Red Cedar

Red cedar, judging from the present day distribution of large, old trees, survived on vertical bluffs along the Wisconsin and Mississippi Rivers. A cedar was found growing on
the ledge of Du Charme bluff, along the Mississippi River, shown in Figure E-3. If the prairie at the top or lower slope of this bluff were to be opened up by grazing, a dense stand of cedars would move in, as they have moved into many grazed pastures in Wisconsin.

The high importance of cedar in the left-most sector of the savanna gradient shows an almost pure red cedar stand which occurs as the cedar seedlings move into the edge of the bluff prairie, and, especially on steep slopes with fine sand soils, occupy a habitat which is probably too dry for any other available Wisconsin tree. Further back from the bluff edge, cedar comes in contact with black and bur oaks, upland basswood, white birch and both species of poplar.

The lower importance of cedar seedlings compared to saplings and mature trees indicates the deciduous forest will in the future gain at the expense of cedar, unless perhaps there are dry spells which allow only the cedar saplings to survive.

Cedar can move into oak openings on plateaus in the driftless area which have been grazed. Figure E-4 shows open grown white oaks with an understory of young cedars.

White Elm

An occasional old open grown elm with deliquescent branches arising six to ten feet above the ground was seen
in a few low meadows. These elms were found in stands with large open grown swamp white oaks and younger elms and ashes. There is a good probability that these stands in earlier days were burned and that, therefore, there are some elm trees which are fire resistant. In most cases, however, where older elms were noted, a potential fire barrier of some sort could be located. In general the larger older elm trees of southern Wisconsin are in protected bottomlands or swamp hardwoods which were not savannas one hundred years ago.

The elm trees which form the many pastured groves of eastern Wisconsin are all relatively young. The only stand sampled in which there was cutting showed most of the trees to be between 90 and 107 years old. The basal areas of these trees at base were from 600 to 700 square inches.

The movements of elm into swamp meadows was probably originally stimulated by light grazing. Elm seedlings were never found in the field in undisturbed prairies even though there were elms in the vicinity. Seedlings occur frequently in grazed meadows although these meadows are so heavily grazed today that no saplings are present. This suggests that if, at present grazing levels, seedlings are kept cropped off, there must have been periods in the past when grazing was not as heavy and some seedlings could become saplings and mature trees.
Red Ash

Red ash and its variety green ash are, like white elm, recent occupants of the low meadow groves. Grazing is apparently necessary for ash seedlings since they were never found in the field in low prairies although they were occasionally noted on hummocks in sedge meadows. In some ungrazed meadowlands around the Lake Poygan area there are quite a few scattered young ash trees while on the raised areas of these meadows there are thickly grown ash and aspen spinnies.

In the elm-ash groves, the ashes are younger than most of the elms and must have come in after the elm invasion. In heavily grazed groves, there were usually a higher number of ash seedlings than of elm although as in the case of elm, there were few to no saplings.

Red Oak

Red oak occurs throughout the length of the savanna gradient although its appearance in the left-most sector is the result of a peculiar type of Driftless Area red oak which grows in cedar glades. In almost every low stand in which red oak was present, it was usually a very large tree. Some of these stands, especially those in bottomlands, showed
evidence of recent burning which suggests that at least some red oaks are fire resistant.

The stands dominated by red oak and those in which it was an important tree were ones which had a higher number of species than the uniform elm-ash groves of the same area of the savanna gradient. This indicates that the red oak stands were formerly closed canopy forests which are recovering from a partial fire degradation and are not the result of recent invasion of grazed meadows.

Aspen

The two species of aspen found in savanna did not seem from field observations to be very restricted in their moisture adaptations, although their occurrence within the savanna gradient is fairly limited. In general, large toothed aspen grows on drier sites in cedar glades and on the edges of dry prairies. Trembling aspen, on the other hand, occurs from dry rock outcrops and cedar glades to low prairies. Both species are fire intolerant and short lived; no older trees were found in savanna. Their seedlings in entering prairie are probably helped by slight grazing. Small copses of either of these species were often found along fences or fenced in cattle trails which were adjacent to undisturbed prairie in which no aspens were present.
These copses were usually thickly grown and uniform in size; with even aged trees. No aspen stands were sampled in the field because they were all, when they reached a tree size of 12 square inch basal area at breast height, closed canopy stands. The forest floor beneath these stands had usually less than a mean of 1,000 foot candles and the prairie herbs had, for the most part, disappeared.

White Birch

White birch reaches its greatest importance with red cedar. It grows in western Wisconsin along ridge tops, bluffs, and rock ledges in steep prairies. Figure E-5 shows a high lime prairie with scattered white birches, the only stand of this kind which was found in field study. The birches in Figure E-5 are growing on a series of small rock ledges. These ledges extend into the hillside and apparently provide ridges for subsurface drainage. In "goat" prairies in Illinois, sycamore grows on similar rock ledges (Evers, 1954) which suggests that the soil around the ledge where the tree roots penetrate is moist from sub-surface flowage. White birch, like aspen, is very fire sensitive and must have escaped former burning by growing on bluffs.

A series of photographs of stands along the savanna tree gradient is shown in Figures E-6 through E-12.
FIGURE E - 1

Photograph of Bur Oak with a Low Limb. The Flowering Forb is Helianthus laetiflorus.
Near Radio Tower, Winona, Minnesota.

ADDITIONAL FIGURE

Bur Oak Open, Near Radio Tower, Winona, Minnesota.
FIGURE E - 2

Photograph of Bur Oak Grub, Near Mazomanie, Wisconsin. Courtesy of Mr. Ralph Dix.
FIGURE E - 3

Photograph of Native Prairie on Bluff, With Open Grown Trees and Scattered Shrubs. Red Cedar is Growing Halfway Down the Bluff Face on a Ledge. Above DuCharme River where it enters the Mississippi River, Wisconsin.

FIGURE E - 4

Photograph of Red Cedar which has entered a White Oak Open Under the Stimulus of Grazing, Near Okee, Wisconsin.
FIGURE E - 5


FIGURE E - 6

Photograph of Cedar Glade, Okee, Wisconsin.
FIGURE E - 7

Photograph of Open With Black (or Hill's )
Oak on Sand. Near Lodi, Wisconsin.

FIGURE E - 8

Photograph of Dry Lime Prairie Which is
Being Invaded by Bur Oak. In Eastern
Minnesota.
Photograph of White Oak Open with Black Oak. Ground Cover Includes Young White and Black Oaks, *Corylus americana*, *Ceanothus americanus*, and *Helianthus strumosus*. Above Du-Charme River where it enters the Mississippi River, Wisconsin.

Photograph of Bur Oak Open. Albion, Wisconsin.
FIGURE E - 11

Photograph of Low Open With Swamp White Oak in Left Foreground and Bur Oak in Right Foreground. Near Hebron, Wisconsin.

FIGURE E - 12

Photograph of Low Open With Swamp White Oak in Foreground and White Elm in Background. Near Hebron, Wisconsin.
### TABLE E - 1

Quantitative Behavior of Major Species by Sets

in which each Species is a Dominant or Co-Dominant

<table>
<thead>
<tr>
<th>Species</th>
<th>Number in Set</th>
<th>J.V</th>
<th>Q.V</th>
<th>Q.a</th>
<th>Q.m</th>
<th>Q.b</th>
<th>U.a</th>
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</thead>
<tbody>
<tr>
<td>1. Juniperus virginiana</td>
<td>07</td>
<td>---</td>
<td>26.5</td>
<td>25.0</td>
<td>7.0</td>
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<tr>
<td>2. Quercus velutina</td>
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<td>---</td>
<td>51.3</td>
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<td>0.8</td>
</tr>
<tr>
<td>3. Quercus alba</td>
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<td>---</td>
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<tr>
<td>4. Quercus macrocarpa</td>
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<td>---</td>
<td>0.0</td>
<td>8.2</td>
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<tr>
<td>5. Quercus bicolor</td>
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<td>2.5</td>
<td>---</td>
<td>61.2</td>
</tr>
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* The figures in the matrix show the mean importance behavior of each species in each of the sets in which the species along the top of the matrix was a dominant or co-dominant.
### TABLE E - 2

Adaptation Values Assigned in the Construction of the Savanna Tree Compositional Gradient

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<td>3. Quercus ellipsoidalis</td>
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<td>4. Betula papyrifera</td>
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<tr>
<td>5. Quercus velutina</td>
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<tr>
<td>6. Corya ovata</td>
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</tr>
<tr>
<td>7. Tilia dryland</td>
<td>2.5</td>
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<tr>
<td>8. Quercus alba</td>
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</tr>
<tr>
<td>9. Quercus macrocarpa</td>
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<tr>
<td>10. Fraxinus americana</td>
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<tr>
<td>11. Quercus rubra</td>
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<td>12. Quercus bicolor</td>
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<td>13. Fraxinus pensylvanica</td>
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<td>14. Tilia americana</td>
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<td>16. Ulmus americana</td>
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## TABLE E - 5

Quantitative Behavior of Trees, Saplings and Seedlings along the Savanna Tree Gradient

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</tr>
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<td>cordiformis</td>
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TABLE II (continued)
**TABLE E-3 (Continued)**

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<tr>
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<td>seedlings</td>
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</tr>
<tr>
<td>39. Salix sp. seedlings</td>
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<tr>
<td>40. Viburnum lentago saplings</td>
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</table>

* The first row designates the Importance Value of the trees of each species on a relative basis. The second row shows the Density plus percent sum of Frequency of the saplings of each species on a relative basis. The third row shows the percent sum of Frequency of the seedlings of each species. If the sapling or seedling rows are absent, there were none present. The last two columns of the sapling and seedling data are vacant because of grazing.*
TABLE E-4

Importance Behavior of Trees in Selected Stands

along the Savanna Gradient

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CHAPTER VI

THE SIZE AND SHAPE OF SAVANNA TREES

Probably the most important complex of factors which influences the distribution of savanna herbs and shrubs is that controlled by the degree and intensity of shading. In studying this shading, measurements of light were augmented, as presented in Chapter IV by direct measurement of canopy coverage per acre; and the influence of varying percentages of canopy cover on tree shape and size was noted.

Of the 680 trees measured for some aspect of their growth form, 484 were bur oaks and the remainder white oaks, with a few black oaks, shagbark hickories and other trees. Open grown white and bur oaks have very similar growth forms and a preliminary tabulation showed that the data in any one stand based upon bur oak alone was not different from that in which the white oaks and the few other trees were included. All the trees sampled in each stand were, therefore, included in the final compilation.

The Influence of Tree Dispersion

Assuming that each tree canopy has approximately the same density of leaves and branches and, therefore, diminishes floor light to the same degree, the mean intensity of light per unit area would be a function of the percent canopy
coverage. The variation around the mean would be, however, dependent on manner of tree dispersion.

The importance of manner of dispersion can be shown in the following example. If trees are contagiously dispersed there will be a higher proportion of the forest floor which will have both higher and lower light intensities than if trees are randomly or regularly dispersed. Contagious dispersions have higher intensities because more of the ground surface receives full sunlight, and have lower intensities because more of the ground is shaded by more than one tree. The deviation around the mean intensity, is, therefore, greater than in random or regular dispersions and the herb and shrub vegetation of a contagious tree dispersion will tend to be much less homogeneous. Of two stands with equal canopy coverages, the one with contagiously dispersed trees will have wider fluctuations between prairie and forest herbs.

Although no tests were made on manner of tree dispersion it seemed in the field that, except in meadows where bur oaks clumped on rises, there was little indication of contagion. The manner of dispersion will, therefore, be considered more or less random to regular for all the sampled stands.
**Canopy Shape**

In calculating the mean canopy coverage per tree, it was first necessary to assume some kind of canopy shape. Bur and white oaks growing in the open have rounded canopies, while, as the canopy closes, competition for light leads to the filling of all available space and a tendency toward an hexagonal shape. Hexagonal canopy shape is difficult to observe in the field since the canopy of any one tree is irregular with much intermixing of branches with other trees. Hexagonal patterning was evident, however, from aerial photographs of swamp white oak stands along the Wisconsin River.

All canopy shapes were, therefore, considered to be hexagonal since there is no way to judge the point at which they cease being circular. To calculate the area of each canopy, it was necessary, therefore, to convert the circular canopy radii measured in the field to the radii of hexagons.

Percent canopy cover was then determined by multiplying the mean canopy area of the trees in a stand by the number of trees per acre and dividing by the number of square feet in an acre. Percent canopy cover is shown in column 5 of Table F-1. The percent coverages vary from 30.3 to 93.3 and thus give a wide range over which to test growth form changes.

Before this can be done, it should be made clear that neither the number of trees per acre nor the mean basal area of tree trunk can be used separately as a measure of canopy...
cover. This can be illustrated by pointing out that the three stands with canopy coverages of from 40 to 50 percent show variations of from 15 to 108 trees per acre and variations in mean basal area of from 656 to 92 square inches. These variations are about as great as those existing anywhere within the entire range of canopy coverage. Mean basal area per acre does, however, generally follow the trend of the closing canopy. The dominance per acre values are shown in column 3 of Table F-1. The distribution of these values in relation to percent canopy coverage is shown in Figure F-1. A uniform trend is evident and the presentation of growth form changes will, therefore, be related to the dominance per acre values.

Growth Form and the Closing of the Canopy

It is evident that growth form relationships must be expressed in relative values since differences in site quality partly contribute to the diversity in size of savanna trees. Two relative measurements will be made to show the changes in shape which can be found from open to closed grown trees.

The most inclusive of these measurements is the ratio of height to canopy diameter. There were many open grown trees which had a canopy which was wider than the tree was tall, although the lowest ratio for a stand was 1.25. This value can be compared with a value of 3.03 for a closed stand in
which the trees were over three times as tall as they were broad. These height to diameter ratios are shown in column 6 of Table F-1 and, as can be expected, there is an increase in the ratio as percent canopy coverage increases.

The other ratio, that of height to basal area, shows the most interesting growth form relationships among the 18 stands. The more open grown a tree, the lower will be the value for its height as a percentage of its basal area. The ratio is shown in column 7 of Table F-1.

The height to basal area ratios are shown plotted against the dominance per acre values of column 3. The resulting figure, F-2, shows a divided trend converging toward the closed canopy end of the gradient. The division illustrates the two major historic manners in which many of the forests of southern Wisconsin have originated. The upper trend line represents stands with a low canopy cover per tree, a low basal area per acre and many small trees per acre. These are stands which have originated from the maturation of oak barrens and grub-lands and are essentially pioneer forest stands which will quickly close their canopies. These stands originally contained few to no open grown trees and have grown from grubs or sprouts with enough light competition to force much of the growth into upward expansion of trunk and limbs. As these stands close their canopy, the number of trees per acre will decrease and the basal area per tree will increase. As can be
seen from Figure F-2, the ratio of height to basal area for these stands will decrease and level off at the area of the closed stands.

The lower trend of Figure F-2 represents, on the other hand, oak openings which have few trees per acre but these trees have a relatively high basal area. As these stands close their canopy, usually with the seeding in of oak or elm species, as grazing opens the soil and fires cease, the number of trees per acre will increase and the mean basal area will decrease. The ratio between height and basal area will, therefore, increase until it levels off in the closed canopy stands.

Figures F-3 through F-6 illustrate the great diversity in size and shape of tree which can be found within oak openings. Figure F-3 was taken in the northern part of Albion (#92B) where the trees are more closely spaced and of a smaller basal area than in the southern part of the stand shown in Figure F-4. From the southern to northern parts of the opening, there is an increase in percent canopy cover from 44 to 66.

A stand with canopy cover similar to the southern part of Albion is Butte de la Chien (#72), Figure F-5. In this stand there are more trees per acre than in Albion but the trees are smaller, with narrower canopies and lower first branches. The photographs presented in Figures F-3 through F-5 are of savannas with old and/or large open grown trees. Figure E-7,
on the other hand, shows a woods which has grown up from grubs or shrubby barrens. While the canopy coverage in a stand of this type can be as low as 74 percent and there is an element of prairie flora present, the stand is a pioneer forest, with many trees per acre (up to 168) and a low mean basal area.

The stand with the most complete canopy coverage is illustrated by the photograph in Figure F-6. This area in southern Dane County was originally an oak opening with a few scattered open grown bur oaks, two of which are still present in the stand. At the time when the land was homesteaded by the parents of the present owner the upper slopes above the stand had grown up into a thick stand of young trees which were cut down as the land was developed for crops. The lower, more poorly drained part of the opening, that shown in Figure F-6, did not contain grubs, or if any grubs or stunted trees were present, they were bur oaks. The owners left the stand undisturbed except in latter years for grazing and the canopy closed with the maturation of the grubs or more likely with the seeding in of an even aged stand of bur oaks. The ages of burs cut at the edge of the stand ranged between 75 and 105 years, with a mean age of 88 years. The closed grown habit of the bur oak trees shown in Figure F-6 is rare for Wisconsin. There are 123 trees per acre and a basal area of 221 square inches. The trees are tall, with a mean of 61 feet, a height to the first limb of 17 feet and a narrow
canopy of 23 feet. The height to canopy and basal area ratios are all the antithesis of the open grown burs of Albion and Butte de le Chien.
FIGURE F - 1

Graph Showing the Relationship Between Dominance Per Acre and Percent Canopy Cover.

FIGURE F - 2

Graph Showing the Relationship Between the Ratio of Height to Basal Area and Dominance Per Acre. The Divided Trend is the Result of Two Separate Historic Origins of Savanna with the Lower Trend Representing Open Stands with a Few Large Trees which Have Closed Their Canopies and the Upper Trend Pioneer Forest which has grown up from the growth of grubs.
FIGURE F - 3

Photograph of Bur Oak Open, Northern part.
Near Albion, Wisconsin. There are 23
Trees Per Acre with a Mean Basal Area of 587
square inches and a Height of 56 feet; the
Percent Canopy Coverage is 66.

FIGURE F - 4

Photograph of Bur Oak Open, Southern Part.
Near Albion, Wisconsin. There are 15 Trees
Per Acre with a Mean Basal Area of 656
square inches and a Height of 55 feet, the
Percent Canopy Coverage is 44.
FIGURE F - 5

Photograph of Bur Oak Open Near Wyalusing, Wisconsin. There are 49 Trees Per Acre and a Mean Basal Area of 151 square inches and a Percent Canopy Coverage of 40. Understory plants to the Right are *Rhus glabra* and *Andropogon gerardi* and to the Left are *Sorghastrum nutans* and *Solidago rigida*.

FIGURE F - 6

Photograph of Bur Oak Forest with Closed Grown Trees. Near Basco, Wisconsin. There are 123 Trees Per Acre with a Mean Basal Area of 221 square inches and a Canopy Coverage of 93 percent. The mean Tree Height is 61 feet.
**TABLE F - 1**

Tree Size and Shape in Savanna Stands

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* T/A is trees per acre; MBA is mean basal area in square inches; D/A is dominance per acre; TH is tree height in feet; % CC is percent canopy cover; H/D is ratio of height to diameter of canopy; H/BA is ratio of height to basal area. Stands are arranged in table in order of increasing dominance per acre values.
CHAPTER VII

TAXONOMIC VARIATION IN SAVANNA TREES

One of the most interesting aspects of three summers of field work in Wisconsin was the observation of the tremendous variability in the characters useful in identifying tree species, a variability often noted by Wisconsin field workers. In some species, this variability is probably induced upon a genetically homogeneous population by varying biotic and physical conditions and would disappear if transplant experiments into a uniform environment were undertaken. Within other species, however, there is an apparent continuous interchange of characters across specific boundaries and identification becomes impossible.

The examples of character interchange in Wisconsin seem to occur within two basic situations: that of a population which is moving apart genetically and which shows a great heterogeneity among its diagnostic characters and its ecologic behavior; and that of a population of interfertile "species", which in the past have undergone geographic or ecologic isolation, and then have reunited with a resultant hybridization and introgression which have obscured the original specific boundaries.
Variability Within Diverging Populations

There are several savanna species which can be clearly recognized as separate entities and which nevertheless show clinal movement of morphologic and ecologic characters. *Tilia americana*, for example, occurs in the Driftless Area not only in mesic to moist closed canopy forests but in fairly open forests on steep north and east facing slopes and in cedar glades on south-west facing slopes and ravines. The frequency distribution pattern of *Tilia* in Table E-3 shows a bimodality into a dryland and moistland *Tilia* which either indicates two distinct populations or the same population with the central part of its amplitude excluded by a consideration of its behavior only within savanna.

Two populations could be historically possible if the moistland *Tilia* during glacial advance was either destroyed or retreated to the southeast. In either case, the *Tilia* which re-entered Wisconsin following glaciation may have built up sufficient differences to separate it from the *Tilia* which is thought to have remained during this time in the Driftless Area. Unfortunately, when the cedar glades which contained *Tilia* were sampled, the existence of a separate complex was not suspected and no specimens were taken. In general, though, the dryland *Tilia* had fairly pubescent leaves half the size of *Tilia americana* and the trees were often many-trunked and under 30 feet in height with a round top. All of these
differences, however, might be related to the circumstance of being open grown and growing in a "bleak" habitat.

All, or most, of the *Tilia* may have come, however, from the Driftless Area and have moved into central and eastern Wisconsin following glaciation as a member of the Northern Hardwood Forest or some as yet undesignated Boreal Forest -- Northern Hardwood mixture. If this movement occurred, then the Wisconsin *Tilia* could be part of one heterogeneous population. Within this population an even cline of diagnostic characters should be observed from the dryland Driftless *Tilia* to the *Tilia* of closed canopy drained forests in both western and eastern Wisconsin and then to the *Tilia* of the Northern Hardwoods, swamp hardwoods and bottomland forests. The bimodality of its savanna distribution would then be founded off by an inclusion of its entire amplitude behavior.

**Variability Within Reuniting Populations**

There have been many recent historic factors which have led to rapid and widespread geographic and ecologic shiftings in the tree populations of eastern North America. Many of these factors are climatic and are related to the geographically shifting balances of relative strength and weakness which the boreal, gulf and western air masses maintain among themselves. Perhaps directly related to patterns of air mass movement are other factors including advancing and receding glaciation, the
north and southward movement of the Caribbean Sea onto the Coastal Plain and the east and westward fluctuation of drought. All these factors induce a constant diverging and reuniting of similar parts of many species complexes. (All "species" of the black or white oak group are in this case considered one species complex.) The net result of these movements is the failure of any one part of a population to keep its distinctive genes from diffusing throughout the population. This, of course, does not mean that all parts of a species complex come to resemble each other -- some sexual barriers become established and some trees in the complex are sufficiently distinct to prevent much mixing. But, on the whole, between the end points of the population there are independent multidimensional gene flows and, therefore, reticulate and not linearly branching phylogenies.

Within the black oak group most, if not all, of the "species" are interfertile and many hybridization studies have been made, mostly on fairly divergent populations with a good set of diagnostic characters (see especially the articles by Muller and others in Evolution). The Wisconsin black oaks are yet unstudied, although it is the opinion of field workers here that if there are several separate species, it will require subtle techniques to ascertain their genetic make-ups.
An attempt to pick a set of characters which could separate any member of the Wisconsin black oak group was undertaken by Brown (1951). He found that the characters used to identify *Quercus ellipsoidalis*, *Quercus velutina*, and *Quercus rubra* varied with the geographic location of the taxonomist and also apparently with the ecologic conditions under which he collected. A diagnostic character for a species in one region was often applied to another species in a different region and among these three species there were movements of characters similar to those described for the sugar maple complex by Desmarais (1952).

In the savannas, these species were considered separate entities but they can as well be regarded as one species with a fairly wide amplitude. In general the cline between *Quercus ellipsoidalis* and *Quercus velutina* was so even that no distinct possible hybrids were seen. Between *Quercus velutina* and *Quercus rubra*, however, although there is also continuous variation, intermediates seem to be more common, suggesting recent hybridization. These intermediates are very common in the Driftless Area and have a pale orange-pink cambium; a smooth bark only partly broken into plates; and acorns, buds and leaves, which are exactly intermediate in size and shape. The acorn, for example, has a cup which is almost turbinate and never flat like *Quercus rubra*, but which covers usually less than one-third of the acorn and is larger than that
described for *Quercus velutina*. An observation of these oaks in forests showed they were also intermediate in their ecologic position and could have been assigned an upland hardwood adaptation number of 3 or 4.

Some of the lower right-hand portion of the *Quercus velutina* distribution in Table E-3 might belong to *Quercus rubra* although, in general, *Quercus rubra* stays out of savanna because of its fire susceptibility.

The above example is of a complex with complete interspecific variability. Within the white oak group, however, hybridization was often noted. Between *Quercus alba* and *Quercus macrocarpa* there seems to have been an extensive gene flow from the F-1's back to the *Quercus alba* parent. Throughout southern Wisconsin many white oaks were found with leaves varying from a typical white oak shape (i.e., as shown in taxonomy books) to a shape medium between white oak and a typical Wisconsin bur oak leaf. The leaves were often more leathery than normal white oak leaves, but there was little pubescence on the underside. Some white oaks showed the peculiar half and half leaf with each side the shape of one of the parents. The acorns of many white oaks showed a deeper cupping and a greater fringing than is characteristic of the species. The variability in the time of leaf fall, hairiness of buds and thickness and tightness of bark has already been discussed in Chapter V as a possible indication of introgression.
The white oaks not clearly F-1's and having the greatest proportion of bur characters were found on upland areas and usually on south and west slopes in fairly open stands. Those trees which were distinctly intermediate, the hybrid *Quercus bebbiana*, grew mostly toward the lower part of the savanna gradient (Table E-3). Here the ecologic advantage of a bur-white hybrid would lie in the combination of the fire tolerance and the tolerance of poor drainage of bur oak with the ability of white oak to withstand medium shading.

The most common recognizable hybrid in the savannas is *X Quercus schuettei*, a cross between *Quercus macrocarpa* and *Quercus bicolor*. The frequency distribution pattern of *X Quercus schuettei* shows in Table E-3 an amplitude width similar to *Quercus bicolor* but peaking more strongly toward the left, where *Quercus macrocarpa* is found. The survival of this hybrid could be the result of a utilization of an intermediate habitat although both parent species occupy the same gradient area and no hybrids were found occurring by themselves without one or both parents present. *X Quercus schuettei* was found with greatest presence and frequency in Jefferson County along the Rock River, was less frequent in the meadows of Jefferson, Waukesha, and Fond du Lac Counties, and occurred occasionally on the sand terraces of the Wisconsin River in Dane and Sauk Counties. It varied from
several to many trees per stand, one stand on the Rock River in which collections were made contained almost half X Quercus schueetlai. The ecologic advantage of such a cross could be in the fire resistance of bur combined with the flooding tolerance of swamp white oak.

There is as great a possibility, however, that the hybrid has no adaptive advantage and is occupying no intermediate habitat, but is the expected result of two interfertile members of the white oak group occurring, because of their overlapping amplitudes, in the same habitat and subsequently hybridizing. The greater abundance of the hybrid in the eastern meadows and river valleys as contrasted to its low abundance along the Wisconsin River is likely the result of a greater amount of bur oak in the eastern meadows as compared to its almost complete absence along the Wisconsin River. Although oak pollen can travel long distances the chances for pollination rapidly diminish as the distance increases. It seems reasonable, that given an equal amount of Quercus bicolor both in the eastern meadows and along the Wisconsin River (which seems to be the case) the relative number of F-1's, if chance is the only factor, will be proportional to the square of the mean distance of Quercus macrocarpa from Quercus bicolor.

The field determination of X Quercus schueetlai is not difficult and is based on an intermediate peduncle length of
from 10 to 25 mm., combined with leaves which are intermediate in shape with a widening of the leaf more nearly toward the middle instead of the strong apical widening of bur oak. There are deeper sinuses than are usual for a swamp white oak leaf, but there is a partial or complete absence of the deep central sinus of the bur oak leaf. In addition, half and half leaves are sometimes seen. Most of the hybrids observed in the field showed on any one tree great variability in the shape of individual leaves and this was the best clue to their possible hybrid nature. Other useful diagnostic characters seemed to occur independently in the hybrids.

The occurrence of many bur characters in trees which could be identified with reasonable certainty as swamp white oak led to a study of a possible introgression from the F-1 back to one or both of its parents. A total of 230 acorns were collected from 28 trees in 14 stands. Each of the trees was identified in the field as parent or hybrid. Measurement of peduncle length, width and length of acorn, and length of fringe on acorn cup were made on each acorn.

The measurements of width and length were very uniform and showed little correlation with the identification of the trees or with the location or habitat of the stand. The lack of relationship to geographic location was in accord with field observations which showed swamp white oak as well as bur
oak to be taxonomically similar from eastern to western Wisconsin. These observations lend further weight to the evidence for a Driftless Area glacial refugium. If the Wisconsin bur oak had entered following glaciation from the south and east, it should resemble the bur oaks of that area. It is, however, clearly distinguishable from the Wabash Valley and Central Illinois bur which has gray slightly flaky bark and much larger acorn cups.

The best evidence for introgression came from a comparison of peduncle length and length of acorn fringe. The pictograph technique of Anderson (1949) was used, in Figure G-1, to show the variability of a single character for each of the parents as contrasted to the varying combinations of both peduncle length and fringe length which the hybrids show. From the pictograph, introgression seems to be moving toward swamp white oak as there is a sharp break in peduncle lengths between the hybrids and bur oak. This sharp break is not present in the movement toward swamp white oak.

Accepting an intermediate peduncle length as a characteristic of the hybrids, a frequency distribution of number of acorns in relation to peduncle length can be shown. Figure G-2 gives the peduncle lengths of acorns of trees identified in the field as bur oak, hybrid, or swamp white oak. Again, the clear separation of bur oak from the hybrid is evident, while the F-1 hybrids also show a distinct amplitude. The distribution of peduncle lengths for trees identified as swamp white
oak shows a multi-modal pattern, however, which suggests, as does the evidence from Figure G-1, the presence of introgression from backcrossing between the hybrids and the swamp white oak parent.
CHAPTER VIII

THE SAVANNA ORIGIN OF SOME WISCONSIN BOTTOMLAND FOREST

While assisting in the field study of bottomland forests, the author noticed and recorded in many stands, the presence of old open grown swamp white, white, and bur oaks which had the same habit as open grown oaks in the upland forest after the canopy has closed. An open grown swamp white oak, one of the largest ever measured in Wisconsin, is shown in Figure E-1. This oak was growing in a closed canopy bottomland forest of the Sugar River near Avon.

In addition to the presence of open grown trees, three other lines of evidence are available besides the historic survey which will be made by Ware (1955), to support the possibility that bottomlands were once savanna. The first is the present day occurrence of savanna in bottomland with a composition similar to that found in the fourth and fifth intervals of Table E-3. The second is the general observation from field work that in many bottomlands, the older trees of the more fire susceptible species were often found in places protected by a possible fire barrier, especially behind sloughs, and lastly is the evidence from past and present composition.

Data from 22 stands, which includes all those which contained an old open grown swamp white oak or bur oak was
divided on the basis of percent density of older and younger trees. An arbitrary basal area was chosen for each species to designate an age of 100 years or more. These basal areas were chosen when data from the clearing agency on tree size and shape, The Lakes States Forest Experimental Station at Saint Paul, Minnesota, failed to show any correlation with data gathered in the field from stumps. This lack of correlation is related to the Station's collection of data from only closed grown stands -- the ones which contain merchantible timber. Basal area levels selected are as follows: black, bur, white and swamp white oak -- 300 square inches; red oak -- 400 square inches; cottonwood -- 400 square inches; black ash and bass-wood -- 450 square inches; red and white ash -- 500 square inches; and red and silver maple and red and white elm -- 600 square inches. All trees over these limits were tabulated and their percent densities shown in column 1 of Table H-1. The second column of the table shows percent density of trees in the stands as they are today minus their old trees.

The trees are arranged in the table by subjective judgment in decreasing order of fire resistance. The change in percent composition between older and younger trees of the same species clearly shows the decrease in importance of fire resistant species and the increased importance of fire susceptible ones. It is true that many of the fire susceptible
FIGURE G - 1

Photograph of Peduncle Length and Fringe Length Showing Introgression from the Hybrid back to the Quercus bicolor Parent. The Dots Represent Mean Averages and the Lines Variation Around the Mean. It should be noted that the Hybrids show variation in two directions while the Parents vary in only one Direction. The two Trees with the greatest Variation are Closest to the Quercus bicolor parent.
LENGTH OF PEDUNCLE IN MM

LENGTH OF ACORN CUP FRINGE IN MM

QUERCUS MACROCARPA

X QUERCUS SCHUETTEI

QUERCUS BICOLOR
FIGURE G - 2

Graph of Frequency Distributions of Peduncle Lengths. The Distributions Represent Number of Acorns (at a Constant Number Per Tree) which were identified in the field on the basis of both leaf and acorn characteristics as either of the two parents or the hybrid. The Several Peaks in the Distribution for *Quercus bicolor* are perhaps the Result of Introgression from the Hybrid.
FREQUENCY DISTRIBUTION

NUMBER OF ACORNS SAMPLED

PEDUNCLE LENGTH IN MM

QUERCUS MACROCARPA

QUERCUS SCHUETTEI

QUERCUS BICOLOR
trees are intermediate to climax species while the resistant ones are intermediate to pioneer, but if fire were not a factor in bottomlands 100 years ago there is no reason why there should not have been as many fire susceptible trees of intermediate successional status. A detailed age study was made by Leopold (1941), which shows older trees to be swamp white oak and younger trees to have started about 100 years ago during the time when fires were beginning to come under control in Wisconsin.
FIGURE H - 1

Photograph of Old Open Grown Swamp White Oak in Bottomland Forest. The Tree is a Surviving Member of a Possible Early Savannah.
## TABLE H - 1

**Savanna Origin of Bottomland Forest**

**Past and Present Composition**

<table>
<thead>
<tr>
<th>Species</th>
<th>100 Years</th>
<th>Younger</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Quercus macrocarpa</td>
<td>5.7</td>
<td>2.7*</td>
</tr>
<tr>
<td>2. Quercus schuettei</td>
<td>3.2</td>
<td>0.3</td>
</tr>
<tr>
<td>3. Quercus bicolor</td>
<td>31.7</td>
<td>8.2</td>
</tr>
<tr>
<td>4. Quercus velutina</td>
<td>3.2</td>
<td>0.7</td>
</tr>
<tr>
<td>5. Quercus alba</td>
<td>4.9</td>
<td>1.8</td>
</tr>
<tr>
<td>6. Quercus rubra</td>
<td>11.4</td>
<td>4.4</td>
</tr>
<tr>
<td>7. Acer saccharinum</td>
<td>12.2</td>
<td>17.6</td>
</tr>
<tr>
<td>8. Carya ovata</td>
<td>0.8</td>
<td>3.7</td>
</tr>
<tr>
<td>9. Populus deltoides</td>
<td>1.6</td>
<td>0.1</td>
</tr>
<tr>
<td>10. Ulmus americana</td>
<td>12.2</td>
<td>12.8</td>
</tr>
<tr>
<td>11. Ulmus rubra</td>
<td>3.2</td>
<td>9.6</td>
</tr>
<tr>
<td>12. Acer rubrum</td>
<td>2.4</td>
<td>3.9</td>
</tr>
<tr>
<td>13. Betula nigra</td>
<td>0.0</td>
<td>3.7</td>
</tr>
<tr>
<td>14. Fraxinus pennsylvanica</td>
<td>5.2</td>
<td>4.9</td>
</tr>
<tr>
<td>15. Fraxinus nigra</td>
<td>0.8</td>
<td>6.0</td>
</tr>
<tr>
<td>16. Fraxinus americana</td>
<td>0.8</td>
<td>5.5</td>
</tr>
<tr>
<td>17. Carya cordiformis</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>18. Tilia americana</td>
<td>2.4</td>
<td>8.4</td>
</tr>
<tr>
<td>19. Acer saccharum</td>
<td>0.0</td>
<td>2.1</td>
</tr>
<tr>
<td>20. All other species</td>
<td>0.0</td>
<td>2.6</td>
</tr>
</tbody>
</table>

* Columns show percent density of species older and younger than 100 years in bottomland stands. Total of 1,760 trees.
CHAPTER IX

PHYTOSOCIOLOGY OF HERB AND SHRUB STANDS

In 82 savanna stands, which were sampled in 49 separate geographic locations, there were a total of over 300 shrub and herb species. Only 109 of these species appeared in more than 20 percent of the stands, however, and of these 109 species, 52 accounted for a sum of presence greater than half of the sum of presence for the entire list of species. A list of all species which occurred in three or more stands is shown in Table I of the Appendix. In surveying the 199 species presented in Table I, it should be remembered that the impossibility of drawing a sharp line to separate savanna along its continuously closing canopy led to the inclusion of a few sampled areas which were more nearly like pioneer forest. Some of the species with low presence levels, as Osmunda claytoniana and Eupatorium rugosum are not, therefore, "typical" of savanna although other species with a low presence, like Xanthoxylum americanum and Saladinella rupestris are found in some characteristic savanna stands.

The first column of Table I shows presence within 82 "phytosociologic" stands; that is, all those stands which meet the criterion of homogeneity but were not necessarily geographically distinct. To be counted present in the stand the species was expected to occur in at least one of the sampled quadrats.
The second column of Table I shows the sum of the percent frequencies of each species among the 82 "phytosociologic" stands. These sums of percent frequency are usually considered, along with some evaluation of the aspects of density and dominance, to represent the relative importance of a species. Although no density measurements were taken in the field it was evident that there were great differences in the number of individuals per quadrat. Thus, *Galium boreale* was often more dense than *Amphicarpa bracteata* and *Smilacina stellata* more dense than *Smilacina racemosa*. The aspect of dominance was not of as great importance, since many savanna species, like many prairie species, are fairly comparable in size. There are, however, several large woody shrubs which often have a high dominance which is not reflected by a similarly high level of frequency. These shrubs include *Celastrus scandens*, *Cornus racemosa*, *Corylus americana*, *Rhus glabra* and *Vitis riparia*, and are marked with an asterisk beside the second column of Table I.

Mean frequency per stand of occurrence is shown in column 3 of Table I. It is interesting to note that there is an overall correlation between level of presence and level of mean frequency per stand of occurrence. Species with high presence tend to have fairly high mean frequencies, while the species with low presence have low frequencies. The mean frequency per stand of occurrence of the 20 species with the
highest presence in 29 while the mean frequency of the 20 species with the lowest presence is only 11. There are, however, several species with a low presence which reach very high (mean) frequency levels, among them Aster pilosus, Helianthus grosseserratus and Silphium terebinthinaceum.

The fourth column of Table I shows presence within 49 "geographic" stands; that is, within 49 separate geographic locations at which savanna was sampled. This column was included since there are some species whose level of presence in column I of Table I is inflated by occurrence within some of the phytosociologic stands, which were not geographically separate. Lithospermum canescens, for example, has a percent presence of 61 in column 1 and of 49 in column 4. Comandra richardsiana, on the other hand, increases its percent presence from 62 to 77 by the consideration of only geographic stands.

The fifth column of Table I shows whether the species was included in the Tabulation Forms used to summarize the data from previous studies in Wisconsin of prairie and upland forest. (Gilbert, 1953; Curtis, 1955). Of the 199 species shown in the Table, 94 are listed only on the Prairie Survey Tabulation Form, 34 are found only on the Forest Survey Tabulation Form, 57 are found on both forms and 14 occur on neither.
Of the 42 species which occur in 25 or more stands, 23 are found on both the forest and prairie form, while the rest are, for the most part, prairie species. Of the 100 species of Table I with the lowest presence, however, only 15 occur on both forms. Thus, the general observation that less common species are more likely to be ecologically restricted in their amplitudes is upheld by the data from savannas.

The 14 species which did not occur on either tabulation form were either European plants or native species with a very limited geographic occurrence in Wisconsin, as Symphoricarpos occidentalis in a few western counties. A few species were found in savannas which were probably omitted by oversight from the Prairie Form, as Opuntia fragilis on the dry fine-sand prairies along the Wisconsin River and Campanula rotundifolia of the steep lime prairies of western Wisconsin.

Relation of the Composition of Savanna to That of Prairie and Forest

No species were found in the savanna study which could be considered to be limited in their amplitudes to savanna and, therefore, fidelic. Several species were found which are almost limited to savanna, among them Symphoricarpos occidentalis, Convolvulus spithamaeus, Wulfenia bullii, Ceanothus americanus, Aster sagittifolius and Tephrosia
All of these species are occasionally found in prairie but it is almost always a shrubby prairie, while the species never are found in very closed canopied woods.

Of the 20 most important savanna species by level of sum of percent frequency, 4 are grasses, 4 are woody shrubs, and 12 are broad leaved herbs. Of these 20 species, 10 reach their peak importance in prairie, 6 peak in savanna, and 4 reach peak importance in forest. (See Table I-1).

Of the 109 species in savanna which occur in 20 percent or more of the stands, 27 are composites, 13 are grasses, 10 are legumes, 6 are roses, 6 are lilies, 4 are crowfoots and the remaining 43 species are scattered among 32 families. Floristically, therefore, the important families in savanna are similar to the important families of the prairies.

In general, savanna contains both on a frequency and density basis, less grass and more forbs and woody shrubs than prairie, while it contains more grass, about the same amount of woody shrubs and fewer forbs and woody vines than pioneer to intermediate forest.

Perhaps the best notion of the general physiognomic structure of savanna understory can be gained from the photographs of Figures I-1 and I-2. These pictures were taken standing in the same place at Garwin Heights, with Figure I-1 showing the view toward the open prairie and Figure I-2 showing the view toward savanna.
The Phytosociologic Structure of Savanna Herb Stands

It has been shown that the floristic composition of savanna is a mixture of prairie and forest flora with no fidelic species. It has also been shown that the dominant species of savanna are usually those which appear in both prairie and forest. This section will examine the position of savanna stands in relation to the stands of prairie and forest.

Although savanna contains no fidelic species, there still exists the possibility that its dominant plants only narrowly exceed the arbitrary boundaries of savanna and that these species reach such a great importance within savanna that a discrete association, based on quantitative behavior, could be delineated. This association could be shown by demonstrating that the important species of savanna reach greatest presence only within savanna stands and not within prairie or forest. The possibility of an association was tested in Table I-1 by comparing the percent presence of species within 59 prairies, 49 savannas and 60 pioneer to intermediate forests. The prairie and forest stands were taken from the vegetation files of the Ecology Section at the University. To be counted present the species had to occur in at least one quadrat within the stand.

Of the 76 species in Table I-2, all should reach greatest percent presence within savanna, if there is a genuine
association. Only 32 species peak in savanna, however, with 23 species peaking in prairie, and 21 species peaking in pioneer to intermediate forest.

The possibility of two distinct floras with little mingling must, therefore, be doubted and the alternative of continuous variation be examined. This examination will cover two main areas: that of an actual spatial transition which can be observed and measured in the field; and that of a theoretic transition in the quantitative structure of all savanna stands.

**Spatial Transitions**

All of the seven detailed herb studies mentioned in the methods section were made by following, in the field, a gradient from prairie through savanna and into forest. The spatial distance in the field was divided for each of the seven studies into equal parts and the quantitative behavior of the species determined for each part. These parts have previously been referred to as phytosociologic "stands". Five of the detailed studies included 100 quadrats and these studies were divided into five parts each containing 20 quadrats. For two of these studies, Butte de le Chien and Kettle Moraine, the division was made on the basis of previously established "blocks" as discussed in Chapter IV. For the other three studies, Kenosha, Lake Lula, and Scuppernong, all quadrats
which occurred eight to ten meters from a tree were included in the first part; all quadrats six to eight meters distant in the second part; and so forth.

The remaining two studies which contained 200 and 190 quadrats were divided into ten and nine segments, respectively. The study with 200 quadrats, that of Trempealeau was divided, not on the basis of actual field separation which did not show continuous variation, but of a continuum constructed from a study of mutual species occurrence (Bray, 1956). The Garwin Heights study with 190 quadrats contained four stand segments sampled by scattered quadrats within blocks and five segments based on transects projected beneath the canopies of trees. These segments were arranged into a linear order by a visual trial and error process.

The behavior of all species in each of the seven detailed studies is presented in Tables 2 through 8 of the Appendix. The frequency distribution patterns in Tables 2 through 8 show approximations to normal distribution with a continuous change in dominant species from the prairie to the forest end of each gradient. No summarizing of the gradients of Tables 2 through 8 is possible because they do not cover the same part of a transition, since some are more toward the prairie end and some more toward the forest end. Without any detailed analysis of the patterns it will be stated that, by demonstrating the continuity of change in species dominance from prairie to forest, they add further evidence to the unlikelihood of a savanna association.
Along the savanna tree gradient there is no good correlation between the percent canopy coverage of a stand and its position within the gradient. Any correlation of herb behavior with the order of stands of the tree gradient is, therefore, doubtful, since canopy coverage is a major factor in herb distribution. The distribution of a number of common herbs was plotted along the tree gradient and the result was for the most part bimodal and multi-modal curves. Whatever trends were noticeable followed fairly closely the species patterns of the prairie continuum from dry to mesic (the moist stands were all grazed), which is to be expected since the tree gradient is, in general terms, a dry to moist gradient.

The fortunate circumstance of the availability of forest and prairie herb continua constructed by Gilbert (1953) and Curtis (1955) led to the possibility that savanna herb stands could be shown simultaneously within each continua as part of a two-dimensional ordination.

The assignment of adaptation values for this ordination was based on those values assigned by Gilbert and by Curtis. Prairie adaptation values were based on the continuum table of Curtis. All species which occurred in ten or more savanna "geographic" stands were assigned a value from 1 to 3 depending on whether they peaked in the last three columns of the prairie table, the middle three columns, or the first three
columns. Twenty species were assigned a value of 1, 20 species a value of 2 and 11 species a value of 3. The adaptation values are shown in column 4 of Table I-1. Since only 11 species were assigned a value of 3, the next nine species in Table I which peaked in the first three columns of the prairie continuum were also assigned a value of 3. Forest adaptation values were based in part on those assigned by Gilbert and in part on the behavior of species among the first three columns of Table I-1. The final forest values are shown in column 5 of Table I-1 and include 23 species with a value of 1, 33 with a value of 2, and 21 with a value of 3.

A total of 91 stands (which included some of the pioneer stands of the upland hardwoods) were then assigned positions within the prairie and forest continua. This position was determined by the average adaptation value of the species in each stand after each species had been weighted by its level of frequency.

The position of each of the 91 stands along the forest continuum is shown on the x axis of Figure I-3, while position along the prairie continuum is shown on the y axis of the same figure. The resultant patterns of stand locations in Figure I-3 give a linear distribution in which location along one axis is highly significantly correlated, using the correlation coefficient, r, with location along the other axis.
A linear compression of the stands of Figure 1-3 was, therefore, attempted. A diagonal line was drawn which follows the trend of the appearance of stands within the figure. The position of each stand was then projected, at right angles, onto the line of the diagonal, and the diagonal divided into eight equal parts. The frequency behavior of all savanna species with an occurrence of five or over in geographic stands is shown, for each of the eight gradient parts, in Table I-2. Also shown in Table I-2 are the frequency distribution patterns of some pioneer and intermediate forest species.

As in the spatial transition patterns of Tables 2 through 8, the species peaking toward the extreme left of Table I-2 are those which are of greatest importance within prairie, while those which peak toward the right reach greatest importance in forest. Between the two extremes in Table I-2, there are continuously appearing normal frequency distributions which further demonstrate the continuum nature of the savanna transition.

Photographs showing understory cover in the Kettle Moraine and in two low prairie savannas are presented in Figures 1-4 through 1-6. Additional photographs of high prairie savanna are shown in Figure E-1 and of mesic prairie savanna in Figure F-5. Photographs of herbs under a more closed canopy are shown in Figure I-2 of this Chapter and in Figures E-7 and E-9.
FIGURE I - 1

Photograph of View Toward Prairie. Garwin Heights, Winona, Minnesota. Dominant Grass is *Andropogon gerardii*.

---

FIGURE I - 2

Photograph of View Toward Savanna. Garwin Heights. Forbs in Picture Include *Ratibida pinnata*, *Solidago speciosa*, and *Solidago ulmifolia*. 
FIGURE 1 - 3

Graph of Savanna and Pioneer Forest
Herb and Shrub Stands Showing Locations
Within a Two-dimensional Ordination.
FIGURE I - 4

Photograph of Dry Prairie Savanna, on Kettle Moraine, Nashota, Wisconsin. Grasses include *Stipa spartea* and *Andropogon scoparius* with *Amorpha canescens*.

FIGURE I - 5

Photograph of Low Prairie Savanna, Soupperomng Prairie Preserve, Eagle, Wisconsin. *Corylus americana* on right with *Silphium terebinthinaceum* and young Bur Oak Seedlings.
Photograph of Low Prairie Savanna,
Near Kenosha, Wisconsin. Flowering
Plants in Foreground are Ratibida
pinnata and Liatris pyenostachya.
### TABLE 1 - 1

Presence of Savanna Herbs and Shrubs in Prairie, Savanna and Forest; Assignment of Adaptation Values

<table>
<thead>
<tr>
<th>Species</th>
<th>Pr.</th>
<th>Sa.</th>
<th>Fo.</th>
<th>P.A.</th>
<th>F.A.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Euphorbia corollata</td>
<td>89</td>
<td>84</td>
<td>15</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2. Comandra richardsoniana</td>
<td>59</td>
<td>77</td>
<td>05</td>
<td>2</td>
<td>2</td>
</tr>
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**Additional Values**

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* The first three columns show percent presence in 59 prairies, 49 savannas and 60 pioneer to intermediate forests. To be counted present, the species must occur in at least one quadrat in each stand. The last two columns give the assigned prairie and forest adaptation values. The arrangement of species is after their level of percent presence in savanna.
### TABLE I-2

**Savanna Herb Compositional Gradient**

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<td>104. Rubus strigosus</td>
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</table>

* Column 1 contains only one stand. The meaning of the values in Column 2 is explained in Chapter XI.
CHAPTER X

STUDY OF SCUPPERNONG PRAIRIE PRESERVE

Scuppernong prairie was sampled by laying two transects, one running in a north-south and the other in an east-west direction. These transects crossed each other at right angles and there were two bur oaks at the point of intersection. The short distance between the two oaks was not sampled as a part of the transect. Each transect contained 50 quadrats which were each one meter on a side. The transects were divided into 20 stands, each of which contained a length of five contiguous quadrats.

Eight different arrangements of these 20 stands were made by aligning the stands along linear gradients determined by phytosociologic, environmental, and random factors.

1. Prairie Continuum.

The first gradient is based upon a phytosociologic alignment in which each stand was assigned a position within the prairie continuum constructed by Curtis (1955). The adaptation values used in the continuum construction were the same as those assigned by Curtis and the continuum value for each stand was determined by the mean adaptation value of its included species after each species had been weighted by its level of relative frequency after the method described in Chapter V.
The continuum values are given for each of the 20 Scuppernong stands in column 1 of Table J-1. The values show a range of from 1.89 to 2.87 which is within the mesic-moist area of the prairie continuum.


The second gradient was ascertained by an ordination of a matrix of Quantitative Coefficients of Community. The ordination method was modeled, in part, on the diagonal factoring method of Thurstone (1947, Chapter 4), although it is not in any sense a factor method and does not represent an attempt to draw out basic factorial elements, the existence of which is very much in doubt if a strict cause and effect relationship is to be discarded. Rather, the ordination method attempts to place stands or species within a spatial configuration in which the distance between the stands or the distance between the species is a reflection of degree of phytosociologic relationship. This phytosociologic relationship is represented in distance between stands by degree of similarity of composition, and is represented in distance between species by degree of correspondence of amplitude (Whittaker, 1954; Bray, 1956). Either a stand ordination or a species ordination is sufficient, since from stand orderings the amplitude behavior of species can be determined, while from species orderings, adaptation values can be assigned and stand locations determined.
In general, it is better to use the matrix which has the least entries. Thus, if there are 100 stands with 4,950 matrix entries and 30 prominent species with 435 matrix entries, it will obviously be easier to construct and analyze the species matrix. If, however, there are the same number of stands as there are of prominent species, then it is better to construct a stand matrix, since the use of a species matrix would always require the additional steps of assignment of adaptation values and of continuum construction before stand locations could be determined. The number of stands is less in the Scuppernong study than the number of species with a frequency of 10 percent or greater and a matrix of coefficient values among the 20 stands was, therefore, calculated. There are several coefficients which can be used to measure relative similarity of stand composition, including \( r \), the correlation coefficient. The Quantitative Coefficient of Community of Gleason (1920) was considered to be the best for ordination purposes since it gave the greatest sensitivity over the upper and medium range, while the correlation coefficient was most sensitive over the lower range of values where high sensitivity is not necessary.

The analysis of a matrix of coefficients of community depends on locating two peripheral stands which can be used as reference points between which the other stands can then be arranged by their degree of coefficient relationship with
the peripheral stands. The peripheral stands chosen for the Scuppernong ordination were those which showed the lowest coefficient value with each other and were, therefore, considered to be separated by the greatest relative distance. In addition, these peripheral stands were expected to show a good range of values with the other stands.

The two peripheral stands chosen were numbers 13 and 18, and it was the relative degree of relationship with these two stands which determined the positions of the Scuppernong stands along the first axis.

It is necessary, if the sets of coefficient values with both of these peripheral reference stands are to be averaged and expressed along a common axis, that the coefficient values of one of the reference stands be reversed. This necessity can best be shown by the following hypothetical example.

In Figure J-1, two reference stands are separated by a linear distance of 100 units. A third stand is located along the axis connecting the two reference stands and this stand has a coefficient value of .60 with the first stand and .40 with the second stand. If coefficient value is equated with spatial distance, then the higher the coefficient value, the closer is the relative position of any two stands. The spatial distance away from any stand used as a reference point should, therefore, be expressed in descending magnitude of
coefficient value. This has been done in Figure J-1 where the distance away from reference stand 1 is shown in the upper scale printed beneath the x axis and the distance away from reference stand 2 is shown in the lower scale. Stand number 3 is located then at .60 on the upper scale and at .40 on the lower scale. To express the position of stand 3 solely in terms of the upper scale it is, therefore, necessary to reverse the unit values shown on the lower scale. This can be done by subtracting any value on the lower scale from the highest value which it is possible within the study for the coefficient to attain and adding this resultant to the lowest value which it is possible for the coefficient to attain. In our example, this means subtracting the value of .40 from 1.00 and adding this value to 0.0 for a reversed value, expressed in terms of the upper scale, of .60. Stand number 3 in Figure J-1 is now found occurring at position .60 along the upper scale of the x axis by reason of its coefficient value of .60 with stand 1 and by reason of its reversal coefficient value of .60 with stand 2.

The technique of reversal of coefficient values is especially important if the stand to be located is not on a line connecting the two reference stands. For example, stand number 4 in Figure J-1 is not on this line but occurs directly above the middle point of the x axis. Stand 4 has a coefficient value of .29 with both reference stands 1 and 2. To determine
the location of stand 4 along the x axis without a previous knowledge of its location, it is necessary to reverse the coefficient value of stand 4 in relation to the second reference stand. This is done, as in the previous example, by subtracting its coefficient value with stand 2, which is .29, from the highest coefficient value, 1.00 and adding the result to the lowest value, 0.0. The final reversed value is, therefore, .71. The position of stand 4 along the upper scale of the x axis in Figure J-1 is then determined by averaging its location in relation to the first reference stand, .29, with its location in relation to the second reference stand, .71, for a mean position along the x axis of .50.

This projection technique of stands onto the x axis represents essentially a compass rotation onto the x axis of stand position in relation to the two reference stands. The two rotated x axis positions are then averaged to determine the stand location. The method is completely accurate only when the stand to be rotated is directly above the middle point of the axis, and it very gradually loses accuracy as the stand position moves away from the middle point. This loss is not too important, however, since the situation in which the least accuracy is noted, that of a stand occurring at a right angle above one of the reference stands, is not likely to occur if most stand distribution patterns are ellipsoidal or solid, normal solid normal.
In the Scuppernong ordination, stand number 16 had a coefficient value of .34 with reference stand number 18 and of .47 with reference stand number 13. If the position of stand number 16 is to be determined along a common x axis, it is necessary to reverse the value of .47 by subtracting it from the highest coefficient value, which is .65 and then adding the resultant value to the lowest coefficient value, which is .34, for a final value of .52. The mean position of stand 16 along the x axis is, therefore, .34 plus .52 divided by 2 or .43.

The results of the ordination analysis are shown in column 2 of Table J-1 where there is a range of values from .33 to .65. This range shows a medium to high amount of vegetational similarity among the stands.


The third gradient, based upon level of elevation, is one which in many low prairies exercises a critical control over certain aspects of the physical and biologic environments. A cline of slightly over one meter was measured with an Abney Level and a surveyor's pole from the higher and noticeably drier part of the Scuppernong transects to the lower and noticeably moister parts. Along this cline there are many environmental factors whose expression is controlled by elevational level. Possibly of major importance is a decrease in
drainage pressure, both surface and sub-surface, from the higher to lower parts, with the lower parts being wet almost throughout the year and probably at or near the level of the water table. Other factors which are possibly correlated with this drop in elevation are a decreasing soil permeability, soil aeration, and dried soil weight, and an increasing moisture retaining capacity. The position of each of the Scuppernong stands in relation to the lowest stand is shown in column 3 of Table J-1. The highest stand, number 16, is 11.0 decimeters above the lowest stand, number 18.


The fourth gradient represents an attempted measurement of a direct environmental factor, that of soil water retaining capacity. From three of the five quadrats in each of the 20 stands, a composite sample of three soil cores was taken, making a total of nine cores for each stand. The determination of water retaining capacity on these composites utilized the same technique as is described in Partch (1949). For each stand three tests, one on each of the composite samples, were carried out. Great care was taken that each test be made upon a homogeneous mixture of the ground and sieved soil particles. The range in mean values for water retaining capacity is from .89 to 1.32. The values are shown in column 4 of Table J-1.

The fifth gradient is also based upon the measurement of a direct environmental factor, that of the dried weight of a constant volume of soil. The samples used for the dried weight test were the same as those upon which water-retaining capacity was later measured. The nine soil cores available from each stand were taken with a soil borer and each core had a constant volume. The cores were air dried in the laboratory for several months and were then weighed, each composite sample of three cores being weighed together. The samples from the stands with better drainage can be expected to have less organic matter in relation to their mineral content and, therefore, to maintain a higher weight. The mean weights in grams for the 20 stands are shown in column 5 of Table J-1. There is a variation in mean weight among the stands from 56.9 to 78.9 grams. For both the soil moisture and water retaining tests, the three composite measurements, upon which the mean value for any one stand depended, showed a low mean deviation. The two environmental tests were, therefore, considered to be accurate representations of the soil factors which they attempted to measure.

6.7. Random Order.

The next two gradients were ascertained by two independent and haphazard entries into the random numbers table
listed in Snedecor (1946). These values are given in columns 6 and 7 of Table J-1.

8. Disordered Arrangement.

The next gradient of Table J-1 represents a deliberate attempt to disorder the arrangement of stands; that is, to go beyond a random arrangement and place the stands in the highest possible lack of complexity to each other. Such an arrangement, of course, requires that one know as much about the stands as is needed to arrange them in a highly complex fashion. This disordered arrangement was made by taking groups of stands from the phytosociologic gradients and rearranging them within a linear gradient so that there was an alternation of closely and distantly related stands throughout the new arrangement. This disordered gradient is shown in column 8 of Table J-1.

A correlation test was made among the first five gradients of Table J-1 by comparing the stand positions in any one gradient with the stand positions in any of the other gradients. The correlation matrix using the correlation coefficient, \( r \), (Snedecor, 1946), is shown in Table J-2. The first three gradients have among themselves a highly significant correlation, with values of .75, .78, and .89. The necessary one percent level of significance is .55. It may, therefore, be concluded that the phytosociologic gradients, numbers 1 and 2, and the control gradient, number 3, show
similar stand arrangements and these arrangements are very probably determined by similar underlying factorial complexes. The first three gradients were not, however, correlated with the next two gradients of Table J-1, those based upon environmental measurements. The highest correlation among the first three and next two gradients is .52 and the lowest value is .21, giving a range of values lying beneath the level needed to attain high significance. This suggests that the two environmental gradients do not correspond to and, therefore, do not causally determine the order noted in the phytosociologic ordination gradients. The two environmental gradients, numbers 4 and 5, do, however, give a highly significant correlation with each other which indicates they are probably interactive parts of the same complex.

A further analysis of the eight Scuppernong ordinations will be made in Chapter XV.
FIGURE J - 1

Graph of a Modified Factor Analysis Technique. The Location of Point 4 along the Upper Scale is Determined by Rotating Arcs, which represent the Distance from the Two Endpoints, onto the x Axis. The Mean Position between the Two are Intersections with the x axis is the Location of the Point.
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*The eight columns of Table J-1, show: 1 -- Prairie Continuum Index. 2 -- Sector position, modified factor analysis. 3 -- Elevation from base in decimeters. 4 -- Index of Soil Water Retaining Capacity. 5 -- Weight of constant soil volume in grams. 6 -- Random numbers. 7 -- Random numbers. 8 -- Disordered arrangement of Prairie Continuum in relative values.
### Correlation Matrix of Five Ordered Scuppernong Gradients

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<td>.21</td>
<td>.41</td>
<td>.71</td>
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</table>
Soil Type and Savanna Composition

There is no apparent limitation of savanna to a definite soil type. There is, however, a tendency for some kinds of savanna to be more prevalent in certain soils, but this prevalence is usually induced by many related factors. Thus, in general, red cedar glades occur on fine sandy to sandy loam soils which have a high lime content. This occurrence is related, however, to historic and topographic coincidences.

Red Cedar is limited in distribution to fire protected areas on bluffs, draws, and steep slopes. As a result of past geologic happenings, most areas in Wisconsin which are sufficiently bluffly to protect cedar have a parent material of either overlapping layers of limestone and limey sandstone, or of limey loess which lies on quartzite rocks of the Baraboo Hills.

The original occurrence of bur oaks on deep "prairie" soils and the high prevalence of black-white oak savannas on the thinner, slightly leached soils of medium to steep slopes
is also related, not to a preference of these trees for a definite soil type, but, as discussed in Chapter V, to an interaction between the ecologic amplitude of these species and past historic factors.

**Vegetational Influence on Soil Factors**

The influence of savanna and forest vegetation on some physical and chemical soil factors is shown in Table K-1. The first eight columns show mean values for the eight intervals of the savanna continuum while the next three columns show data from three sections of Gilbert's upland forest herb continuum (1953).

The first five lines of the table show amount of various soil minerals in terms of pounds per acre at an assumed seven inch soil depth. The actual nutrient determinations were made on samples of $A_1$, so the values in the first five lines give the fertility of stands with a constant hypothetical $A_1$ of seven inches.

There is a definite decrease in the pounds per acre of $Mg, P, K,$ and $NH_3$ from the left to right ends of the savanna continuum, while the pattern for Ca shows no significant trend. In a broad sense, this decrease reflects the age of the soils. Many of the stands furthest toward the left of Table K-1, occurred on steep slopes where the parent rock was on or close to the surface. While there was little erosion on these slopes,
there were occasional small patches of bare soil with some
washing and the subsoil often contained small pieces of un-
decomposed rocks. The soils toward the left tend, therefore,
to be younger.

The second factor besides age contributing to decrease
in fertility per unit volume of soil is that of an increased
presence of oak trees from left to right and consequently an
increase in fallen oak leaves in litter. Oak litter does not
contain as high a concentration of calcium as a percent of
dry weight as does the litter of more climax species. The
mean calcium percent of *Quercus velutina* is 1.10 and of
*Quercus alba* is 1.36 as compared to concentrations of 1.81
for *Acer saccharum*, 3.41 for *Carya cordiformis*, and 3.84 for
*Tilia americana* (data from Lutz and Chandler, 1946, and Coile,
1937). Although the pumping of Mg, K, P, and N, by all these
species is approximately the same, the lower calcium content
of black and white oak litter is apparently not sufficient to
buffer the soil and prevent the leaching which is a result of
a pedalfer climate where precipitation slightly exceeds eva-
poration.

Oak leaves also do not decompose very quickly and are
likely to be blown by the wind from a woods and the contained
minerals thereby lost. This loss is especially prevalent in
stands on steep slopes or the edges of bluffs where there is
often a complete absence of litter and a thin humus layer
covered by an extensive growth of moss.
The influence of an increasing amount of black, white, and bur oak leaves on pH is shown in line 11 of Table K-1. A decrease in pH from 8.0 to 6.2 is noted. This trend is reversed, however, as succession proceeds within the upland hardwoods and mesic lime-pumping trees replace the pioneer oaks. This reversal is shown in columns 9, 10, and 11 of row 11, where the pH along the herb continuum of Gilbert shows a recovery from 6.3 to 6.8.

The influence of succession is also evident in the recovery of high levels of Ca and K per seven-inch soil depth in columns 9, 10, and 11 of lines 1 and 4. In so far as fertility per unit volume of soil and pH are concerned, there is a decrease in pounds per acre and in pH as the number of trees increases in savanna and as the soil ages and leaches. This decrease is reversed by an increase in pounds per acre and in pH as the canopy closes and tree succession from oaks to calcium pumping maples, basswoods, and yellowbud hickories takes place.

If, however, the actual fertility per acre in terms of available values of $A_1$ is considered, a slightly different trend is evident. The depth of $A_1$, shown in line 12, increases fairly uniformly from high dry savanna in column 1 to climax upland forest in column 11. When fertility is figured, therefore, in pounds per $A_1$ per acre shown in lines 6 through 10 of Table K-1, a gradual increase in nutrients
to the middle of the savanna gradient is followed by a decrease in pioneer oak forests which is then reversed by an increase to climax forest.

The middle of the savanna gradient includes those stands with a fairly deep $A_1$ and a medium fertility, and which have, therefore, a higher fertility per acre than the stands toward the left of the continuum which have a high fertility per unit volume but are handicapped by a very shallow $A_1$. The right-most area of the savanna gradient, where the oak forest reaches greatest density, shows a moderate soil depth, but a low fertility per unit volume which is not recovered until the development of climax forest.

Along with depth of $A_1$, the water retaining capacity of the soils increases from a low of 55 in a dry cedar glade to a high of 100.4 as the maple forest is approached.

The demonstration that the level of fertility both in concentration per unit volume and in total fertility is as great or greater (with fairly similar soil materials) in maple forest as in savanna with a few trees scattered among a young prairie soil is evidence which requires a reconsideration of the equilibrium concept in soil dynamics. This reconsideration will have to take into account stable prairie or forest which, as an open system in steady state equilibrium, can so completely conserve its essential nutrients that what little is lost, is replaced by subsoil weathering and surface erosion.
during temporary catastrophic destruction of the plant cover. The reconsideration will probably have to come from ecology, however, since the idea of a steady state has been confused in soil science (see: Jenny, 1941, pp. 45-48) with the concept of time and of chemical equilibria (which are functions of a closed system).¹

**Light Intensity and the Closing of the Canopy**

The percent occurrence, by foot candle classes, of the light intensity readings made in savannas are shown in Table K-2. To give some basis for comparison with closed canopy stands, Trempealeau I and Denmark Beech stands are included, as well as several pioneer oak forests, including Ant Woods. By an inspection of the relationship of light intensity values to the frequency distributions of individual species, it was apparent that a decrease in light below 1,000 foot candles gave as great a difference in species frequency as a decrease from 10,000 foot candles to 1,000. This observation can be demonstrated in Table K-4 where the mean difference between the values in the first and second columns is almost as great as the mean difference between the second and third columns. That the difference is not as great is probably the result of the non-inclusion of many

1. A reference was located, after writing this paragraph, in which the concept of steady state equilibrium is applied to soil science. (Nikiforoff, 1942).
species of low light intensity preferences which would have shown high values for column 1 and low values for column 2.

This suggests that an increase in light influences plant distribution in a logarithmic fashion. The first intensity class of Table K-2 should, therefore, include all values from 0 to 100, and the next class from 101 to 1,000, if the entire range of the upland hardwoods were being sampled. Since only savannas were sampled, and only a few readings were available from 0 to 100 foot candles, the first two classes were lumped into a composite of 0 to 1,000 foot candles. If a light study is made upon the entire upland hardwoods, it seems very probable that the class of intensity values from 0 to 100 foot candles will give as significant a separation of species frequency distributions as either the class of 101 to 1,000 or 1,000 to 9,999 give as the savanna opens into prairie.

The distribution of intensity values shown in Table K-2 gives an overall impression of the shift in values by size classes as the canopy closes. A prairie has, of course, a constant illumination under clear skies of 10,000-plus foot candles. As trees appear in a prairie, the ground surface with full sunlight decreases, until by the time a fairly closed canopied forest is reached, as in Ant Woods or Basco, the surface with full sun is less than 10 percent. A further increase in thickness of canopy leads to a complete
absence of ground surface with full sunlight as illustrated in Trempealeau I and Denmark Beech.

The intermediate light intensity class of 1,000 to 9,999 foot candles is filled, for the most part, with measurements of light on ground surfaces which are shaded by the canopy of a single tree. This size class increases from 0 in prairie to a peak of 69 percent in Heron Woods and then decreases, as the canopy continues to close, to a value of 0 in Denmark Beech.

Although no exact separation is possible of the continuous trend from savanna to pioneer forest, an arbitrary distinction can be made at the line of 50 percent occurrence within the class 0 to 1,000 foot candles, with the pioneer forest having a 50 percent or more occurrence within this class. It is of interest to note that this is the area where canopy coverages of 75 to 80 percent are present and where black and white oak reproduction ceases. (Data on oak reproduction from Curtis, 1955).

**Light Intensity by Herb Continuum Interval**

Light intensity values plotted along the herb continuum show an overall decrease in illumination from left to right. The percentage of quadrats with full sun, shown in Table K-3, decreases from 34 to 0 for the closed canopy forest, while
the percentage of quadrats with 1,000 foot candles or less increases from 28 to 92 percent.

**Light Intensity and the Distribution of Individual Species**

It was evident from field observation that the relationship of a species to variations in light intensity could not, in many cases, be separated from the relationship of the species to factors of moisture (including available soil moisture and air humidity). In order, therefore, to demonstrate only the relationship of species distribution and degree of illumination, stands from a limited moisture range were chosen. This limited range was determined by locating the position of stands within the prairie continuum of Curtis (1955) and choosing only stands within the mesic-dry to dry part of the continuum (the area from which the most light measurements were available). Whatever the factors operative within this section of the continuum, it is assumed that a fairly narrow range in moisture conditions is present.

Within Table K-4, therefore, only stands which were western in location and were mesic-dry to dry were included. The percent occurrence by quadrat of each species within the quadrats of the three light intensity size classes is shown in Table K-4. By calculating percent occurrence of species
per quadrat, the mistake of measuring the distribution of the light intensity values, instead of the actual species response, is avoided.

The frequency patterns of the species in Table K-4 give part or all of the light adaptation amplitudes of the included species. Each species peaks in a size class roughly comparable with its position within the savanna continuum of Table I-2, if a size class of 10,000-plus foot candles is equated with the left end of the continuum and a size class of 0 to 1,000 foot candles equated with the right end.

The light intensity amplitudes of species which are within the same genus give interesting insights into possible evolutionary ecologic adaptations. *Andropogon gerardi* and *Andropogon scoparius* both peak in the 10,000-plus class but *Andropogon gerardi* is much more important in the classes with a lower intensity than is *Andropogon scoparius*. Of the four species of *Aster*, each peak in a separate class except the two which reach predominance in the 10,000-plus class. *Helianthus laetiflorus* and *Helianthus strumosus* show amplitudes which peak at opposite extremes of illumination intensity and give frequency patterns which are almost mirror images.

The fourth column of Table K-4 lists the prairie adaptation values of the species as assigned by Curtis (1955).
If the mean adaptation value of all species which peak in the column in Table K-4 with the lowest illumination is calculated, it is found to be 2.6 as compared with values of 3.3 for the medium light size class and 3.9 for the high size class. Within the prairie continuum a value of one indicates predominance toward wet prairie and of five predominance toward dry prairie. The tendency of those species which peak under low illumination to be also species with relatively lower (and, therefore, more moist) prairie adaptation values illustrates the tendency of moist preferring species growing on drier sites to seek out microhabitats with higher soil moisture and a higher relative humidity. A very general classification of species found in prairies, savanna, and pioneer forest can be made on the basis of the interrelations of their light and moisture adaptations.

First, there are low to mesic prairie species which are strict prairie species and cannot or rarely enter shaded places, even when the presence of shade might enable them to expand their distribution into drier sites. These species include all the plants in the first two sections of the prairie continuum of Curtis (1955) which are not designated with a 4 in Table I-2. In addition, there are several low prairie species which, while not moving into shaded areas, can withstand a certain amount of shade if a low prairie is overgrown with brush or thickets. These species have large
Secondly, there are low to mesic plants which can often to occasionally enter dry savannas by growing close to or beneath the canopies of trees. These species are designated by a number 4 in column 9 of Table 1-2.

It is interesting to note that under most phases of the Mid-western climatic swing from moist to dry, growth beneath a tree, because of lower soil moisture evaporation, probably does provide an increase in moisture, compared to areas away from the canopy. During the driest part of the cycle, however, as during the early 1950's, the use of moisture by the tree roots is so efficient that many forbs and grasses die back to the roots within the area of tree root extension, and some species probably do not survive. This death occurs when plants of the same species away from the area of root extension are still living.

Thirdly, there are species of mesic to dry prairie which cannot withstand shading and are only rarely found beneath the canopy of a tree and never found in a closed canopy forest. An increase in soil moisture from shading would be no advantage to these species since they are adapted to dry soil moisture conditions and though they might grow better on moister sites, they cannot compete with species which are
better adapted to moist sites. The species in the third group are designated with a number 2 in column 9 of Table I-2.

Fourthly, there are the species of mesic to dry prairies which can withstand some shading but usually do not penetrate too far into closed canopy forest. These species are designated with a number 3 in column 9 of Table I-2.

And, lastly, designated with a number 5, are the plants of pioneer forest which are never or rarely found in prairie and do not compete successfully in full sunlight.
The present distribution of forest in southern Wisconsin is most easily interpreted if an earlier deciduous forestation of almost the entire region is assumed to have taken place sometime preceding the second Xerothermic Period (ca. 400-1,000 A.D.). The evidence for such an extensive forestation is the widespread though localized distribution of climax maple-basswood forests (with complete complement of climax herbs according to McIntosh, 1950) which are found today in all southern and western counties of Wisconsin. To have reached these widely distributed areas, the climax trees and herbs (which are slowly moving migrants) must have migrated either through stable prairie or have traveled, as discussed by McIntosh (1950), through a fairly continuous intermediate forest in which successional developments were reaching the climax stage. If the alternative of a prairie migration is considered doubtful, then some general picture of a continuous forest must be drawn.

If one assumes for the period before the second Xerothermic, a climate very similar to the one today with perhaps a little more rainfall, a maple-basswood forest, with mosaic patches of pioneer to intermediate forest from gap phase destruction, probably covered the entire drained rolling
and flatland areas of the region. Toward the more hilly or less drained areas, however, different vegetation was perhaps more in evidence. On steep slopes with south-west exposures (especially in the Driftless Area) the chances for development of a maple forest would be almost as remote as they are today, and if any trees were present, they probably formed a fairly open canopy. On many of these slopes prairie might have existed, as considered by Anderson (1954), in continuous occupancy since the first Xerothermic Period. On the slightly less steep and less exposed slopes, much of the land was probably covered, as it is today, either with intermediate forest dominated by red, white and black oaks, red elm, shagbark hickory and cherry, or with climax forest in which many intermediate species were still present.

On poorly drained land, if a maple forest was capable of developing, the successional paths would not be through the intermediate tree species of the upland, but through the trees of the swamp hardwoods which were tolerant of poor drainage, as white elm, red and black ash, and hackberry.

If the southern forest originally existed as has been outlined, then the distribution of forest when European men arrived in Wisconsin can be interpreted in accord with the constant and widespread burning activities of Indians.

The moistland climax and intermediate forests, since none of their species are fire resistant, or are grub formers,
would be destroyed with the exception of the areas protected behind natural barriers. As this destruction took place, prairie would move in accompanied in places by bur oak and swamp white oak, which had been too shade intolerant to grow in the original moistland forests except as pioneer species during gap phase destruction.

Toward the mesic forests, dominated by sugar maple, the trees were also fire susceptible and except for an occasional white oak or red oak, the fires would completely and quickly level all forests not fire protected. Into this area prairie moved, again accompanied by bur oak which had been growing in areas of pioneer forest or on steep dry prairie slopes where it was pioneering as it still does today.

The appearance of a complete flora of mesic prairie plants to replace the maple forests is not difficult to explain, since the moisture amplitudes of all mesic prairie plants encompass either the dryest or most moist end of the prairie continuum and could thus enter the maple forest areas from dry slope prairies or from lowland prairies and sedge meadows.

Proceeding toward the steep land forests where development had not necessarily reached the sugar maple climax, a different picture would be evident. The intermediate trees of these areas, as black and white oak, shagbark hickory, and to a lesser extent, red oak (McIntosh, 1950), are capable of vigorous stump sprouting and, more important, their seedlings
can form grubs. A burning of these forests would result not in true prairie but in a partial degradation into barrens and grublands with occasional trees maturing into open grown adults.

When, therefore, European man arrived and stopped the fires, the lowlands were mostly prairie with scattered groves, and the only tree growth which came about as a result of European occupation was from the seeding in of elm and ash following grazing. The drained flat and rolling lands were prairie with bur oak opens and occasional open grown red, white, and black oaks. These lands, because of their high fertility, were used almost immediately for agriculture. If not plowed or heavily grazed, they grew up to thick bur oak or mixed oak stands from grubs, as in Basco Woods and as mentioned by Muir, or they seeded in to oaks, elms and aspens as mentioned by Cheney.

The more hilly areas, however, those which were not used immediately for agriculture and which contained oak and hickory grubs, sprouted into the thick woodlands as described by Stout and Cottam, whose rapid appearance astonished the settlers in the 1870’s and 1880’s.

Besides the evidence from the historic review in Chapter II, the following information from the study of savanna supports the preceding historic outline.
(1) The tendency for white and black oak to be together and for white oak not to occur in savanna with bur oak suggests these two types of savanna have different origins. As discussed in Chapter V, the closing of the canopy leads to a rapid exclusion of bur oak. A burning of a subsequent intermediate forest would not find any bur oak present and any future entrance of bur oak would take place into black or white oak grublands.

(2) In many bur opens there are a few old black and/or white oaks which have perhaps grown from the root systems of trees of an original forest, or from seedlings which started in forest but which grew to maturity after grub formation in the open.

(3) While not presented in the chapter on herbs, field observations showed a scattering of maple woods herbs in prairies in Green County, and seemed to indicate, as did the evidence of Hilgard (no date) and Gleason (1912), a former maple forest occupancy.

The origin of savanna is, therefore, in part as Gleason (1923) suggests — a reduction of forest to parkland conditions. This reduction takes place with trees capable of stump sprouting and with seedlings which can form grubs. In part, however, the reduction of forest is probably completely to prairie with a subsequent or concomitant invasion of bur oak, or in the moister areas, of swamp white oak.
The more recent origin of savanna, since the cessation of fire is, as previously discussed, dependent on either a migration of trees into prairie, (in cedar glades), or on a seeding in of elm and ash under grazing.

Despite these various modes of origin, the quantitative composition of savanna tree stands has been shown within a single gradient. Along this gradient, many trees, because of the predominant influence of a single factor, occur in fairly pure stands. Where quantitative stand composition shows a mixture of species, however, the patterns of tree importance behavior show a continuous ordered intergradation.

Even though all savanna trees are pioneer or intermediate species, there is no way to tie in savanna with the upland hardwoods continuum of Curtis and McIntosh (1951) by a consideration of composition, since in savanna a white oak open can be very similar in environment and in herb and shrub composition to a bur oak open, but in forest, a white oak woods is very different from a bur oak woods.

The manner of savanna origin determines the nature of the accompanying shrub and herb communities. Savanna as a migrant and savanna resulting from fire are in every sense integrated communities; their herbs and shrubs are not European weeds nor are they pioneer native plants. The understory of savanna, barring changes in the canopy cover, is as stable as that of
any of the communities along the prairie continuum of Curtis (1955).

Fire susceptible savanna originating as the result of grazing is usually covered, however, with a weedy understory. If grazing was originally light and then ceased, a recovery of prairie vegetation might be possible, although no such stands were found in Wisconsin.

The herbs and shrubs of savanna, as shown in Chapter IX, show a clearly intermediate relationship to prairie and to pioneer forest. Few species show a limitation to savanna, and most stands were composed of varying mixtures of plants previously found in either prairie or forest.

The continuum arrangement of frequency distributions along the savanna herb gradient gives additional confirmation to the postulate of normal ecologic distribution and suggests that regardless of the complex of factors which determines the structure of any community, the quantitative behavior of its species will give a normal response if the community is placed in its correct theoretic position in relation to other existent communities. The possibility for a prediction of all possible community structures is thereby apparent.

Finally, it is interesting to note that although both trees and herbs can be shown along compositional gradients, these gradients do not follow in identical directions. The
tree gradient is essentially a moisture gradient which
follows a range in conditions from dry to moist similar
to that present in the prairie continuum of Curtis (1955).
The herb gradient, however, travels from species characteristics of relatively high light and low moisture to those of relatively low light and high moisture. The intermediate areas of the herb gradient as demonstrated in the chapter on environmental correlations, contain stands where a lower soil moisture is compensated by a higher degree of shading or where a high soil moisture is compensated by a low degree of shading. A description of a savanna association based upon the combined composition of trees and understory would, therefore, be meaningless, since within the limitations of moisture amplitudes, any possible tree composition could be linked together with any possible herb composition.
CHAPTER XIII

GENERAL BIOLOGIC THEORY AND THE CONCEPTS
OF ORDER AND COMPLEXITY

The field of ecology has often both contributed to and benefited by the continuing effort of the biological sciences to achieve a much needed aim: the establishment of a theory and a methodology which are independent from that held by the physical sciences. One of the outstanding ecologic contributions to this effort was the Holistic concept of the biotic community as an emergent unit unpredictable in terms of a sum of its parts. This discussion will attempt to examine two concepts which seem to form a basic part of many recent biologic theories and then to apply these concepts to the information gained in the study of savannas. It is hoped that this application may be of value to the field of ecology and may, perhaps, in some way further the establishment of an unified biologic theory.

The Organismic viewpoint of Bertalanffy (1952) is the most comprehensive of the more recent theories and with the appearance of a promised logical and mathematical foundation should, regardless of its ultimate adequacy, challenge the basic assumptions under which ecologists conduct their experiments and with which they interpret their results. The Organismic Theory proposes "the conception of the
### TABLE K - 1

Soil Data Summary

<table>
<thead>
<tr>
<th></th>
<th>Along Savanna Continuum</th>
<th>Along Gilbert Herb Continuum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><strong>Fertility in Pounds Per Acre if Seven-Inch Soil Depth</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca.</td>
<td>6000</td>
<td>4250</td>
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<tr>
<td>Mg.</td>
<td>1200</td>
<td>1066</td>
</tr>
<tr>
<td>P.</td>
<td>400</td>
<td>123</td>
</tr>
<tr>
<td>K.</td>
<td>220</td>
<td>200</td>
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<td>NH₃.</td>
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<table>
<thead>
<tr>
<th></th>
<th>Fertility in Pounds Per A₁ Per Acre</th>
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</thead>
<tbody>
<tr>
<td>Ca.</td>
<td>120</td>
</tr>
<tr>
<td>Mg.</td>
<td>36</td>
</tr>
<tr>
<td>P.</td>
<td>12</td>
</tr>
<tr>
<td>K.</td>
<td>07</td>
</tr>
<tr>
<td>NH₃.</td>
<td>01</td>
</tr>
</tbody>
</table>

| PH.                  | 8.0 | 7.3 | 7.2 | 7.2 | 6.1 | 7.3 | 6.2 | 6.3 | 6.9  | 6.8  |
| AI.                  | 2/8 | 6/8 | 11/8| 17/8| 22/8| 9/8 | 20/8| 17/8| 18/8 | 25/8 | 32/8 |
| WRC.                 | 55  | 57  | 73  | 83  | 65  | ---| 75  | 87  | 60   | 100  | ---- |

* Values for A₁ in line 12 are given in eighth-inches. WRC indicates water retaining capacity.
<table>
<thead>
<tr>
<th>Stand</th>
<th>% Occurrence in Foot-Candle Classes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-1000</td>
</tr>
<tr>
<td>Any prairie</td>
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</tr>
<tr>
<td>Scuppernong</td>
<td>10</td>
</tr>
<tr>
<td>Nashota</td>
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<td>Kenosha</td>
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<td>Lake Lula</td>
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<td>Albion</td>
<td>22</td>
</tr>
<tr>
<td>Garwin Heights II</td>
<td>28</td>
</tr>
<tr>
<td>Hager City</td>
<td>38</td>
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<tr>
<td>Trempealeau III</td>
<td>54</td>
</tr>
<tr>
<td>Heron</td>
<td>27</td>
</tr>
<tr>
<td>Basco (CP)</td>
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<tr>
<td>Columbia Golf</td>
<td>56</td>
</tr>
<tr>
<td>Garwin Heights I</td>
<td>56</td>
</tr>
<tr>
<td>Ant Woods</td>
<td>64</td>
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<td>Butte de le Chien</td>
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<tr>
<td>Fountain City</td>
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<td>Trempealeau II</td>
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<tr>
<td>Du Charme</td>
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<tr>
<td>Brownsville</td>
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<tr>
<td>Trempealeau I</td>
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<tr>
<td>Denmark Beech</td>
<td>100</td>
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* Values in columns 1 through 3 show percent of light readings in each stand which are within the designated interval.
### TABLE K - 3

Light Intensity by Savanna Herb Continuum Interval

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<thead>
<tr>
<th>Interval</th>
<th>% Occurrence in Foot-Candle Classes</th>
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<tbody>
<tr>
<td></td>
<td>0-1000</td>
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<tr>
<td>1.</td>
<td>--</td>
</tr>
<tr>
<td>2.</td>
<td>28</td>
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<tr>
<td>3.</td>
<td>48</td>
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<tr>
<td>4.</td>
<td>47</td>
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<tr>
<td>5.</td>
<td>68</td>
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<tr>
<td>6.</td>
<td>88</td>
</tr>
<tr>
<td>7.</td>
<td>--</td>
</tr>
<tr>
<td>8.</td>
<td>92</td>
</tr>
<tr>
<td>Species</td>
<td>0-1000</td>
</tr>
<tr>
<td>---------------------------------------------</td>
<td>--------</td>
</tr>
<tr>
<td>Amorpha canescens</td>
<td>28.2</td>
</tr>
<tr>
<td>Amphicarpa bracteata</td>
<td>60.7</td>
</tr>
<tr>
<td>Andropogon gerardi</td>
<td>20.7</td>
</tr>
<tr>
<td>Andropogon scoparius</td>
<td>08.4</td>
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<tr>
<td>Anemone cylindrica</td>
<td>27.6</td>
</tr>
<tr>
<td>Antennaria sp.</td>
<td>10.6</td>
</tr>
<tr>
<td>Apocynum androsaemifolia</td>
<td>19.3</td>
</tr>
<tr>
<td>Aralia nudicaulis</td>
<td>35.4</td>
</tr>
<tr>
<td>Aster azureus</td>
<td>37.0</td>
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<tr>
<td>Aster ericoides</td>
<td>18.8</td>
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<tr>
<td>Aster laevia</td>
<td>39.9</td>
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<tr>
<td>Aster sericeus</td>
<td>01.6</td>
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<tr>
<td>Bouteloua curtipendula</td>
<td>08.8</td>
</tr>
<tr>
<td>Carex penlandiana</td>
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<tr>
<td>Geanothus americanus</td>
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<tr>
<td>Gelastrus scandens</td>
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<td>Comandra richardiana</td>
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<tr>
<td>Coreopsis palmata</td>
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<tr>
<td>Elymus canadensis</td>
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<tr>
<td>Fragaria virginiana</td>
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<td>Galium boreale</td>
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<tr>
<td>Geranium maculatum</td>
<td>23.2</td>
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<tr>
<td>Helianthus laetiflorus</td>
<td>23.6</td>
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<tr>
<td>Helianthus strumosus</td>
<td>55.2</td>
</tr>
<tr>
<td>Species</td>
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<tr>
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<td>61.2</td>
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<td>02.2</td>
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<tr>
<td>30. Lespedeza capitata</td>
<td>31.8</td>
</tr>
<tr>
<td>31. Lithospermum canescens</td>
<td>16.4</td>
</tr>
<tr>
<td>32. Monarda fistulosa</td>
<td>37.0</td>
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<tr>
<td>33. Muhlenbergia cuspidata</td>
<td>01.9</td>
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<tr>
<td>34. Panicum leibergii</td>
<td>16.1</td>
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<tr>
<td>35. Petalostemum candidum</td>
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<td>37. Phlox pilosa</td>
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<td>38. Pteridium aquililimum</td>
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<td>39. Ratibida pinnata</td>
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<td>40. Rhus glabra</td>
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<td>41. Rosa arkansana</td>
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<td>43. Smilacina stellata</td>
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<td>44. Solidago ulmifolia</td>
<td>39.6</td>
</tr>
<tr>
<td>45. Stipa spartea</td>
<td>21.2</td>
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* Numbers across top designate light intensity by foot-candle intervals. Column P.A. shows the prairie adaptation numbers of the species. Values in columns 1 through 3 are percent occurrence in quadrats with light intensity within designated interval.
system as a whole as opposed to the analytic and summative points of view; the dynamic conception as opposed to the static and machine-theoretical conceptions; the consideration of the organism as a primary activity as opposed to the conception of its primary reactivity." (See: Bertalanffy, 1952, pp. 18-19; and the comments of Egler, 1953.)

A fundamental concern of Organismic Theory is the exact relationship of biologic systems to each other and to the physical systems from which they originate. The relationship is discussed by Bertalanffy in an attempt to locate the level at which biologic behavior appears: "On the other hand, passing from molecules, which are defined chemically to the material and dynamic microcosm of the living cell, we come into a realm of entirely new phenomena. Although there is no absolute discontinuity, there is, if we can picture the transition in the form of a curve, a steep ascent from a lower to a higher level." (Bertalanffy, 1952, p. 131.)

Among biophysicists, however, Pirie (1937) and Bernal (1951) believe this transition between levels to be even and continuous.

The relationship is also explored by Engelmann (1953) in an excellent review of scientific method and theory with the conclusion, in part, that "only in terms of a spatio-temporal delineation of the two systems can we assign a definite region of the wider system [i.e., physical] to the
subsystem [i.e., biologic]." If this is not done the sub-
systems will appear "in different spatial areas of the total
system" and the phenomena would be reduced to "causal in-
fluences of the dynamics of one system on that of the other
one." (See: Engelmann, 1953, p. 85.)

The emphasis upon a means of distinguishing the bio-
logical from the physical aspects of a living system reflects
the belief of Bertalanffy and Engelmann that biologic be-
havior should not be interpreted within a philosophy of
mechanism and of cause and effect determination. "Mechanist
reductionism in any form, either at the dividing line between
biological and physical, or between behavioral [social] and
biological events, must be unequivocally rejected. For, if
events, occurring on one level of organization are reduced to
events occurring on a different level, the first type of
event is simply lost in the process. Without a definition of,
let us say, metabolism, on the purely biological level, it is
impossible to investigate the physico-chemical concomitants of
metabolism. If biological events are considered nothing but a
particular kind of physical event, then the essential difference
between an ape and a piece of iron ore, a difference without
which the field of biology has no meaning, has disappeared."
(See: Engelmann, 1953, p. 17.) Almost identical viewpoints
can be found in the essays: "What Is Life" by Schrödinger,
(1948, p. 76); and "A Physicist Looks at Biology" by Delbrück, (1949).

The most elaborate recent defence of mechanist biology has been made by Nagel (1950-1951), who, while favorable to Organismic viewpoints and contributions, does not think it has proven that biologic behavior can never be explained in physico-chemical terms. Nagel asserts that reduction is possible within the physical realm (he gives the example of the specific heat of solids explainable in terms of the quantum theory) and, therefore, by analogy, there is no reason why biologic events cannot someday be reduced to physical explanations. If this reduction is possible, however, it will probably not be on the level of defineability with each biologic action (as cell division) explainable by physical concepts (as electric charge), but on the level of underlying theory. And on the theoretic level, there must first be a formulation of general scientific or general system theory before this reduction can take place. If such system theory is ever produced, it is unlikely that either its methodology or its postulates will be the same as those held by present day field theories in physics, (which were not set up with any intention of accounting for biologic behavior). The Organismic objection is not to a future overall scientific framework but to present day transference of organizational concepts from one level to another.
The influence of mechanism in ecology, although steadily diminishing, is still very strong. A paper, which states "...soil phosphate is the factor which selects the vegetation with the possible exception of certain of the small patches of rainforest which may be climatically controlled", (Beadle, 1954), is one of the latest examples. Recently, however, the interrelationship of factors within a complex is being stressed. Whittaker (1954) states: "It may also be recognized, however, that the factors are isolates from the environmental complex, defined and determined to some extent by our ideas of what is important to plants and our means of instrumentation." He then discusses the interdependence of factors concluding, in part, that: "Along most of the gradients of environment we study, it is the environmental complex which is changing in various, more or less interrelated, ways, and not simply a factor changing in intensity." (Whittaker, 1954, p. 190.)

**General Scientific Theory**

The rejection of mechanism in most modern biologic theories is not followed by the acceptance of a vitalist, extra-naturalist outlook (as originally advocated by Driesch and more recently by Lillie, 1948), but is usually replaced with a theory which is independent of both these viewpoints. Engelmann and Bertalanffy believe the development of an
unified biologic theory depends upon the construction of a
general scientific theory which is adequate for the des-
cription of the dynamic aspects of all scientific phenomenon,
physical, biological, or social.

From an examination of the metaphysical premises of
Western science, Engelmann concludes that a general scienti-
fic theory must be based upon a "double delineation of any
phenomena which we observe. We can delineate such a pheno-
menon either as an emergent at the intersection of its
constituent elements, or as a differentiation from a field
with regard to which it is a constituent." (Engelmann, 1953,
p. 127.)

The theory of emergent configurations, different in
structure from any possible combination of intersecting
particles is well known in ecology from the concept of
Holism. An emergentist theory does not include any state-
ment about an inevitable complexity increase, however, for
the emergent unit may be less complex. The Holist viewpoint
of the whole as greater (i.e., more complex) than the sum of
its parts, is, therefore, not justified, nor does the ana-
logy of a community as an organism which must always progress
and cannot regress necessarily apply.

A good general description of an organism in terms of
field theory has been given by Bertalanffy (1952, p. 124):
"A living organism, however, only appears to be persistent
and invariable; in truth it is the manifestation of a perpetual flow.... Living forms are not in being, they are happening; they are the expression of a perpetual stream of matter and energy which passes the organism and at the same time constitutes it." The need for a mathematical application of wave mechanics to biology was expressed by Bertalanffy (1952, p. 113), and a series of differential equations was proposed by him as a part of his General System Theory (1950a). These equations are essentially a statement of the interrelatedness of basic phenomena and are so general that the biologic units which must be substituted within the equations are, for the most part, not yet known.

The theory of field determination has not been often expressed in ecology. This is, in part, the result of the complexity of biologic behavior on the community level, since the ability to differentiate from a field depends upon the field configuration, within which the differentiation takes place, being completely accessible to the observer. (Engelmann, 1953, p. 127.) But the lack of an ecologic field theory can also be related to the mechanist concentration upon causality and the sampling of single factorial environmental gradients with a consequent neglect of community structure analysis. It is only recently that enough quantitative information about community composition has been available (See: Curtis and McIntosh, 1951; also the
works of Ramensky, 1930; Kulczynsky, 1927; and Motyka, 1950) to allow for an analysis of field determination. The future development of this approach appears to lie, for plant ecology, in the construction of matrices of Quantitative Coefficients of Community from which a field configuration with a fluid differentiating structure can be delineated. The movement of patterns of quantitative species behavior within this differentiating structure would then perhaps be correspondent to the wave phenomenon of classical field theory.

The logical method which Engelmann and Bertalanffy believe necessary for general theory construction is a hypothetico-deductive or postulational system. (See: Engelmann, 1953, chapters 3, 4, and 5 for a justification of the use of a deductive logic; also see: Wisdom, 1952.) From the general scientific theories a set of postulates are to be formulated -- a set which is capable of "direction", "leading from the postulates through the logical operation of theoretical deduction and the extra-logical operation of empirical identification to the common sense phenomena which are to be integrated." (Engelmann, 1953, p. 149.)

The present development of a logical and mathematical treatment of biologic emergent and field theory is, however, very incomplete (Engelmann, 1953, p. 156, 162) and there is a consequent confusion of postulates with first and second
order theorems. A strictly logical deductive procedure is, therefore, not yet possible, and general biologic theory is today concerned with the non-mathematical transformation of these theories into workable biologic concepts.

**Order and Complexity**

The form in which these concepts have appeared most often recently is that of two independent measurements; order and complexity. (Pringle, 1951; Bertalanffy, 1952.) Pringle, from an examination of the mathematical theory of communication and from a study of the thermodynamics of open systems, outlines these concepts and their evolutionary significance.

The order of a living system refers essentially to its energy relations. A statement of order includes a description of the amount and kinds of energy entering and leaving the system; and of the movements, equilibria, and availability of energy within the system. In a narrower sense, however, order refers to availability and is synonymous with low levels of entropy. Entropy is a measure of the distance which a system maintains from maximum energy disorder; the higher the entropy, the greater the disorder. Maximum disorder is reached at that point when energy pockets are dissipated to their lowest relative level and are diffused throughout the system in a random homogeneous mixture.
Entropy is also defined as a number which indicates the number of states or positions which are possible in a system at a given situation. The lower the number of distinguishable particles and the greater the number of positions which any one particle is free to occupy, the greater is the entropy of a system.

The complexity of a system is determined by its "amount of 'structural' information" or "the number of parameters" which are needed "to define it fully in time and space". (Pringle, 1951, p. 176.) It is emphasized by Pringle that "the measure of complexity is of the statement about the system and is not the complexity of the system itself, an expression which has no scientifically discoverable meaning." (Pringle, 1951, p. 176.)

The complexity of a statement is thought by Pringle to be dependent upon the effort used in study and it seems reasonable to suppose that this "effort" includes the adequacy of one's biologic concepts and that, therefore, with the same amount of experimental information several statements of varying complexity can be made.

The relationship of order and complexity is an independent one; the level of each of these attributes is not necessarily related to the level of the other and either of these attributes may change without a consequent change in the other. (Needham, 1943; Pringle, 1951; Klein, 1954;
Burgers, 1954.) Burgers in discussing the relationship of order and complexity accepts Klein's definition of entropy: "the entropy is low when the number of energy states, in which there is a non-negligible probability of finding the system is small." He then concludes that it is conceivable that "under comparable conditions a more highly organized system may have a greater number of distinguishable states than a less organized system and thus have a greater entropy."

The nature of this order-complexity relationship is of great importance to biology because it has often been maintained that an increase in order must inevitably accompany the increased states of organization which occur during evolution or succession. It has also been maintained (Needham, 1943) that organization may increase only with a loss in order. This is a contention which ignores the ability of an organism to achieve a time-independent steady state and the possibility that different organisms might exist at the same level of organization and still have varying entropies.
CHAPTER XIV

ORDER AND COMMUNITY STRUCTURE

Recent research on the energy relationships of organisms has resulted in the conception of the open steady system developed by Bertalanffy (1934, 1950b), Burton (1939), Reiner and Spiegelman (1945), Prigogine (1947), and Schrödinger (1948). Their work was influenced, in part, according to Wisdom (1951) by the earlier research of Cannon (1926) and Hill (1930), who originally described the organism as being in a state of steady motion which cannot be considered as a dynamical stable equilibrium.

It is evident that a community shows the properties of an open system. It has a high degree of interrelationship of its various parts; it displays self-regulation by maintaining "a constant ratio of components in a continuous flow of materials" with the composition "independent of, and maintained constant in, a varying import of materials", and it re-establishes a steady state after a disturbance or a stimulus. (Bertalanffy, 1950b). The community also exhibits equifinality, though not in the sense that different initial conditions will always end in the same final state; i.e., all trends inevitably moving toward the climax. Rather, a steady state, at a given level of order, can be attained from a number of different initial states, and can
be restored from different kinds of disturbance to a pre-existent level of order.

The process of order increase has been discussed by Pringle (1951) and will be briefly summarized: The rate of formation and of destruction of a unit is not directly proportional to the quantity of the unit present. If there is variation in the formation and destruction rates accompanied by a competition for energy, then a change in level of negative entropy is possible and a system can increase its order. Of evolutionary significance is the fact that a more rapidly forming energy unit or a less rapidly disappearing unit can, regardless of the probability of its emergence, become established. The same dynamics would also apply to community growth and maturation.

The growth of a community, in its approach toward a steady state, shows some interesting energy relationships. The general formula for these relationships was worked out by Prigogine (1947) and is given in Bertalanffy (1950b). In terms of this formula, initial community development, from the time when no living organisms are present to the time where there is a fairly complete plant cover, shows an overall increase in order which is possible because negative change in entropy by import is greater than positive change through irreversible processes. As further development proceeds, the order of the community continues to
increase, although at a progressively slower rate until the
positive change of entropy by import is equaled by the
negative change through irreversible processes and a steady
state is reached -- a state in which entropy change is at a
minimum.

The energy dynamics of community order increase have
been discussed by Sears (1949) with especial emphasis on
the capability of an increasing re-utilization efficiency to
reduce the relative loss through production of non-available
energy forms; and, therefore, to postpone the time when a
steady state is attained. Thus, continued order increase
does not alone depend on an increased amount of photosynthe-
sis, but is also dependent on the number and kinds of
organisms and their ability to create and occupy new energy
niches and to increase the number and complexity of the
paths of energy exchange.

The capacity of biotic communities for developing from
lower to higher states of order is a function of the ability
of individual organisms, (which are more rapidly forming or
less rapidly disappearing energy units), to be present near
the community and to enter and survive in it. The community
during succession thereby recapitulates the conditions of
the past under which every organism had its evolutionary
emergence, although this recapitulation does not necessarily
follow any kind of historic sequence.
It is of interest here to note that once a community has attained a steady state, the transport of material into it is equal, both in composition and in quantity, to the loss of material by outflow through irreversible processes. In most stable communities (though not in Carboniferous forests or present day bogs), the CO\textsubscript{2} removed from the air by photosynthesis is exactly replaced into the air by the CO\textsubscript{2} released in respiration. The same balance applies also to oxygen, nitrogen, etc. Inorganic substances have a similar equilibrium. The entrance into the community of soil minerals through subsoil breakdown and pumping by plant roots is balanced by a loss from erosion and/or leaching. In the equations for material transport listed by Bertalanffy (1950), the equality of matter intake and outflow leads to a simplification of the final equation, no. 5, to \( \frac{K_1}{K_2} \), and, therefore, to a description of matter transport in terms of the equilibrium constant. An obvious basis is provided, then, for a differentiation between a biotic community and an individual organism; a community, once it reaches a steady state, must be an open system only in regard to energy; whereas an organism, to retain life, must always be open to matter as well as energy exchange.

A further means of differentiation between community and organism lies in the dynamics of their maintenance of a steady state. An organism, once it reaches maturity,
undergoes oscillations from its state of steady motion — oscillations which come about when a self-correcting mechanism "overshoots its mark too far", and the "error it makes is commensurate with the one it is correcting". (Wisdom, 1951). Biotic communities, on the other hand, do not oscillate in the above sense since they cannot overshoot their steady state, if it is in a climax condition without a further evolutionary development. They do show, however, a well known fluctuation away from a climax steady state, from the narrow fluctuations of the deciduous forest with its gap phase replacement, to the wider fluctuations which can occur in the boreal forest with its complete catastrophic replacement.

A generalized understanding of the dynamics of a steady state has long been a part of ecologic thinking with an early statement, that of Cooper (1926), and, more recently, Whittaker (1953). An application has been made by Lemmel (1939), who discussed the energy relations of the Dauerwald, which is a continuing or permanent forest which maintains itself though there is a change in its individuals, (i.e., the self-reproducing community families to American ecology but a new concept in German forestry.)

Sears (1949) gave a good description of the energy dynamics of a developing community, and included some of the mechanisms which insure increased re-utilization efficiency.
He also outlined the changes which community growth impresses on the order of the physical environment, as illustrated by soil stabilization and climatic modification. A well known essay, *Odyssey*, describing energy changes through the journeys of a molecule has been given by Leopold (1949). The general field of biologic energy relations and their importance to conservation has been reviewed by Curtis (1950). The most extensive measurements of energy balances have been made in the field of limnology and can be found in the works of Juday, Clarke, Lindemann, Hutchinson and others as reviewed in Allee, et. al., (1949).

In discussing the energy relations of the savannas, it is first necessary to point out that the attainment of a steady state implies nothing as to the level of negative entropy; a steady state only describes a system in which entropy change is at a minimum. A bucket into which water is flowing is in a steady state as long as the water leaving the bucket equals the water entering it. This applies whether the outflow opening is at the middle of the bucket or at the top. All self-reproducing communities are in a steady state -- both those which have reached climax conditions and those in which change is so slow as to be unobservable. The savannas are, for the most part, in a steady state, held there either because the continued presence of fire and/or grazing prevents any further
development, or because in their role as invaders of previously treeless areas, the savannas move very slowly.

The areas of the savanna gradient from which sapling and seedling data is available (Table E-5) show that the trees predominant in any one area are more or less reproducing themselves. These figures are, however, mean averages, and there are, within all areas of the savanna gradient, individual stands where a definite succession toward more shade-tolerant and more fire-susceptible trees is taking place.

Heavily grazed savannas, devoid of reproduction, cannot maintain themselves. Whether or not the loss of trees from the area results in a decrease in order depends on the level of order assigned to the two formations to which savanna is intermediate, forest and prairie. This level of order, as previously mentioned, is a direct function of the order possessed by individual organisms and represents the energy retained in the community during the time when negative entropy change was greater than positive change. This retained energy must, however, be available for utilization.

Thus, total organic matter, though a relatively simple measure, cannot be used in the comparison of forest and prairie. For example, the forest stores a large amount of energy in its wood, litter and soil organic matter, while the prairie stores only in litter and soil. It is probable
that a climax forest in Wisconsin can approximate the high organic matter levels of the prairie soil, and with the addition of its wood can outweigh the prairie in total matter. Much of the energy locked in the wood is not, however, directly available and is not being utilized by animals or plants which are capable of releasing it. This energy is 'down the sink' as effectively as if it were dissipated to heat and diffused from the community.

Another possible basis for comparison would be the total amount of photosynthesis. This comparison has been made in Allee, et. al. (1949), but is biased by the guess-work which was used to derive the daily glucose production of a tall grass prairie from the known production of a corn field and of a deciduous forest from the estimated production of an apple orchard. Furthermore, the comparison which found the tall grass prairie with a glucose production of 15,000 pounds per acre and the deciduous forest having a production of 22,500 pounds per acre, was based on a growing season for the forest of 180 days and for the prairie of only 150 days -- a situation which does not apply in the prairie-forest border regions of Wisconsin. Until more accurate estimates are available the assumption will be made here that the total photosynthesis of a stable tall grass prairie would be very close to that of a climax forest within the same environmental complex.
The main difference, then, would lie in the ability of the re-utilization processes of these communities to increase their order by postponing the time when less through irreversible processes equals the gain by import. The greater vertical coverage of the forest might indicate that it had a larger number of energy niches with greater numbers and kinds of organisms. The prairie, however, within a much smaller space probably possesses highly organized energy chains and displays much of the layering, in regard to smaller organisms, which the forest shows. The light of full sun both on the tops of trees and over the prairie grass is 10,000-plus foot candles, while the light on the prairie and forest floor has a median of less than 1,000 foot candles, although the forest shows a lower mean value. This light layering is paralleled by other environmental microgradients, and in less than two vertical meters, the prairie shows great diversities in arthropods and other invertebrates as well as a rich soil biota and vertebrate fauna.

The possibility that the prairie has, through evolutionary processes, made a more efficient use of its available energy through a more consistent and a longer term emergence of more rapidly utilizing units, should not be overlooked. Even if the tall grass prairie in the Middle West exists in a less "favorable" habitat than the forest, it could, nevertheless, through a more complete evolution, exist at a
higher level of order. This possibility can be illustrated by a hypothetical example taken from the Productivity Table (no. 46) in Allee, et. al. (1949). For purposes of the example, the productivity of the photosynthetic plants of Cedar Bog Lake is considered to be 240 g - cal / cm² / year and of Lake Mendota to lie at a higher value of 250. If the re-utilization efficiencies of these lakes remained the same as is listed in the table, then the Cedar Bog Lake, though it had the lower productivity, would have the higher order with a total energy on all levels of 279.0 g - cal / cm² / year compared with the lower total for Lake Mendota of 273.0.

The experimental determination of relative levels of order cannot be based on a single measure of the adsorption and transformation of light energy but must also consider the re-utilization of this energy. A single measure for comparison might, therefore, be found in the average time between the entrance into the system, (that is, the community and not the individual plant), of every light particle and the exit from the system of the particle or an equivalent amount of heat. This average time should be comparable to the period between the entrance of a molecule of CO₂ in photosynthesis and its exit in respiration. A technique using a given amount of tagged CO₂ molecules should not be too difficult to devise. The CO₂, released into different
communities at the same time, could then be tested for over periodic intervals and the community, which retains the highest concentration of the tagged molecules for the longest period of time, would have the highest level of order.

Until suitable experimentation is carried out the question of the relative levels of order of prairies, savanna and forest must remain unsettled. If forest and prairie are fairly comparable in level of order, then the savanna can be summarized as existing in a steady state at a level of order nearly or exactly equal with stable deciduous forest and prairie.
CHAPTER XV

COMPLEXITY AND COMMUNITY STRUCTURE

A complexity description of a living system usually starts with a statement about the position of the system within the scheme of biologic emergence. There seems to be little questioning of the placement of the community on the highest heirarchical level within this scheme and, therefore, of the designation of the biotic community as the most completely organized of all biologic phenomena. There is still, however, some doubt in ecology of the relationship of the community to lower levels, especially to that of the individual organism.

Using the principles of heirarchical order as defined by Woodger (1937), Bertalanffy (1952) discusses this relationship. While admitting many of the points of similarity (discussed by Phillips, 1935), Bertalanffy, nevertheless, concludes that a community is not a super-organism or a quasi-organism because it is not integrated as closely as an organism and its development is determined to a much greater extent by external conditions. The basis of the similarity lies in the fundamental properties previously listed which both the organism and the community share as open systems.

The relationship of biotic communities to lower levels (including the immediately lower level of populations of
individual organisms) can be further clarified by an application of Feibleman's Theory of Integrative Levels (1954). Feibleman outlines a series of general organizational laws, based on the essay by Novikoff (1945), which state that a higher level both organizes and directs the level or levels beneath it, and is, at the same time, dependent on the mechanism and continuance of the lower levels. Thus, both the positions of individual organisms within a community and the adaptive and evolutionary direction taken by these organisms are determined by community conditions. On the other hand, a community cannot exist without the continued life of its organisms nor be analyzed without a consideration of their mechanisms. Feibleman also outlines general dynamic laws which include the statement: "A disturbance introduced into an organization at any level reverberates at all the levels it covers," and general descriptive statements including the observation that the higher the level, the smaller its population of units and the more complex these units. The preceding concepts are well known and illustrated in ecology.

The Analysis of Complexity

Any statement which can be analyzed for complexity refers to those features of a system which are "ordered" and are, therefore, capable of verification; that is, to those
features which maintain a certain amount of structural constancy (Pringle, 1951).

An increase in these ordered relationships can occur either when existent units or events are rearranged or when new units or events have appeared in the system and have persisted. This persistence can take place in three ways: by an occurrence in only a part of the system and a survival there; by an occurrence throughout the system but a survival in only a part (Pringle, 1951); or by an occurrence throughout the system and survival throughout. This last possibility is usually remote except in systems with a very low complexity, and it is doubtful whether such a situation could occur in any biotic communities but the most pioneer and most unstable.

The process of complexity description consists in finding, with a given amount of effort, the statement which gives the most information about a system. The traditional empiric approach has included in this statement the numbers and kinds of units or events, their distribution within the system, and the dynamics of their interactions. An examination of one of these system characteristics, that of distribution, will be made here to show the value to phytosociology of a complexity analysis.

Since distribution within a system is a description of appearance among parts, the statement which conveys the most
information about distribution will be the one which shows the greatest "ordered and verifiable difference" (Pringle, 1954) among these parts; that is, the greatest heterogeneity. With a given amount of experimental data there are probably a large number of statements, with varying complexities, which can be made about distribution within a system; one or a relative few of these statements must ultimately be selected. This selection depends, essentially, on finding an objective technique for quantifying complexity differences.

**Ordered Differences Among Parts**

The technique which will be examined here is one which divides the system into parts and assigns numerical values to the units or events existent within these parts. That statement which shows the greatest ordered differences among these parts can then be considered to be the most complex. The shape of an "ordered" pattern relating to the ecologic distribution of species has frequently been assumed and demonstrated to be normal. (Curtis, 1951; Whittaker, 1954; Bray, 1956).

A justification for the assumption of normality can be gained in part from Pringle's description of the process of complexity increase. In spite of his assertion that the complexity of a system has no discoverable innate meaning, Pringle believes a living system can change from lower to
higher states of organization because of the characteristic attribute of evolution. Complexity may increase either when there are uniform conditions for emergence, but non-uniform conditions for survival, or when the conditions for survival are uniform but there is a non-uniform emergence. Whatever factorial conditions govern emergence and survival, it is apparent that a normal distribution would be an expected result, if each factorial complex is more expressive in one part of a system than another and decreases in a normal fashion away from that part.

If, in the natural world, the factorial complexes which govern biologic action are entirely physical and are strictly causally determinative, then any pattern of biologic behavior can be expected to follow whatever distribution patterns physical phenomenon display. It can be observed, however, that those physical factors which influence plant behavior have no clear normal pattern but show a fairly continuous distribution with almost all possible shades of factorial expression existing somewhere in the world, though not in any continuous geographic order.

Biologic normality is, therefore, usually considered to be based upon the evolutionary emergence and adaptation of a species within a narrow range of the broadly continuous physical milieu. Within its biologic amplitude each species reaches a maximum expression and decreases away from this peak in a normal pattern.
In specific ecologic terms, distributional normality is the result of an ecologic determination (and, therefore, limitation) of the fairly wide biologic amplitudes possessed by most species. This ecologic determination is expressed by competition and cooperation within a community situation and has been discussed by Curtis (1955) in interpreting the normal patterning of the presence distribution of species which occur along a prairie continuum. Biologic normality can, therefore, be interpreted, if the strictly causal action of physical factors is rejected, as the result of the interaction of physical and biotic factors, with normality in some way a consequence of the dynamic aspects of this interaction. Both Goodall (1954a) and Whittaker (1954) have recently stressed the interplay of biotic and physical factors within a complex and have criticized a mechanistic explanation of plant distribution.

The relative complexities of several phytosociologic ordinations will, therefore, be assessed by the degree to which they present the distribution of species in the most highly ordered, i.e., normal, fashion. In addition, other non-phytosociologic manipulations will be examined as a basis for a comparison of the adequacy of the biologic theories behind the various techniques.
The Sum of the Ordered Differences

The technique of the sum of the ordered differences was applied to the study of Scuppernong Prairie Preserve outlined in Chapter X. The eight gradients presented in this chapter were each divided into five equal parts. The mean frequency of the ten most common Scuppernong species in each of the five parts was then calculated and recorded in the first five columns of Table 0-1. The number of gradient parts chosen was a compromise between a low number (two or three) which would smooth over and obscure many of the ordered relationships and a high number (ten or twenty) which would reveal these relationships but would include a low level of predictability of any one species in any one part of the gradient.

In Table 0-1, the sixth through eighth columns represent an attempt to assess the complexity of each species pattern for each of the gradients.

In assessing the relative complexity of these distribution patterns, with only five points to judge the shape of each pattern, it is necessary to accept a broad definition of the meaning of normality. The definition was, therefore, enlarged to include all patterns showing a continuous increase, a continuous decrease, or a continuous increase followed by a continuous decrease.

This enlarged definition of normality was applied in calculating the sum of the ordered differences within each
frequency distribution pattern of Table 0-1. The ordered differences are shown in column 6 of the table and were calculated by adding all those differences between the frequency values of each of the sections in each ordination, which were part of a normal distribution. Thus, the frequency distribution of *Sanicula marilandica* L. in the third arrangement shows a continuous decrease from 100 to 0, for a sum of ordered differences of 100. Further examples of ordered patterns are those of *Tradescantia ohiensis* Raf. in the third arrangement which shows a continuous increase from 10 to 67 for a sum of ordered differences of 57 and of *Aster leavis* L. which shows in the second arrangement, an increase from 13 to 70, followed by a decrease to 28 for a sum of ordered differences of 107.

The sum of the disordered differences of each frequency distribution pattern is shown in column 7 of Table 0-1. The disorder of a frequency distribution is considered to be the amount by which its values deviate from a normal pattern. The trend of this normal pattern was considered to be, using the broad definition of normality, the movement from the highest to the lowest value, if the highest value occurred at either of the ends of the pattern. If it did not occur at either end, the trend was considered to be the movement between the highest value in each pattern and the lowest value on either side of the highest value.
In the frequency distribution of \textit{Sanicula marilandica}, in the first arrangement of Table 0-1, there is an overall downward trend from 100 to 7 in which a decrease to 70 is reversed by an increase to 80 before the movement again continues downward. In this case, the disorder is considered to be 10; the amount by which the value of 80 rises above the value of 70 in obstructing the continuity of this downward trend. In the pattern of \textit{Phlox pilosa} L. in the seventh arrangement there is a trend from a high value of 70 to low values on either side of 20 and 13. To both sides of the highest value, the downward trend is reversed by subsequent rises, from 20 to 54 and from 13 to 44. The disorder of the pattern is, therefore, considered to be 34 plus 51 or 65, the minimum amount by which these subsequent rises obstruct the uniformity of the downward trends.

\textbf{Positive and Negative Complexity}

The ordered differences of column 6 of Table 0-1 can be considered to represent positive complexity, while the disordered differences of column 7 represent negative complexity. The total complexity of each arrangement is, therefore, shown in column 8 as the sum of the positive and negative complexities. \textit{Sanicula marilandica} in the first arrangement, which has a positive complexity of 93 and a negative complexity of 10 has, therefore, a total complexity of 83.
The sum of the positive, negative and total complexities of the 10 species of each of the eight arrangements is shown in the first three columns of Table 0-2. The total complexity varies from a low of 239 for arrangement 8, which was deliberately disordered, to a high of 623 for arrangement 1 which was based on position within a previously constructed continuum.

Discussion

The high relative complexities in Table 0-2 of the phytosociologic ordinations, 1 and 2, are an expected result of arrangements which are determined by a direct attempt to understand the total configuration of factors which influence plant behavior.

The third arrangement which is determined by elevational control also shows a relatively high complexity, which demonstrates the importance of difference in levels on the distribution of plants in low prairie.

The fourth arrangement, determined by a measurement of soil water retaining capacity gives a complexity midway between the phytosociologic and random ordinations, while the fifth arrangement, determined by measurement of dried soil weight, is only slightly more complex than the random arrangements. The lower complexity of these two ordinations which are based upon direct environmental measurements, illustrate the relatively lower amount of information which is available,
if only supposedly causal influences of the physical upon
the biologic level are considered and the biologic subsys-
tems are consequently fractured and realigned in different
spatial areas of the total system. Goodall (1954) comes to
a similar conclusion in his factor analysis of Australian
Victorian Mallee: "It is not to be expected, however, that
sociologic factors -- or even the distribution of individual
species of plants -- can be closely related to any single,
simply measureable environmental factor."

The values of the two random arrangements, numbers 6 and
7, can be considered the expected complexities of arrangements
made with no knowledge of the vegetation. They form an in-
teresting base for comparison with the highly ordered arrange-
ments, numbers 1, 2, and 3, which show approximately twice the
complexity of the random arrangements.

The deliberately disordered arrangement, number 8, gives
a much lower complexity than is shown by the random arrange-
ments. Such a low value was made possible, as previously dis-
cussed, only by the use of a fairly complete knowledge of the
vegetation.

Non-Ordered Differences Among Parts

If the patterns in Table 0-1 are judged for complexity
on the basis of non-ordered differences among parts, a dif-
ferent complexity heirarchy of arrangements is attained.
Since the frequency distributions are not expected to conform to a normal pattern, a simple sum of the differences among the frequencies of each section was calculated and recorded in column 9 of Table 0-1. The total non-ordered sum of differences of each of the eight arrangements is shown in column 4 of Table 0-2. From column 4 it can be seen that arrangements 1 and 8, the phytosociologic and the deliberately disordered arrangements, have the highest non-ordered sum of differences. The random arrangements show the lowest non-ordered sum of differences, with the values for the other arrangements scattered in between.

If, in the final evaluation of the amount of information conveyed by each of the eight ordinations, the assumption of ecologic distributional normality is not made, there is no reason for preferring the patterns of the first arrangement over those of the eighth arrangement. Yet, if the frequency distributions of these two arrangements are extracted from Table 0-1 and compared, it is evident that the patterns of the first arrangement can be described in accordance with their shape and their tendency towards location in the various areas of the arrangement. The patterns of the eighth arrangement could not be described in this way; nothing can actually be said about them except that they have no uniform shape and show no real preference among the sections of the arrangement.
A possible justification, then, of using the sum of the ordered differences method as a practical measure of distributional complexity is that the arrangement which is judged by the method to be the most complex gives a reasonable or expected (i.e., normal) picture of frequency distribution patterns.

The ability of a number of different arrangements to give a high complexity leads to the possibility that no single final statement is possible in describing species frequency distribution and that the differential structure mentioned earlier must, therefore, be considered. The search for a method which will handle such a situation is a part of current botanical research at the University of Wisconsin. As a partial approach to this method, it can be realized that the fundamental similarity in patterns of the first three gradients of Table 0-1 suggests that the position of any one stand among the three gradients fluctuates within a fairly narrow orbit relative to the fluctuations of the other stands.

A number of additional one-dimensional arrangements for the Scuppernong stands were, therefore, tried, in an attempt to further increase the complexity shown in rows 1, 2, 3, of Table 0-1. These arrangements were determined by slightly varying the positions of one or two stands from their original position within the most complex gradient. None of these additional arrangements were of a greatly increased complexity
over the 623 for gradient 1. The high complexities of these additional gradients again suggests that there is no one final arrangement which is more correct than a number of other arrangements.

**Two-Dimensional Ordinations**

Many of the frequency patterns in the more complex gradients do not show an orderly, normal transition as can be seen in the bimodal patterns of *Aster ericoides* or *Silphium terebinthinaceum*.

These bimodalities are closely related to the presence, at the intersection of the two Scuppernong transects, of a bur oak tree. The possibility that another dimension reflecting the influence of the tree could be added which would remove many of the irregularities of the more complex gradients within the single dimensional ordinations must be considered. A new dimension was accordingly added for the first three gradients of Table 0-1.

The first gradient was augmented by a new axis based upon the behavior of the Scuppernong herb and shrub species along the herb gradient of the southern upland hardwoods established by Gilbert (1953). The adaptation numbers assigned by Gilbert were used, after slight modification to include information gained from the study of oak-openings, to assign each stand a place in the upland herb continuum. As in the placement of
stands within the prairie continuum of the x axis, the adaptation value of each species was weighted by its relative frequency. The position of each stand within the forest continuum is shown in column 1 of Table 0-3. A two-dimensional arrangement of the Scuppernong stands is now possible with location along the x axis determined by position within column 1 of Table 0-1 and location along the y axis determined by position within column 1 of Table 0-3.

The second gradient of Table 0-1 was similarly expanded into two dimensions. This was accomplished by locating the peripheral tendencies within the matrix which were most at variance with the initial peripheral tendencies upon which the first dimension was based. Two stands were located which were very distantly related, not only to each other, but also to the peripheral stands which were used for the reference stands of the first axis. A new axis was then constructed, using the same technique as was previously described for the ordination method of gradient 2 of Table 0-1. These y axis values are shown in column 2 of Table 0-3. Again each of the Scuppernong stands can be arranged along both an x and y axis, as determined by their position in column 2 of Table 0-1 and column 2 of Table 0-3.

The third gradient was augmented by the addition of a dimension representing distance from the bur oak tree which was located in the center of the two intersecting Scuppernong
transects. The tree can be considered in the same way as is elevation, namely as a control over certain definite environmental factors. The presence of the tree influences light intensity, relative air humidity, air movement, soil moisture, and soil permeability. The absolute values assigned to represent distance from the tree are shown in column 3 of Table 0-3. A two-dimensional ordination representing the controlling influence of elevation and tree presence is now possible. Position along the x axis of this ordination is shown in column 3 of Table 0-1 and along the y axis is shown in column 3 of Table 0-3.

The position of each stand within each of the three two-dimensional ordinations was then plotted. The observed similarity of relative position of stands in each of these new arrangements suggested the possibility that the three ordinations could be superimposed to form a single two-dimensional model within which each stand occurred three times.

Before this superimposition could be accomplished it was first necessary to rotate the axes of the arrangements so that the diamond shaped or spindle patterns, often found in two-dimensional ordinations, could be re-oriented. These patterns seem to occur because there is a good probability that if factorial complexes are interactive two of the corners of a stand ordination will only sparsely be filled. This can be illustrated by the following example. In this example, complex X and complex
Y are interactive and complex X expresses itself increasingly along the x axis while complex Y expresses itself increasing-
ly along the y axis. Given the interactiveness of these complexes, there is, therefore, a low probability that a stand location will be determined entirely by a high level of com-
plex X and a very low level of complex Y, or entirely by high Y and low X. The lower right-hand and upper left-hand corners of two-dimensional ordinations are, therefore, not likely to be very well filled.

Since a 45 degree rotation of the x and y axes will eli-
minate the sparsely filled corners and more nearly enclose the spindle pattern, rotations were made on each of the three phytosociologic ordinations. These rotated stand ordinations were then superimposed within one graph.

This graph is shown in Figure 0-1. As can be seen from Figure 0-1, most of the stands fluctuate within a rather small orbit although there are a few stands, as numbers 8 and 12, which swing more widely.

The frequencies of a few of the more common species within the composite ordination of Figure 0-1 are shown in Figures 0-2 through 0-7. Since each stand contained only five quadrata, the frequencies are listed as 0 to 5. The species chosen for Figures 0-2 through 0-7 are ones which peak strongly toward the various extremities of the composite stand ordina-
tion. Each frequency distribution shows some approximation to part of a solid normal pattern.
To further demonstrate these two-dimensional patterns, the composite ordination of Figure 0-1 was divided into nine equal sized rectangular cells and the percent frequencies of every Scuppernong species with a frequency of five percent or over was plotted for each of the cells. The upper right-hand cell which contained only one stand was not used. Each of the other cells contained four or more stands.

The two-dimensional cell patterns are shown in Table 0-4. Again, as in Figures 0-2 through 0-7, there is a suggestion of parts of solid normal distributions. Many of the patterns of Table 0-4 iron out the inconsistencies which were noted for the frequency distributions in one dimension, as the bi-modal pattern for Silphium terebinthinaceum is reshaped in the second dimension to a single modal trend.
FIGURE 0 - 1

Graph of Stand Locations of Scuppernong Savanna within Superimposed Ordinations. Note the Narrow Fluctuations of Stand Positions within Relatively Small Orbits.
FIGURE 0 - 2

Graph of Frequency Distribution Pattern of *Aster lasvis*. A Value of 5 Represents 100 Percent Frequency. Points of locations of frequency values are correspondent in Figures 0-2 through 0-7 to position within the superimposed ordinations of Figure 0-1.
FIGURE 0 - 3

Graph of Frequency Distribution Pattern
of *Petalostemum purpureum*.
FIGURE 0 - 4

Graph of Frequency Distribution Pattern of *Galium boreale*.
FIGURE 0 - 5

Graph of Frequency Distribution Pattern of *Ratibida pinnata*. 
FIGURE 0 - 6

Graph of Frequency Distribution Pattern
of *Sanicula marilandica*. 
FIGURE 0 - 7

Graph of Frequency Distribution Pattern
of *Dodecatheon meadia*.
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* Columns 1 through 5 show the relative frequencies of species within the five equal sections of each of the eight ordinations. Column 6 shows the ordered differences of each frequency distribution, column 7 the disordered differences, column 8 the total differences (total complexity), and column 9 the non-ordered differences.
TABLE 0 - 2

Total Relative Complexity and Non-Ordered Differences of Each Ordination

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* The column symbols are the same as in Table 0 - 1, with TD indicating the total relative complexity of the ten frequency distribution patterns of each of the eight ordinations. As in Table 0 - 1, ND indicates the total non-ordered differences.
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**TABLE 0-4**

Scuppernong Herb Frequency Distributions in Two Dimensions
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CHAPTER XVI

CONCLUSIONS

The central theme of Chapters 13, 14, and 15 has been the suggestion of reasons for examining the biotic community on its own level, and the examination of two concepts which might be helpful in this study. The primary reason for regarding community behavior as non-reducible to physico-chemical terms is the same as is applicable to all hierarchical levels of biologic phenomena: the emergence of life from the chemical organic world constitutes a "steep ascent" from a lower to a higher level of organization and, until a general scientific theory is formulated, demands an independent theory and methodology.

The acceptance of biologic behavior on its own level has always been a part of American ecologic thinking, especially in the early writings of Gleason (1913) and in the emphasis on the "Phytometer" as a primary measure, and instrumentation as a secondary measure, by Clements (1935). More recently, a renewed interest in community structure analysis has been evident in the writings of Curtis, Whittaker, and Goodall. This interest has paralleled, in a general way, the two major delineations of scientific phenomena, emergence and field differentiation, outlined by Engelmann (1953). That such a dual approach is existent in ecology can best be demonstrated
by observing that when the first continuum paper was published by Curtis and McIntosh it was interpreted by the Ecology Journal Club at the University of Illinois as a statistically elaborate statement of succession, (Bell, 1953), and by the Japanese ecologists, Horikawa and Okutomi (1955), as a demonstration of the compositional relationships of plant communities regardless of successional aspects.

Emergentist theory has been prominent in ecologic thinking about the evolution of the individual species and the concomitant successional development of the community. The general concepts of order and complexity applied to community development show an overall pattern of an increase in order (negative entropy) accompanying an increase in complexity as the community proceeds from incipient to terminal stages. At each new successional phase, more rapidly utilizing or less rapidly disappearing energy units appear and regardless of the probability of their emergence become established. During this establishment, the historic conditions under which each species had its evolutionary emergence are recapitulated. Complexity generally, though not necessarily, increases as development proceeds, largely because a more complete description of community dynamics (biotic interrelationships) is needed.

The concept of a climax community, the keystone of successional theory, has, therefore, been enriched by a more
exact description in terms of order and complexity, especially by the application of the concept of steady state or flux equilibrium. Divested of its almost mystical position within the Clementsian classification system, the climax concept remains a necessary part of community analysis from an emergentist viewpoint.

A mathematically unsophisticated approach to an analysis based on the theory of field differentiation was presented in a series of ordinations of herb frequency data from a low prairie savanna. A test of relative complexity was outlined and applied to the ordinations and the inability of single environmental factors to give as high a complexity as phytosociologic ordinations was demonstrated. This is considered additional reason for not basing a community explanation upon a non-biologic basis.

To present a differential approach to relative stand location, the three phytosociologic ordinations were expanded into two dimensions and then superimposed within a single framework. Within this framework each stand fluctuated within a fairly narrow orbit and each orbit maintained a fixed relationship with the other orbits. The patterns of species frequency distribution within the framework can be considered to resemble the solid normal distributions suggested by Whittaker (1954).
The savanna vegetation of Wisconsin, embracing all grasslands in which there are scattered open grown trees, has been studied with a sampling of 59 tree stands and 84 herb and shrub stands containing 1,760 one-by-one meter quadrats. Tree stands were sampled by the random pairs method and herb stands by quadrats laid at random within the stands or contiguously along transects which extend from prairie through savanna and into forest. Some herb data was gathered from transects projected from beneath the canopies of isolated trees into prairie.

Soil samples of the A1 layer were collected and 4,000 light readings were made, 946 of which were taken over sampled herb quadrats.

Although most tree stands were strongly dominated by one species, a compositional gradient was constructed which showed, for the tree species, a series of intergrading normal frequency distributions. Major species along this gradient in order of dominance were: Juniperus virginiana*, Betula papyrifera, Quercus velutina*, Quercus alba*, Carya ovata, Quercus macrocarpa*, Quercus rubra, Quercus bicolor", Fraxinus pennsylvanica, Ulmus americana* and Acer saccharinum. The species marked with an asterisk made up 90 percent of the total Importance Value in savanna.
Four major historic origins of savanna were outlined; (1) The complete destruction by fire of climax forest or intermediate moistland forest (neither of which contain fire resistant species capable of grub formation) and an invasion of prairie with a subsequent or concomitant entrance of *Quercus macrocarpa* or *Quercus bicolor*, this entrance helped by ability to form grubs. (2) The degradation by fire of intermediate dryland forest to brushland containing the grubs or stump sprouts of *Quercus alba*, *Quercus velutina*, *Quercus ellipsoidalis*, *Carya ovata*, and to a lesser extent *Quercus rubra*. Within this brushland occasional trees were able to reach adult size. (3) The invasion of dry prairie by *Quercus macrocarpa*. (4) The entrance, after the cessation of fire and usually under the stimulus of grazing, of *Juniperus virginiana* and *Betula papyrifera* into dry prairie, and of *Ulmus americana* and *Fraxinus pennsylvanica* into moist prairie.

Hybridization was noted between *Quercus macrocarpa* and *Quercus bicolor* and introgression was demonstrated as taking place from the hybrid to the parent, *Quercus bicolor*.

Three hundred species of herbs and shrubs were found in savanna, all of which had been previously recorded from prairies or upland forests in Wisconsin.

Spatial gradients showing transition as it exists in the field between prairie and forest were constructed for 44 herb stands in seven geographic locations.
A two-dimensional theoretic gradient was made by assigning 92 herb stands (including some pioneer forests) positions along axes determined by previously established prairie and upland forest continua.

Within the theoretic gradient, a linear trend was noted from stands with species characteristic of high light intensities and low soil and air moistures, to stands with species of lower light intensities and higher soil and air moistures. Intermediate areas showed a spindle-shaped widening in which stands with high light intensity compensated by high soil moisture were found along with stands in which a lower soil moisture was moderated by lower light intensities.

Both the spatial gradients and the theoretic gradient showed herb species frequency distributions which gave a continuum pattern and showed an even interchange in species dominance from prairie to forest.

A decrease in fertility per unit volume of $A_l$ was shown for Ca, Mg, P, K, and NH$_2$, along the herb gradient from prairie to pioneer forest. This decrease, which reached its maximum amount in pioneer oak forests was shown to be reversed and original levels of fertility were regained as development proceeded to the maple-basswood forest.

Light measurements showed species to have, within a range of uniform soil moisture, definite light intensity amplitudes. Many species of moist prairie were found under the canopies of trees in savannas with a relatively low soil moisture.
A general theory which is adequate to explain scientific phenomena on any level, physical, biologic or social, is believed by Engelmann to be based on a delineation of a phenomenon, either as an emergent at the intersection of its constituent elements or as a differentiation from a field.

The theory of emergent configurations has appeared in ecology in the concepts of Holism and hierarchical levels of organization and in the concept of succession.

The theory of field determination has not been often expressed because of a mechanist concentration on causality and the sampling of single factor environmental gradients with a consequent neglect of community structure analysis. A possible future ecologic development of field theory appears to be in the analysis of matrices of Quantitative Coefficients of Community from which a fluid structure for the placement of stands or species can be determined.

Since the logical development of emergent and field theory for biology (though promised by Bertalanffy) is as yet incomplete, two recent concepts, order (the number of distinguishable particles and the number of positions which any particle is free to occupy) and complexity (the number of parameters needed to fully describe a system) were applied to the field of ecology.

The development of a community in terms of entropy change and the attainment of a steady state was described. A separation of a community from an individual organism (with which a
community has been held analogous) on the basis of energy
dynamics was attempted.

A technique for analyzing complexity on the basis of
the sum of the ordered (i.e., normal) differences among
parts was outlined. The technique was applied to eight
ordinations of a set of herb data. Phytosociologic arrange-
ments which were based upon a previously constructed con-
tinuum and on a modified factor analysis showed a higher
complexity than arrangements based upon environmental
measurements which in turn were more complex than random
ordinations.
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APPENDIX
### TABLE I
Herb and Shrub Species of Wisconsin Savanna

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* P.P. indicates presence within 82 "phytosociologic" stands; E. % F. indicates the sum of the percent frequencies within these 82 stands; M.F. indicates the mean frequency within stands of occurrence; P.G. indicates presence within 49 "geographic" stands; T.F. indicates presence on tabulation forms, P designates prairie form, F designates forest form, B designates both forms, and N designates neither form. Numbers marked with an asterisk (*) in column 2 are species with large growth habits which are liable to be relatively more important than their frequency values indicate.
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**Spatial Transitions -- Frequency Distribution Patterns**

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Kettle Moraine

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TITLE OF THESIS  THE SAVANNA VEGETATION OF WISCONSIN AND AN APPLICATION
OF THE CONCEPTS ORDER AND COMPLEXITY TO THE FIELD
OF ECOLOGY  JOHN ROGER BRAY

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Date  Aug 13, 1955  Signed  
Professor in charge of thesis