THE PHYTOSOCIOLOGY OF
DRY LIME PRAIRIES OF WISCONSIN

by

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". . . . toward the west the country has the general elevation of river bluffs. It is wooded with oak--with tracks of prairie and lies in ridges, some of which are entirely covered with grass and destitute of forest trees."

Schoolcraft, 1821
writing of the country
at La Montaigne qui
Trempe dans L'Eau.

INTRODUCTION

The interesting juxtaposition of grassland and forest in the midwestern area of North America has long been a topic of interest to plant geographers and ecologists. Southern and western Wisconsin is a part of this ecotone. Harshberger (1911) defines a prairie as a "heavily grassed area (a closed formation), destitute of forest growth, but existing in the midst of a wooded region, where the climatic conditions are favorable to the growth of timber, but where, on account of the exclusiveness of the grasses and their success against all competitors coupled with ecologic, physiographic, and historic influences rather than want of water and soil conditions, the spread of forest trees has been prevented."

The location of the prairie as it existed in Wisconsin at the time of settlement by European man is shown on a map (Fig. 1) which has been constructed from the records of the original land survey of the state. The relation of the prairies in Wisconsin to the more extensive areas of grassland to the south and west is shown in Figure 2. The vegetation of southwestern Wisconsin of a hundred years ago consisted of a mosaic of prairie, oak savanna, and hardwood forest. This region has been termed by Curtis and McIntosh (1951) the prairie-forest floristic

Figure 1

Native vegetation of Wisconsin as it existed around 1840. Map by J. T. Curtis, based on surveyors' records.

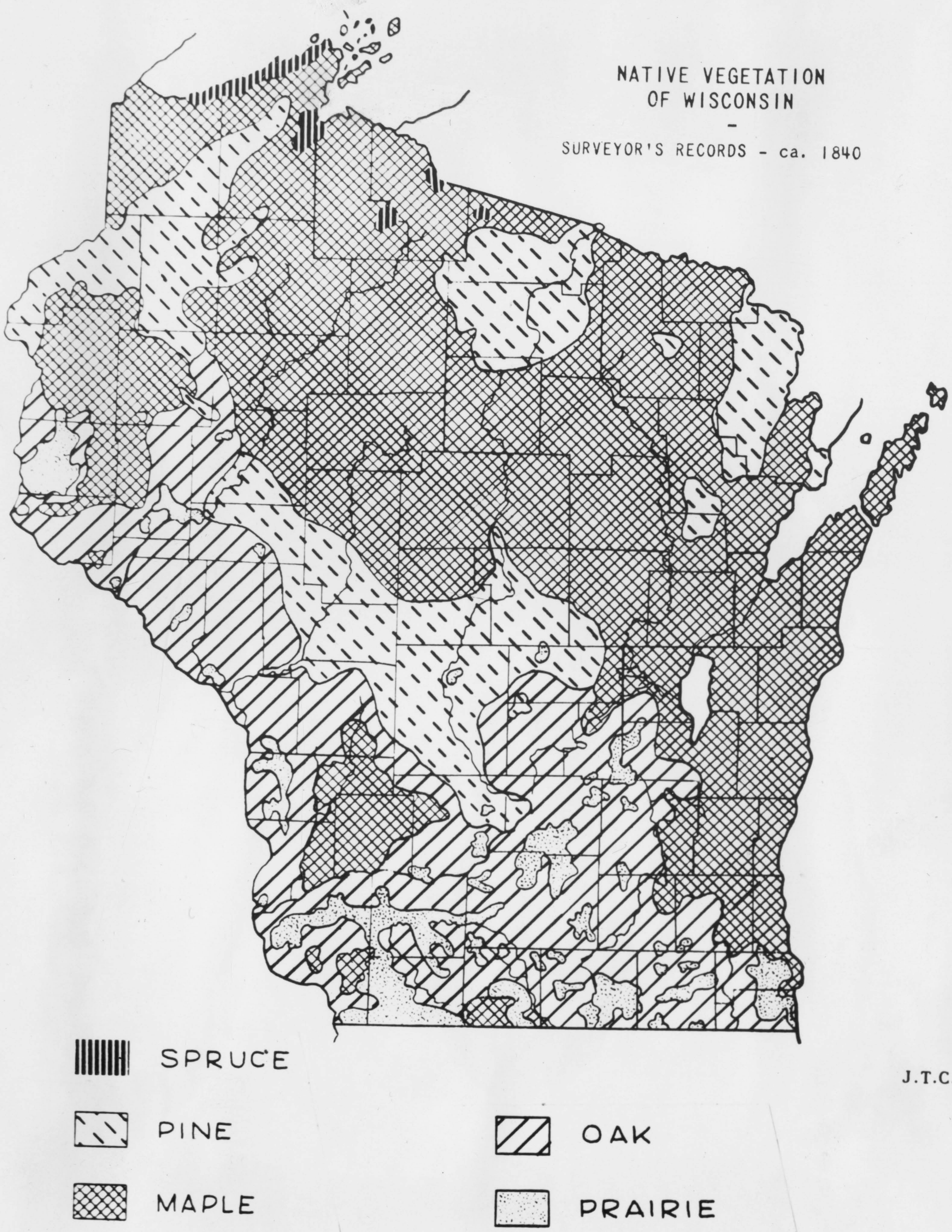
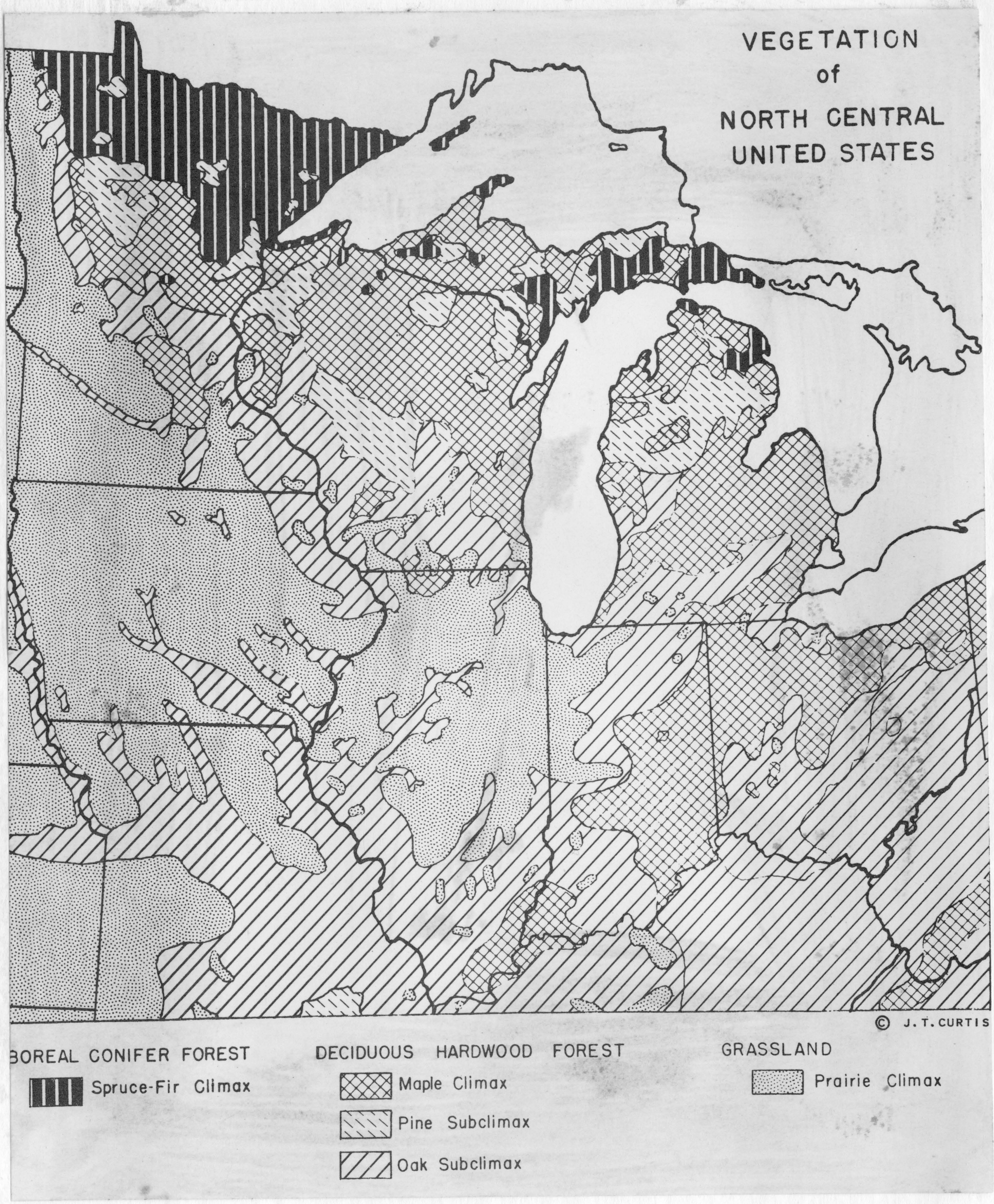

NATIVE VEGETATION
OF WISCONSIN
-
SURVEYOR'S RECORDS - ca. 1840
SPRUCE
PINE
MAPLE
OAK
PRAIRIE
J.T.C.

Figure 2

Major vegetation types of the Midwest.


VEGETATION
of
NORTH CENTRAL
UNITED STATES
© J. T. CURTIS
BOREAL CONIFER FOREST
Spruce-Fir Climax
DECIDUOUS HARDWOOD FOREST
Maple Climax
Pine Subclimax
Oak Subclimax
GRASSLAND
Prairie Climax

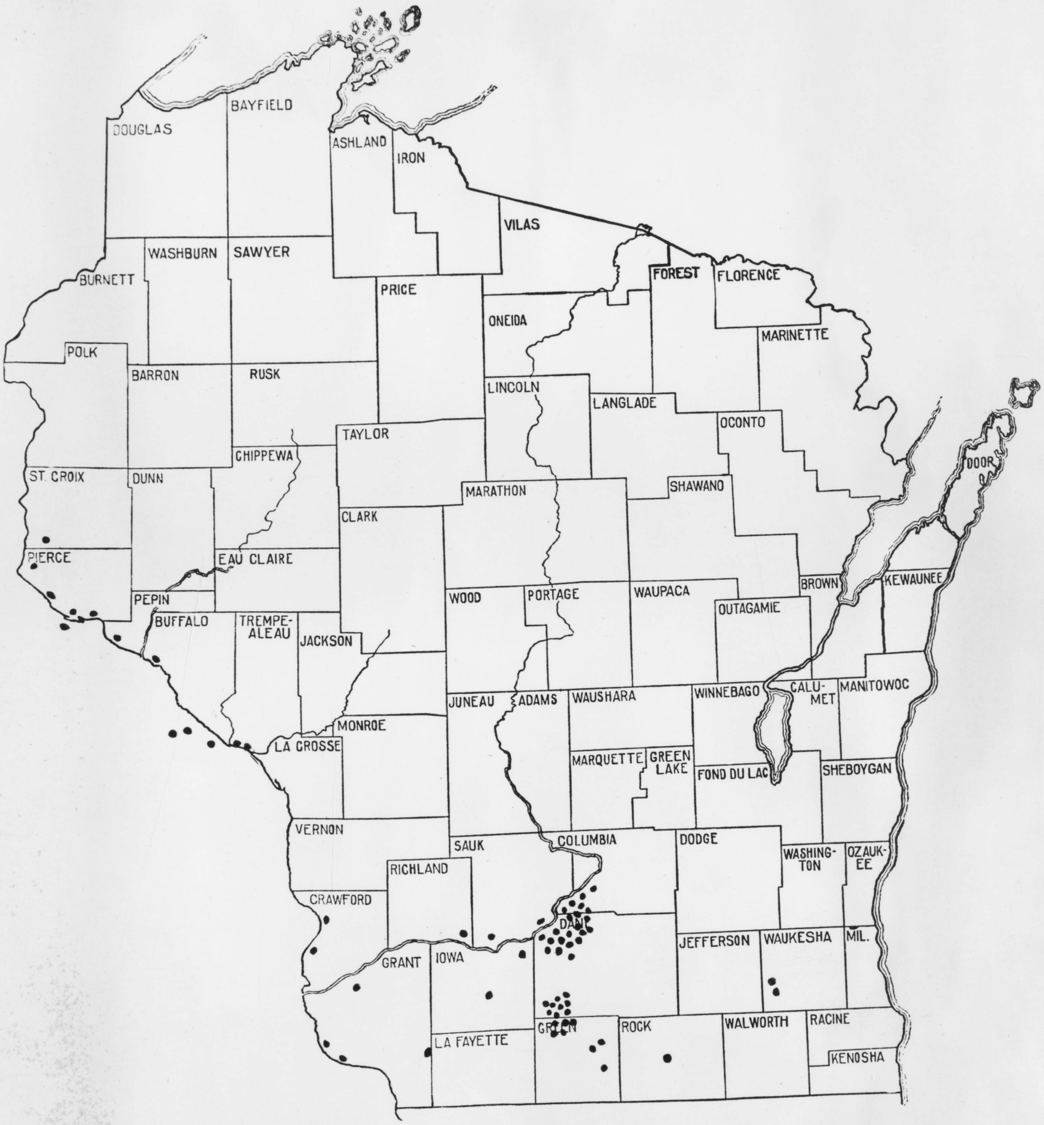
province. The rapid and complete settlement of the midwest has long since converted the larger prairie areas into cultivated fields, so that only small isolated and scattered remnants of native grassland remain.

In a preliminary study of these relic prairies, Curtis and Greene (1949) have enumerated four rather distinct types: the low prairie, found on poorly drained flatlands; the high prairie, found on internally well-drained uplands; the sand prairie, on sandy soils of glacial lake beds and river terraces; and dry lime prairies, which are located in areas of very thin soil over dolomitic bedrock or calcareous gravel and have excessive surface drainage.

It is with the phytosociology of the dry lime prairies of southwestern Wisconsin that this study deals. A total of 64 stands have been studied, ranging in location from the kettle moraine of southeastern Wisconsin to Pierce and St. Croix Counties in western Wisconsin and including several stands in northwestern Illinois, northeastern Iowa, and southeastern Minnesota (Fig. 3). These stands, which vary in size from slightly more than an acre to over 10 acres, consist of prairie vegetation which has been neither grazed nor plowed and which grows in a very shallow soil over a dolomitic bedrock or coarse calcareous gravel. Figures 4, 5, 6, and 7 show typical landscape types in which thin soil prairies can be found. It is in the rugged topography of the Driftless Area of southwestern Wisconsin, on the steep limestone-capped

Figure 3

Location of stands included in present study.


DOUGLAS
BAYFIELD
ASHLAND
IRON
VILAS
WASHBURN
SAWYER
BURNETT
PRICE
FOREST
FLORENCE
ONEIDA
MARINETTE
POLK
BARRON
RUSK
LINCOLN
LANGLADE
OCONTO
TAYLOR
CHIPPEWA
DOOR
ST. CROIX
DUNN
MARATHON
SHAWANO
CLARK
PIERCE
EAU CLAIRE
PEPIN
BUFFALO
TREMPE-
ALEAU
JACKSON
WOOD
PORTAGE
WAUPACA
OUTAGAMIE
BROWN
KEWAUNEE
JUNEAU
ADAMS
WAUSHARA
WINNEBAGO
CALU-
MET
MANITOWOC
MONROE
LA CROSSE
MARQUETTE
GREEN
LAKE
FOND DU LAC
SHEBOYGAN
VERNON
SAUK
COLUMBIA
DODGE
WASHING-
TON
OZAUK-
EE
RICHLAND
CRAWFORD
DANE
GRANT
IOWA
JEFFERSON
WAUKESHA
MIL.
LA FAYETTE
GREEN
ROCK
WALWORTH
RACINE
KENOSHA

hills and ridges, that very many of the dry lime prairies are located. They exist as isolated bits of prairie vegetation near cultivated fields, pastures, and on ridges in wooded areas; they have escaped the plow because of the shallow soil and steep slope and have not become pasture because of some quirk of ownership or location.

Under the present conditions of climate and intense land utilization in the area studied, the fate of the prairies is rather uncertain. Several dry lime prairies have become gaping limestone quarries since this study was started, and the search for suitable unused areas as sites for additional quarries is not likely to diminish. Fortunately some of the larger and better stands are located in state parks.

No minimum number of species was used as a criterion in deciding whether or not a particular stand be included in the study. The average number of species per stand for the 64 stands studied is 60. Only a very few stands have as few species as 35, and many have over 85 species.

Because of the obvious relation to the underlying limestone (dolomite) bedrock in the stands studied early, the term lime prairie was used to distinguish this rather distinct type from the deep-soil, very wet, and very sandy prairie. A criterion used later in certain instances where the relation to the bedrock was not especially clear was a field determination of the soil pH. This was found to be at least 7.5 and in most cases 8.0; thus the name lime prairie

Figure 4

General aspect of country in which dry lime prairies are located. Most of treeless and wooded hillsides are heavily grazed.

Figure 5

Steep, southwest-facing bluffs along the Mississippi River. Most of the bluffs are heavily forested.

seems justified. The soil found on these prairies varies from a silt of loessal origin to a fine calcareous sand.

This is an introductory study of a still prevalent but disappearing plant community, located within an area of fairly uniform climate and topography. This study has attempted, first of all, to locate the best stands of dry lime prairie, and secondly, to demonstrate certain facts concerning the phytosociology of prairie vegetation in the prairie-forest floristic province of southwestern Wisconsin.

Figure 6

A small remnant prairie at a bend in a country road. This is in northern Dane County and is glaciated. Most of the area is heavily farmed.

Figure 7

Steep, southwest-facing bluffs in Driftless Area in eastern Minnesota.

REVIEW OF THE LITERATURE

Historical

According to Camp (1947) no ecological study can be said to be well rounded unless it takes into account the history of the region under study "in the light of its geo-structure and climate, as well as its natural biota and the development of all of these through both space and time." Historical references have been used in a number of significant ecological papers (Dyksterhuis, 1946, Gardner, 1951, and Beilmann and Brenner, 1951) to point out how the vegetation of an area has changed since settlement by European man. The writings of early travellers in the area covered by the present study are numerous and extremely interesting. Although most of the descriptions are general in nature, it is possible, by examining many of them, to reconstruct a rather vivid picture of what southwestern Wisconsin was like prior to settlement. The following consists of excerpts from this voluminous literature, edited to show what the observations of the early explorers and travellers were.

Many of the earliest descriptions of prairies are of those seen along the rivers, on the broad, flat, and sandy terraces. For instance, as early as 1683 Father Hennepin (Shea, 1853) described the Mississippi River as running "between two chains of mountains, quite small here, which wind with the river, and in some places pretty far from the banks, so that between the mountains and the river there are large prairies, where you often see herds of wild cattle browsing. . . . Beyond these mountains you discover vast plains." At Prairie du Chien there was seen "a beautiful, even, grassy meadow of six miles in length by one or two broad" (Latrobe, 1833), having "grass that must have been at least six feet high" (Lanman, 1847). At the site of the present village of Trempealeau there was "an extensive prairie having few or no trees extending east and west about twenty five miles and from five to six miles wide" (Featherstonhaugh, 1847). Extensive prairies are described at La Crosse, Lake Pepin, and at Bay City. In 1781 Carver describes "fine meadows" along the Chippewa River where larger droves of buffaloes and elk were feeding than he had seen on any other parts of his travels. The country of "vast plains" as described by Hennepin is also described by Zebulon Pike in 1810 (Coues, 1895) when he climbed the bluffs behind the prairies at Winona, Minnesota:

> "We crossed first a dry flat prairie; when we arrived at the hills we ascended them, from which we had a most sublime and beautiful prospect. On the right we saw the mountains which we passed in the morning and the prairie in the rear, like distant clouds, the mountains at the Prairie La Crosse; on our left and under our feet the valley between

two barren hills through which the Mississippi wound itself. . . ."

There are numerous references to "barren hillsides" and to treeless slopes. Undoubtedly these include some of the dry lime prairies studied in this paper. Guigna's voyage of 1728 (Shea, 1861) gives us several of these descriptions. "The Ouisconsin is quite a handsome river. . . . Its shores are either steep, bare mountains, or low points with a sandy shore." Later, the valley of the Mississippi is described: "This beautiful river extends between two chains of high, bare, and very sterile mountains. . . . Its center is occupied by a chain of well wooded islands." In travelling down the Wisconsin, probably in the vicinity of Sauk City, Carver (1781) describes the terrain: "For miles nothing was to be seen but lesser mountains, which appeared at a distance like haycocks, they being free from trees . . . . and only a few groves of hickery and stunted oaks covered some of the vallies." At Trempealeau, Schoolcraft (1821) describes the view from the heights there: ". . . . toward the west the country has the general elevation of river bluffs. It is covered with oak--with tracts of prairie, and lies in ridges, some of which are entirely covered with grass and destitute of trees." In the region of Lake Pepin, Lanman (1847) describes a cone-shaped "mountain" which is "completely covered to the extreme summit by a carpet of grass" and the country in general as being "surrounded by undulating hills, covered with velvety grass to their summits and abounding with almost every variety of game." On the way up the Mississippi from Prairie du Chien to St. Paul, Caird (1859) mentions the numerous limestone ridges and their change in appearance: "In many places this ridge retires a short way from the water, its sharp edge disappears, and a round grassy face, smooth and regular as a lawn, runs up to within twenty feet of the top." In Volume II of the Geology of Wisconsin (1873-77) Irving points out that the prairie areas need not necessarily be flat but can include "both lowland and bold outlying bluffs."

References to the more extensive flat to rolling upland prairie areas, which were made whenever the earlier travellers climbed up out of the river valleys, become much more numerous when overland travel becomes common. Featherstonhaugh (1847) describes what must have been a common and exciting experience: "I landed on one of these gentle lawn-like slopes, and, ascending to the summit, had an immense extent of prairie-land before me, covered with wild grass." In travelling overland from Chicago to Prairie du Chien, Keating (1824) speaks of being led "in a general north-westerly direction, at first through thin woods, which gradually disappeared, their place being supplied by an extensive and apparently boundless prairie, which occupied us a whole day in crossing it. The woods consisted of small oaks and was without undergrowth, the prairie was undulated and extended itself along the dividing ridge between the streams tributary to the Mississippi and those which fall into the Rock river."

This extensive prairie along which extended the Military Road, built in 1835 from Green Bay to Prairie du Chien, occupied much of the level to gently south-sloping upland of the cuesta of the Galena-Platteville dolomites. From the mound at Belmont, in Lafayette County, Smith (1837) describes this expanse of prairie:

"The view from this mound . . . . beggars all description. An ocean of prairie surrounds the spectator whose vision is not limited to less than thirty or forty miles. This great sea of verdure is interspersed with delightfully varying undulations, like the vast waves of the ocean, and every here and there, sinking in the hollows or creating the swells, appear spots of trees, as if planted by the hand of art for the purpose of ornamenting this naturally splendid scene."

The geologist David Dale Owen (1848) wrote vividly of the prairie scenery in the upper Mississippi Valley:

"We find the luxuriant sward clothing even down to the water's edge the hill slope. We have steep cliffs shooting up through it in mural escarpments. . . . We have clumps of trees, disposed with an effect that might baffle the landscape gardener, now crowning the grassy height, now dotting the green slope with partial and isolated shade. . . . From the hill tops the intervening valleys wear the aspect of cultivated meadows and rich pasture grounds, irrigated by frequent rivulets that wend their way through fields of wild hay, fringed with flourishing willows. . . . On the summit levels spreads the wide prairie, decked with flowers of the gayest hue; its long and undulating waves stretching away till sky and meadow mingle in the distant horizon. The whole combination suggests the idea, not of an aboriginal wilderness inhabited by savage tribes, but of a country lately under a high state of cultivation and suddenly deserted by its inhabitants."

The extensive deep-soil prairies in northern Dane and Columbia Counties, the Dane and Arlington prairies, have been early described by Irving (1877):

"The prairie areas are by no means always flat; indeed, the flat prairies are the exception, and have chiefly been noticed along the bottom land of the Wisconsin river. The ordinary prairie, however, as in northern Dane and eastern Columbia county, is very rolling, commonly showing abrupt changes of level, even up to fifty or a hundred feet. In many cases, for instance, ... the prairie area includes both lowland and bold outlying bluffs. . . . This large prairie area is for the most part on high land, occupying the summit of the water sheds between the Wisconsin and Rock Rivers. It is nearly always underlain by the Lower Magnesian limestone, whose irregular upper surface contributes much to the rolling character of the prairie."

Besides the references to wide spreading, open prairies, many of the early references describe the oak savannas and oak forests. Carver's reference to the land's being covered with grass with a few groves of trees interspersed becomes one of the most commonly met-with descriptions. The oak groves "may be passed over in any direction in a wheel carriage with ease and safety as if you were driving through a plantation of fruit or forest trees, set or growing irregularly" (Smith, 1837).

In his voyage down the Wisconsin, Featherstonhaugh (1836) describes the valley in the vicinity of Helena (near the present city of Spring Green) as being bordered on both sides by "well-wooded coves or vales, called by the French coulees." Keating (1824) notes the forests along the streams in the general prairie area traversed from Chicago to Prairie du Chien and describes the land as he descends from the prairie on the Military Ridge to the Wisconsin River thus: "We descended a rough, steep, hilly ground which was covered with a heavy timber, and with very thick underwood, consisting chiefly of young oaks and aspens." The same area has been described by Smith (1837) as being "well timbered with numerous oak openings, and some miles of thick and well set wood."

In describing the country above Prairie du Chien, Keating (1824) notes that although "the country is generally prairie land, the hills and valleys are in some places covered with a scattering growth of fine timber, consisting of white, red, and post oak, hickory, white walnut, sugar tree, maple, white and blue ash, American box, etc." Further, in going overland from Prairie du Chien to Fort Snelling on the St. Peters River (the Minnesota), he describes the forests traversed to consist "principally of oak, basswood, ash, elm, white walnut, sugar tree, maple, birch, aspen, with a thick undergrowth of hazel and hickory."

Early Observations on the Ecology of the Prairie

References to the vegetation types which European man found on his arrival in the prairie-forest border area imply that it was a mosaic of grassland, oak savanna, and some thick timber. The references which follow attempt to show that many of the early travellers were aware of such ecological factors as exposure, drainage, and disturbance.

In travelling westward over the prairie peninsula, Flint (1828) observed that "in Indiana the proportion of prairie land is far greater than in Ohio; and in Illinois it has an immense disproportion over the timbered country." Flint also gives us good descriptions of his three categories of vegetation of the upper Mississippi Valley: the thickly timbered, the barrens, and the prairie. He divided the prairie into three types: the heathy or bushy, the wet, and the dry or rolling prairie.

The well-wooded and protected coves along both the Wisconsin and Mississippi rivers and the well-wooded islands in both of these streams are well described by Featherstonhaugh (1836, 1847). The roughly dissected country between the gently rolling prairie of the Military Ridge and the Wisconsin River, which was covered with a "heavy timber and very thick underwood," has already been mentioned in references by Keating (1824) and Smith (1837).

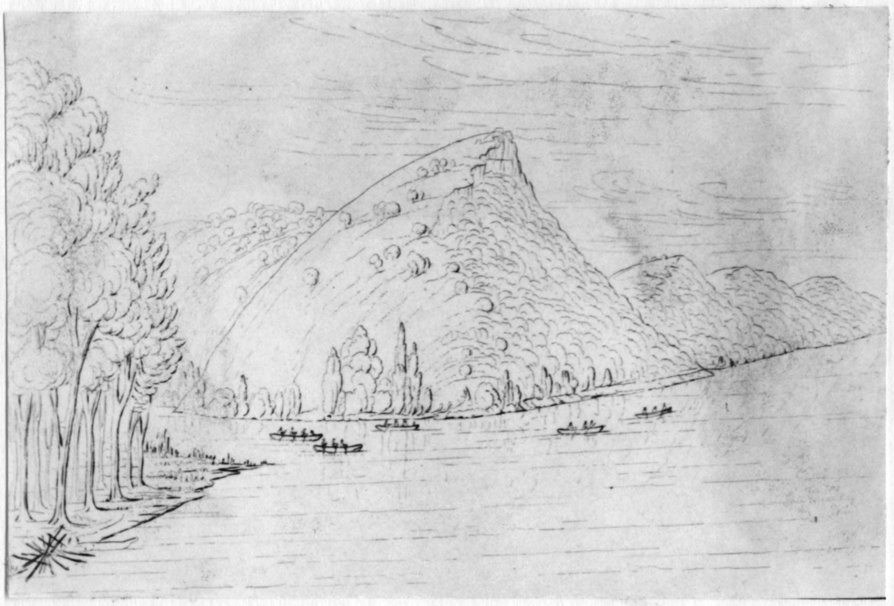
Exposure

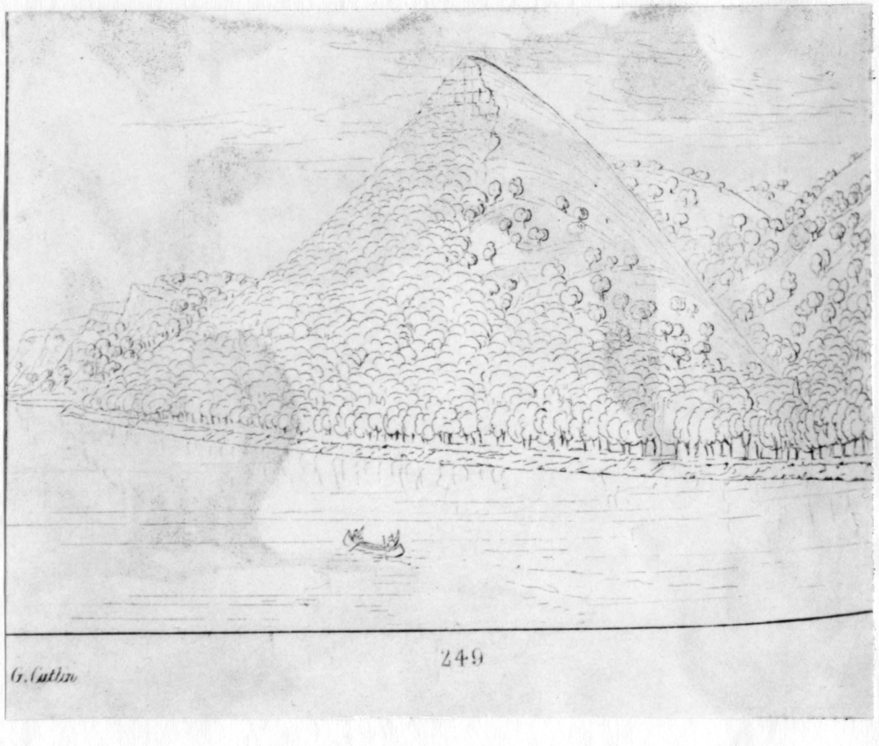
One of the earliest references to a difference in the vegetation of two sides of a slope is found in the description of a portion of Buffalo County (23N R 13W) in the field notes of the original land survey of Wisconsin, dated 1847: "This township is very hilly, rough, and in many places brushy. There is a constant succession of hills from the south to the north end of the township, some barely bare of vegetation of trees, and some pretty thickly timbered, chiefly with black oak and aspen, though generally bare on the south side to the summit and brushy or timbered on the north side." Lanman (1847) noted the difference between the eastern and western slopes of the Mississippi Valley, the prevalence of barren hills on the east and the "opposite side . . . where the eye is gratified by a range of wood-covered bluffs, rising directly from the margins of the stream." Owen (1852) has also described this relation between forest and exposure on the Mississippi bluffs: ". . . bold exposures of rock with grassy banks beneath are for the most part only on the south and western sides of the hills; the northern and eastern declivities are more generally overgrown with trees and shrubbery." As an explanation to this phenomenon, Owen reasons that "the alternate thawing and freezing on the sunny side has caused a more rapid decay of the rock, while scaling and splitting off, sometimes in large masses, slips down the side of the hill; and this, together with the rapid transition from heat to cold on the southern exposure probably prevents trees from coming to maturity on that side." Winchell (Geology of Minnesota, 1876), in discussing the geology of Houston County, comments on this observation also: "It is noticeable that many of the valleys, particularly those running east and west . . . have the bluffs along the north side destitute, or nearly so, of timber, but are heavily timbered on the opposite bluffs on the south side."

The aspect of these exposed, treeless southern and western slopes and timbered northern and eastern exposures has been preserved for us by Owen (1848), Catlin (1866), and others (Figs. 8 and 9). That some of these have not changed greatly can be seen by comparing a plate of the famed Maiden's Rock on Lake Pepin from Keating (1824) with a photograph of that bluff as it appears today (Figs. 10 and 11).

Figures 8 and 9

Plates from Catlin's works (1848) showing relation of forest and grassland to slope and exposure along the Mississippi River.





G. Catlin

A further factor which is related to the location of prairie and forest and exposure is the influence of drainage patterns on their position. Strong (1877) has indicated this relationship in the area known as the mineral lands of southwestern Wisconsin on a map (Fig. 12) which shows the main body of prairie to be located on the exposed upland areas between the streams. The descriptions of this general area by Owen (1839) confirm this distribution: ". . . south of the principal dividing ridges, on which the military road runs, the country is mostly prairie, except on the streams where we generally find a belt of timber" and, "The country on the Peccatonnica river affords the greatest supply of timber in any portion of the mineral district in Wisconsin."

Indian Fires

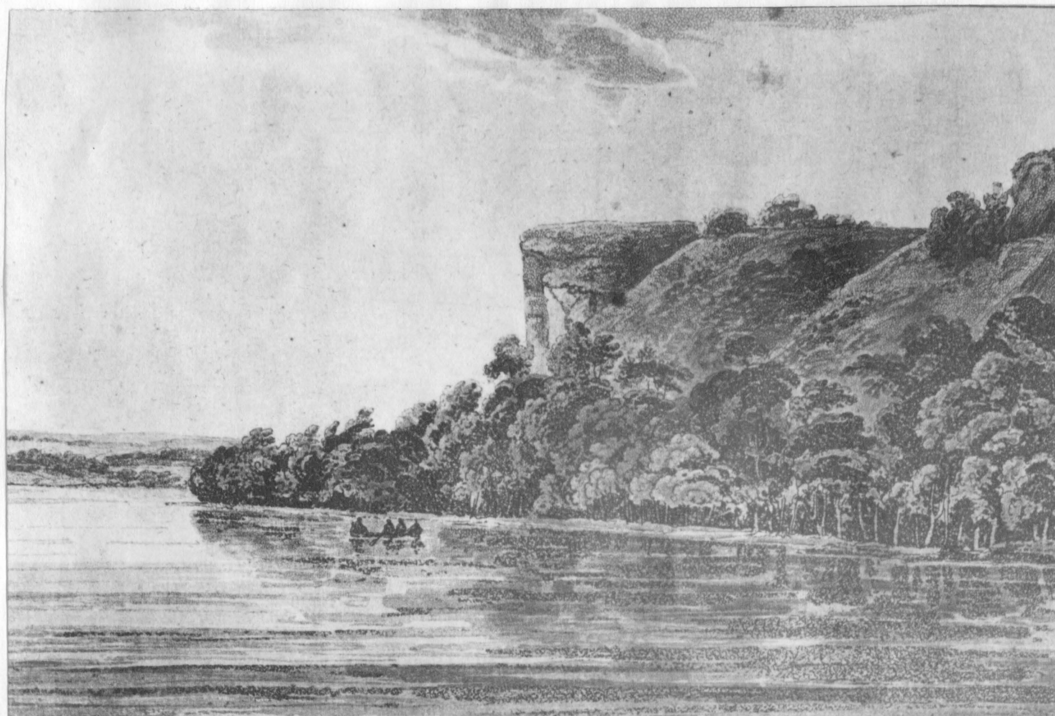
Perhaps no single factor regarding the milieu of the natives of the prairie-forest province is as often referred to as the annual fires set by the Indians for driving game. The intimate relationships between primitive man and his environment--the prairies, open forests, game, and fire as a weapon--need to be thoroughly examined in the light of ethno-ecology. The complete story of the postglacial development of the vegetation of the middle west cannot be unfolded until these relationships are better understood. According to Caird (1859), "so long back as we have knowledge of the country it has been the custom of the Indian to set fire to the prairie grass in autumn, after frost has set in,

Figure 10

Plate from Keating (1824) showing a view of Maiden Rock bluff on the upper Mississippi.

Figure 11

Present-day view of Maiden Rock bluff.



Pub. by H.C. Carey & I.Lea 1824. Engrav'd by J. H

THE MAIDEN'S ROCK ON THE MISSISSIPPI.

the fire spreading with wonderful rapidity, covering vast districts of the country, and filling the atmosphere for weeks with smoke."

Something of the probable extent of the Indian fires is indicated in a journal by Faux, written in 1818, from Indiana (Thwaites, 1904-07): "The season, called the Indian summer, which here commences in October, by a dark blue hazy atmosphere, is caused by millions of acres, for thousands of miles around, being in a wide-spreading, flaming, blazing, smoking fire, rising up through wood and prairie, hill and dale, to the tops of low shrubs and high trees, which are kindled by the coarse, thick, long, prairie grass and dying leaves, at every point of the compass, and far beyond the foot of civilization, darkening the air, heavens, and earth, over the whole extent of the northern and part of the southern continent, from the Atlantic to the Pacific, and in neighborhoods contiguous to the all-devouring conflagration, filling the whole horizon with yellow, palpable, tangible smoke, ashes, and vapour . . . for many days, or until the winter rains descend to quench the fires."

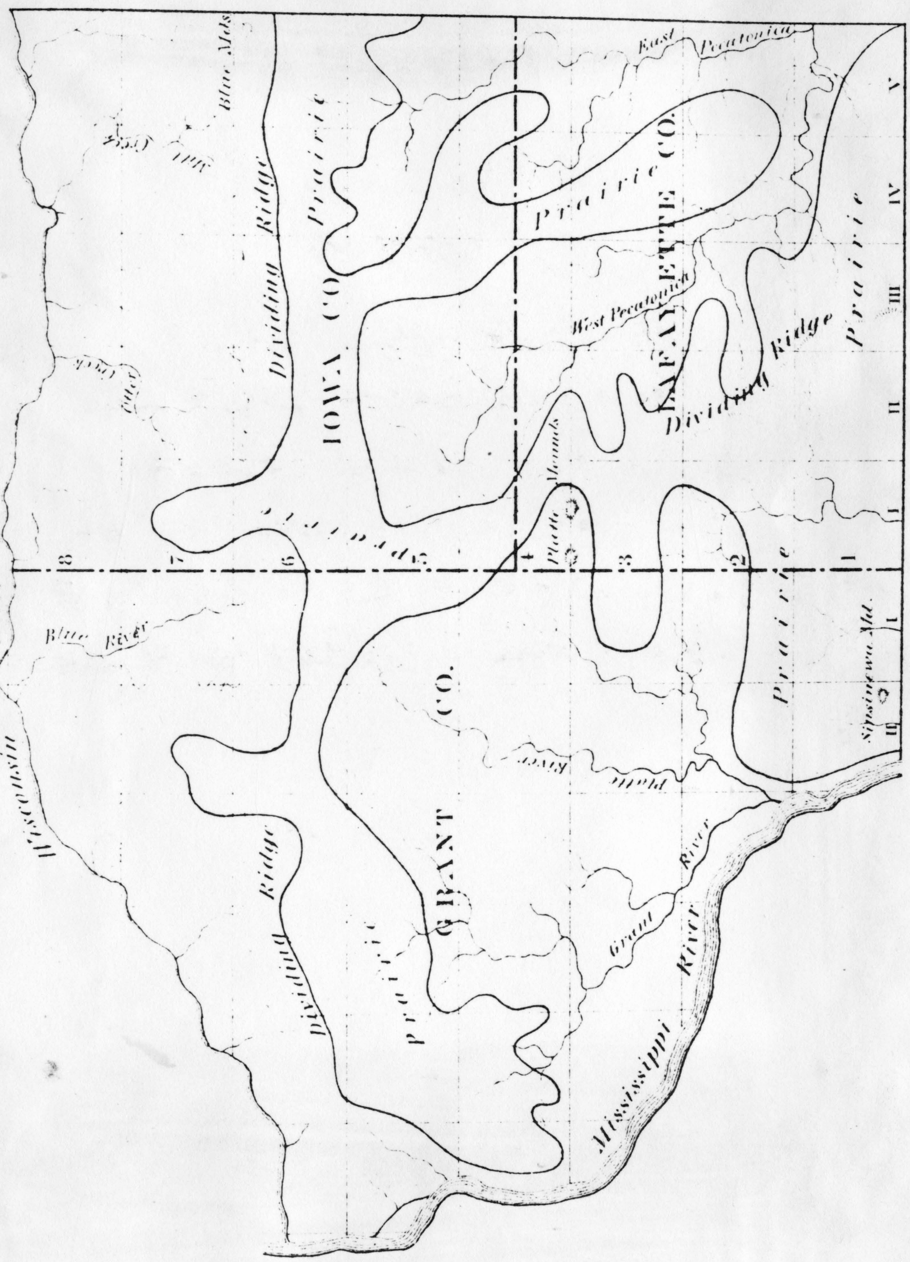
Latrobe (1833) describes a fire burning the prairie on the west shore of Lake Pepin as seen from the top of Maiden Rock bluff:

> "As we looked upon the summit early in the morning, across the troubled surface of the lake . . . a dense column of smoke from the opposite gave us in-

Figure 12

Map of the mineral lands of southwestern Wisconsin after Strong (1877). This shows an interesting relationship between the prairie and the Military Ridge and the other high ridges between the streams and valleys.

OUTLINE MAP
of the
LEAD REGION
Exhibiting the Drainage and the Distribution of Prairie and Forest.



timation that the Prairies were on fire. The spread of the conflagration on the low grounds opposite, which drew our attention at intervals during the day, continued unabated; and as evening approached, other columns of smoke springing up in all directions, both on the summit of the opposite range of mountains and in the valleys at their feet, showed us that the Indians had taken advantage of the driving wind to fire the country for a great many miles inland. . . . On the opposite side of the troubled sheet of water . . . the range of western bluffs was seen to incline inland . . . leaving a wide tract of country, partly forest and prairie, between their feet and the shore. A singularly conical and prominent hill rose abruptly from the middle of the plain. Around this detached eminence, which, swathed as it was in the smoke of the burning prairies beyond, seemed like a volcano, the fire had been concentrating itself during the earlier hours of the day, now advancing in one direction 'till checked by a dense tract of forest or a river, and then rushing on in another, and rolling over the summit or the base of the mountains. At sunset, the flame seemed to have gathered full strength, and to have reached a long tract of level grassy prairie nearer the shore, upon which it then swiftly advanced, leaving a black path in its trail. . . . In one place the progress of the fire, effectively checked by a small river, died away or edged over the country with slower progress. In another, after being seemingly choked, it would burst forth with redoubled fury, sending bright jets of flame far on the wind. . . . We calculated at this time that the fire spread over a tract nearly twelve miles in length, while the distant glare upon the clouded horizon showed that it was raging far inland. The whole evening the lake, the Maiden's Rock, the clouds, and the recesses of the glen were illuminated by the flames, while, gaining the rank growth on the borders of the lake and the brow of the distant mountains, the country opposite blazed like tinder in the wind; and from the summit of the Maiden's Rock, which we had again ascended before we retired to rest, the scene was fearfully grand."

Later and farther down the Mississippi, Latrobe gives us another vivid picture of the burning of the prairies: " . . . the golden haze of Indian summer had been scattered . . . and the prairies on all sides, above and below, were all blackened or burning. As you glanced up the side valleys, through which the broad tributaries pour into the main river from the east and the west, the summits of the hills were half obscured by the wreaths of smoke rising from the lower grounds."

An Indian fire from Kenosha County, in southeastern

Wisconsin is described for us by Lothrop (1856):

> "After the first frost, in the autumn of 1835, had killed the millions of tons of grass west of us, we began, at Pike River, to see the rising smoke at a distance. The Indians probably had fired the prairies as early as they could for hunting purposes. It was sometime in the latter part of September. We began to see the advancing fire towards evening on the prairie, three miles west of us; and, before twelve o'clock, it became a serious affair. The wind was from the south-west, and pretty strong, and the fire progressed rapidly. The blaze and burning fragments being blown by the wind, caught the tops of the high grass, and raging fire continued to advance so swiftly that a deer would hardly escape it. About nine o'clock in the evening it reached the woods, which extended back from the lake half a mile, where the rich foliage and fallen leaves fed the flame to a great height. Some precaution had been used for the protection of our shanties and stacks of hay; but we saw, as the flood of flames poured in, that we were not sufficiently prepared. Coverlets and blankets were thrown into the water and spread over the hay. . . . The roaring terror came through the woods with awful grandeur. Large trees, as well as all smaller vegetation, quickly fell before the ruthless invader."

Again, the fury of a fast-moving prairie fire is described to us by an anonymous author travelling through the United States and Canada in 1828 (Gleason, 1913): "The flames advanced very rapidly, continued to spread, and before they had arrived opposite to the place where I stood, formed a blaze of fire nearly a mile in length. How shall I describe the sublime spectacle that then presented itself? I have seen the old Atlantic in his fury, a thunderstorm in the Alps, and the cataracts of Niagara; but nothing could be compared to what I saw at this moment. The line of flame rushed through the long grass with tremendous violence, and a noise like thunder; while over the fire there hovered a dense cloud of smoke. The wind, which even previously had been high, was increased by the blaze which it fanned; and with such vehemence did it drive along the flames, that large masses of them appeared actually to leap forward and dart into the grass, several yards in advance of the line. It passed me like a whirlwind, and with a fury I shall never forget."

Both the effect of these repeated and often widespreading fires on the advance of the prairie and the encroachment of the prairie by forest on the cessation of the fires receive attention in the early literature. In 1825 Loomis (Gleason, 1913) observed that "the heat and fury of the flames driven by a westerly wind far into the timbered land . . . has no doubt for many centuries added to the quantity of open land found throughout this part of America."

Smith (1837) remarks that although the want of timber is the chief disadvantage to the settlement of the prairies, "the timber of the country is of the most rapid growth if the annual fires of the prairies are prevented or subdued." Also, Bradford (1846) notes that "the soil is of such fertility that in a few years, if the fires are kept out, there will be an abundant growth (of trees) for all purposes. In the Gazeteer of Missouri, published in 1823, it is stated that the St. Louis country is generally prairie; yet in fifteen years after that date, it was almost wholly covered with a thrifty growth of timber. The same is the case with other places."

This aspect of the dynamics of the grassland-forest borders as determined by fires seems well understood by Owen (1852):

> "The timber in the whole mineral district, on both sides of the Mississippi, grows in those situations which are least exposed to fire, and to the blast of winds which sweep over the extensive prairies. . . . The annual fires which have undoubtedly been kept up by the aborigines for ages past, have also, no doubt, . . . kept open our vast western prairies; for those parts of the western country which were originally prairie, and where the fires have been kept out for twenty years or more, are now covered with thick groves of small trees. The American aspen, in the

whole district of mineral lands, seems to be the pioneer tree which first invades the prairie. In many places we see copses of this tree in the broad prairie, like little islands in a vast lake. And almost everywhere in the prairie we see little shoots of it of one year's growth, which would soon be trees were it not for the annual fires. When once the prairie sward has been broken by this kind of tree, others come in one after another; the prairie changes to the thicket; and in a few years it becomes the vast wilderness, the boundless contiguity of shade."

Wright (1875) has expressed well the role of fire in converting timber into prairie: "Again, fire has killed the trees over wide areas on which grass was growing, exhibiting before our eyes nature's simple method of converting woodland into prairie. The reverse process is just as simple. When prairies are no longer swept over by fire, timber springs up, reconverting prairie into woodland. Grass, with fire as its ally, can beat timber. Timber can beat grass when it has no fire to fight."

The Bison

The grasslands and oak savannas of southwestern Wisconsin were a basic part of a wonderfully integrated biome in which such large mammals as the deer, elk, and bison were hunted by the native Americans, who, in turn, by using fire, kept open vast areas as prairie. Moyer (1910) quotes the geologist Shaler who stated the idea that "the American Indian before the advent of the whites had advanced to such a degree of culture that they had begun to regard the great herds of bison somewhat in the light of domestic animals, and that they purposely set fire to the prairie and forest opening to make better pasturage."

References to the presence of bison in the prairie-forest border are fairly numerous. The former range of this animal in Wisconsin has been described by Shorger (1937) who, by making use of historical references, has shown the range to be an area corresponding to the prairie-forest province. Gleason (1913) quotes Hennepin's comments on the Indian's use of fire to hunt the wild bison in the accounts of his travels in Illinois in 1679. Carver's statement regarding the "larger droves of buffaloes and elks" along the Chippewa River "than I had observed in any part of my travels," printed in 1781, has already been mentioned. Coues (1895), writing of the Pike expedition of 1810 to the area just south of the Chippewa River, states "that in the seventeenth and eighteenth centuries there were plenty of buffalo in this part of the Mississippi." According to Coues, they were exterminated or driven off after Fort St. Anthony was built in 1819.

Some indications of the numbers of bison in the entire area of their range are noted from Butler's <u>Wild North Land</u>

(1878): "The earth had never elsewhere seen such an accumulation of animal life as this northern continent must have exhibited five or six centuries ago, when, from the Great Slave Lake to the Gulf of Florida, millions upon millions of bisons roamed the wilderness," and from Hornaday's Extermination of the American Bison (1887): "Of all the quadrupeds that have ever lived upon the earth, probably no other species has ever marshalled such innumerable hosts as those of the American bison. It would have been as easy to count or to estimate the leaves in a forest as to calculate the number of buffalo at any given time during the history of the species, previous to 1870."

Commenting on the passing of the bison, Featherstonhaugh (1847) is prophetic regarding the disappearance of many wild things:

> "In every direction the country was covered with long wild grass; the buffalo, that formerly used to keep it down, has been driven to the other side of the Mississippi. . . . This state of things will not last long, for the American population will soon drive the Indian after the buffalo, and the cultivated grasses will take the place of the wild ones."

Prehistoric Man

It would be extremely valuable to be able to say just when early man began using fire in the prairie-forest border region as an aid to hunting or to clearing land for agriculture, when these fires became widespread enough to begin pushing back the forest, and just when the bison made its appearance in any large numbers. By the many accounts of early travelers in this region we know that extensive prairies existed in a region capable of supporting forests, that the natives regularly set fire to the prairie, and that considerable populations of bison, elk, and deer existed in the prairies and savannas.

That there have been concentrations of peoples living in this area for a long time before the arrival of European man has been noted by the numerous references to the earthen mounds of these prehistoric peoples. In 1828 Keating noticed a series of mounds in the vicinity of the Fox River of Illinois in a land largely prairie though "handsomely wooded in the neighborhood of the river." Also, along the Wisconsin River, about four miles above its mouth, Keating noted the presence of many more mounds which were "generally from six to eight feet high and eight to twelve feet in diameter." Commenting on the many mounds he saw along Lake Pepin, Keating states that they "attest to the former existence of a very dense population along the lake." The contemporary Indians apparently knew nothing of the builders of these mounds and are not in a "habit of constructing the works of a similar character and are unacquainted with the utility of them." Bradford (1846) noticed the numerous tumuli existing from the Blue Mounds eastward to the Four Lakes where "the country abounds with the earthwork antiquities, the origin of which the present aborigines are as ignorant as ourselves."

The probable effect of the mound builders on the vegetation has been expressed by Lapham (1855): "Whether the greater extent of treeless country in former times was owing to natural or artificial causes it is difficult to determine; but the great extent of ancient works within the depths of the present forests seem to indicate that the country was at least kept free from trees by the agency of man."

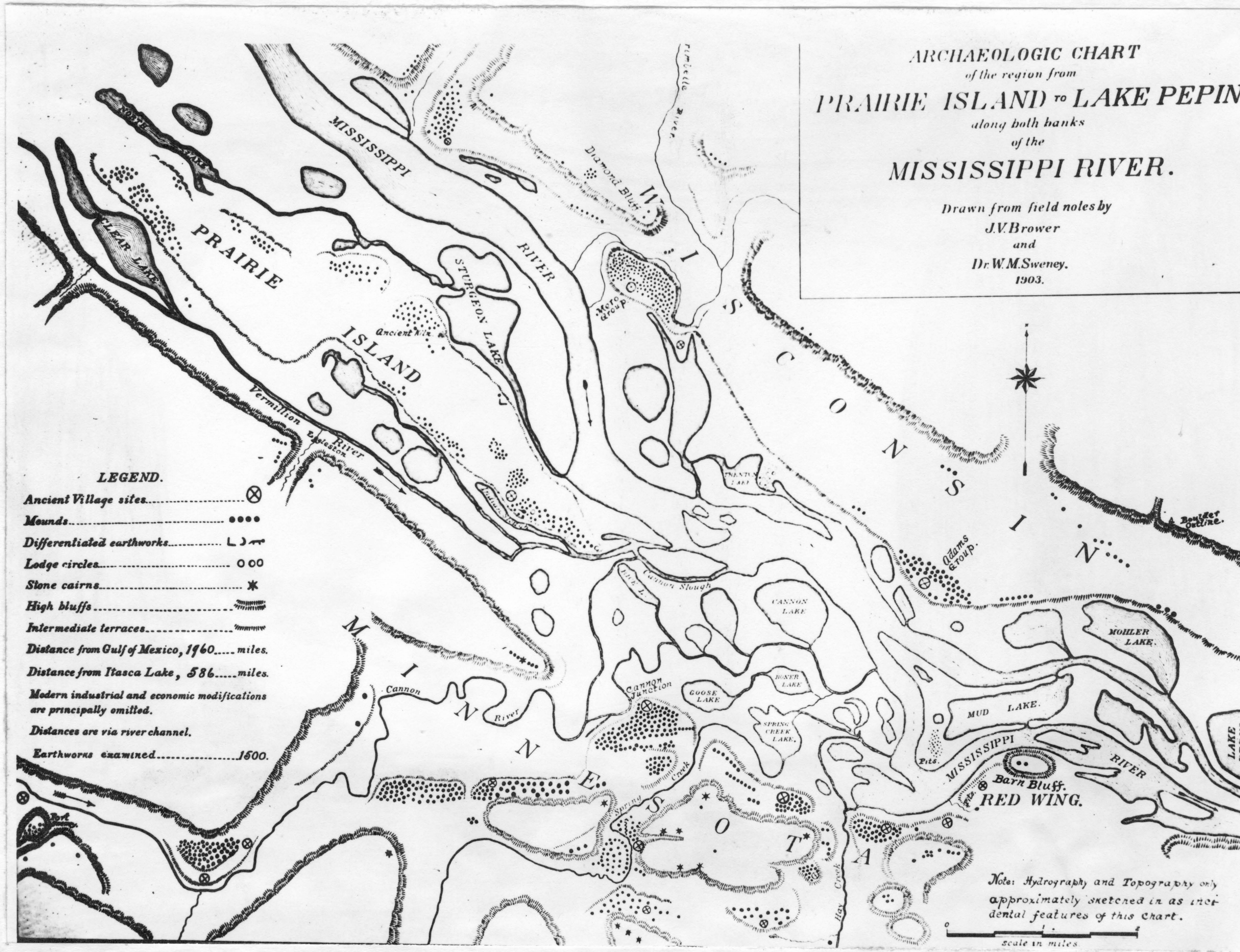
Several early workers (Gale, 1867, Stuntz, 1883) give added information about the mound builders. Gale suggests that the large number of mounds in Wisconsin, and particularly in the upper Mississippi Valley, indicates a heavy population which practiced an advanced type of agriculture. In 1867 over ten thousand mounds were already noticed within the state of Wisconsin, and nearly all of these were in the prairie-forest province, on or near the richest tables of land and near a permanent supply of water. Many of these mounds are near the modern cities of Racine, Madison, Prairie du Chien, La Crosse, and Trempealeau. According to Stuntz, they did not live entirely by the chase but cultivated the land. They "introduced and cultivated certain fruits, planted and protected certain forest trees such as the oak, sugar maple, and linden in regions far beyond where they are indigenous."

Blair (1911) has given us a picture of the agricultural habits of the Sauks and Foxes, tribes the Europeans met in the prairie-forest region, which, if it does not necessarily suggest a kinship of these Indians with the mound builders, does show us that the tribes the white men met were agricultural as well as hunting people: "They leave their villages as soon as the corn, beans, etc. are ripe and taken care of . . . and go off to the wintering grounds . . . it being previously determined on in council what particular ground each party shall hunt on. They return to their villages in the month of April and, after putting their lodges in order, commence preparing the ground to receive the seed. They usually raise from seven to eight thousand bushels of corn, besides beans, pumpkins, etc."

Although a number of ideas regarding the probable fate of the mound builders can be found in the early literature, it is not the purpose of this study to discuss all of these. Gale suggests that they were probably pushed out of the upper Mississippi Valley by the Winnebago confederacy which was, in turn, pushed down by the Dakotas. Shaler (1899), however, discusses a fate brought about by a factor other than an invading tribe or nation. This idea is mentioned here because it represents early thinking regarding interrelationships among various environmental factors. According to Shaler, "some of the Indians a few centuries before the coming of the whites . . . were in a rather higher state of advance than that in which they were found by the first Europeans. . . . The Ohio and Mississippi valleys abound with the tumuli and fortifications which indicate that the people had been

Figure 13

Map from Brower (1903) which shows an unusually high concentration of Indian mounds in the vicinity of Red Wing, Minnesota. A great many prairie remnants can be found in this vicinity today.


ARCHAEOLOGIC CHART
of the region from
PRAIRIE ISLAND TO LAKE PEPIN
along both banks
of the
MISSISSIPPI RIVER.
Drawn from field notes by
J.V. Brower
and
Dr. W.M. Sweney.
1903.
LEGEND.
Ancient Village sites
Mounds
Differentiated earthworks
Lodge circles
Stone cairns
High bluffs
Intermediate terraces
Distance from Gulf of Mexico, 1760 miles.
Distance from Itasca Lake, 586 miles.
Modern industrial and economic modifications are principally omitted.
Distances are via river channel.
Earthworks examined 1500.
Note: Hydrography and Topography only approximately sketched in as incidental features of this Chart.
scale in miles
PRAIRIE
ISLAND
CLEAR LAKE
MISSISSIPPI
RIVER
STURGEON LAKE
Ancient Kiln
Vermillion River
Diamond Bluff
Mero Group
WISCONSIN
Adams Group
Cannon Slough
CANNON LAKE
MOHLER LAKE
MUD LAKE
GOOSE LAKE
SPRING CREEK LAKE
Cannon Junction
Cannon River
MINNESOTA
Spring Creek
Hay Creek
Barn Bluff
RED WING
MISSISSIPPI
RIVER
LAKE PEPIN
Pits

more numerous . . . and that they depended more upon agriculture and less on the chase than their successors." It was Shaler's belief that the bison, which was quite numerous east of the Mississippi when the first Europeans arrived, was absent from this area until about 1000 A.D. The mound builders, therefore, did not know the bison, for no remains of his bones or pictures are found among their effects. With eastward migration of the bison at this time, the once sedentary agricultural peoples adopted a hunting culture. Although they kept some of the agricultural practices, they made the hunting of large mammals their primary source of food. They stepped up the burning of the prairies to favor pasturage for these wild herds, extending the grasslands "eastward into Ohio and Kentucky and probably even into the Carolinas." This idea raises more questions than it answers, perhaps, but it is interesting to note that at least one recent writer (Roe, 1951) favors the recent advent of the bison east of the Mississippi.

A map (Fig. 13) taken from Brower (1903) shows the location of a rather large number of mounds near the present city of Red Wing, Minnesota, where several prairies included in the present study are found. The presence of so many mounds in such a small area indicates at least a concentration of peoples in this region. Their use of fire to clear land for agricultural purposes or to hunt game (or for both of these ventures) would certainly keep back the encroaching forests and maintain and extend the grassland vegetation.

In the foregoing discussions there have been no attempts made to arrange references to the prairie in a chronological order. The earliest voyagers arrived in the 1670's, and a period of over 100 years elapsed before the numerous observations of the early 1800's were made. It is not known that there was any great lessening of the Indian fires in this interval, but if there had been a decrease in the numbers and extent of the fires during this time, it seems very probable that much of the open prairie could have been encroached upon at this time. That the prairie fires had not ceased even after settlement by the white man is shown by the numerous accounts of the settlers' fears of the raging fires. However, even a few years of diminution of the fires because of upheavals and movements among the native tribes would have allowed a certain number of oak grubs and pioneer trees to grow up and invade the prairie in some areas at least.

The excerpts which follow are from the very earliest references to the prairie in this area; many of them give the impression of vast open prairie areas, but in all of them are there references to scattered groves of trees. Although a great many of these early accounts were examined, it does not seem safe to conclude from these that there were any great differences between the amount of open country then and a century later.

In 1673 Father Marquette travelled from Green Bay to the Mississippi by way of the Fox and Wisconsin rivers. Stopping at the Mascouten Indian village, which was located "three leagues from a River (the Wisconsin) which discharged into the Mississippi," he describes the view from this place, which was located on a hill: "On every side prairies, extending farther than the eye can see, interspersed with groves or with lofty trees. The soil is very fertile and yields much Indian corn." This same view is described by Father Claude Allouez in 1670-71 in the Jesuit Relations (Thwaites, 1896-1901) who exclaims that "the Fire Nation is erroneously so called . . . its correct name being Maskoutenech, which means a treeless country." Again, in the Relations of 1678, Father Claudius Dablon notes that the Indians dwelling in this area had so little bark for cabins that reeds were used instead. And again the view is described: "The view is beautiful and very picturesque, for from the eminence on which it (the village) is perched, the eye discovers on every side prairies, spreading away beyond the reach, interspersed with thickets or groves of lofty trees."

Travelling down the Fox River of northeastern Illinois in 1670, Father Claude Allouez (Jesuit Relations, volume LX) states: " . . . we enter the fairest land possible to behold, in every direction, prairies only, as far as the eye can reach, cut by a river which gently winds through it . . . The region of forests is passed when one arrives here, and nothing but little groves, planted hills present themselves at intervals, as if to offer their shade to the traveller. In these rich pasture-lands are found buffaloes, called

Pisikiou, which greatly resemble our bulls in size and strength."

In the writings of Father Louis Hennepin are many references to prairies. In 1683 he commented on the prairies along the Illinois River: "It is lined with hills, whose sides are covered with fine large trees. On ascending these hills, you discover prairies further than the eye can reach, studded at intervals with groves of tall trees, apparently planted there intentionally" (Shea, 1853). He further comments on the same general area: "We found a vast Plain, on which nothing grows but only some Herbs, which were dry at that time, and burnt, because the Miamis set them on fire every Year in their hunting wild Bulls. . . . The buffalo were very refreshing and full of Juice, especially in Autumn; for having grazed all Summer long in those vast Meadows, where the Herbs are as high as they, they are very fat" (Thwaites, 1903).

Of the country near Lake Winnebago in eastern Wisconsin, Hennepin states: "We passed four lakes . . . on the banks of which the Miamis formerly resided. We found Maskoutens, Kickapous, and Outaougamy there, who sow Indian corn for their subsistence. All this country is as fine as that of the Islinois" (Shea, 1853).

La Salle, in 1677, in a letter to the minister Colbert, writes of an area near Fort Frontenac, near Lake Ontario: "It is nearly all so beautiful and fertile, so free from forests and so full of meadows, brooks and rivers, so abounding in fish, game, and venison, that one can find there in plenty all that is needful for the support of flourishing colonies. . . . And there are even native cattle, which, instead of hair, have a fine wool." Later, in the same year, he describes the country along the Illinois River: " . . . on the right hand and on the left stretched the boundless prairie, dotted with leafless groves and bordered by gray wintry forests, scorched by the fire kindled in the dried grass by the Indian hunters and strewn with the carcasses of the bleached skulls of innumerable buffalo. . . . The edges of the river were full of their hoof prints, . . . and at night the horizon glowed with distant fires" (Parkman, 1879).

REVIEW OF THE LITERATURE

Ecological

Papers dealing with the prairie in the prairie-forest border region, while rather numerous, are mostly descriptive in nature, giving lists of species found, and including usually a discussion regarding the probable origin of the prairie in this region. Ideas concerning this origin seem to be divided between a climatic and a fire origin.

Todd (1878), who reviews the ideas prevalent at that time, argues that although the presence of prairie fires, the amount and distribution of rainfall, the nature of the soil, the temperature and inclination of the surface are all more or less important in explaining the origin of forests and the prairie, the fundamental condition for forest growth is a "constant medium humidity of air and soil." Meehan (1881), however, is convinced that there is nothing in nature to prevent the gradual encroachment of forest over grassy plain in this region and states that the Indians "could not but have perceived that while grassy herbage throve in spite of fires, . . . trees could not follow on burned land. What could be more natural than that they burn the prairies with the object of obtaining food for their wild animals?" Another interesting idea stated by Meehan is that man came into this region soon after the recession of the ice and the glacial lakes and very early made use of fire.

Gleason (1909, 1912, 1913), studying prairie-forest problems in Illinois, favors the fire theory of prairie origins and draws support from travel accounts of early explorers and the distribution of forests chiefly on the eastern sides of north- and south-flowing streams. Also, he discusses a possible sequence of events at the close of the glacial epoch in which the plants of the grassland, completing their cycle of development more rapidly than trees do, were able to migrate eastward with a slowly drying climate at a faster rate than the deciduous forest could. According to Gleason, the migration of forests was restricted largely to two paths, the stream valleys and system of moraines, and, while the forests reached a vastly larger proportion of the state before the Indian fires became widespread, the level-till plains between the streams and moraines were probably grasslands even at the time of the forests' greatest advance. A more detailed discussion of possible migration routes of floras is found in a later paper of Gleason's (1923).

Shimek (1911, 1915, 1925), who studied the prairie in Iowa, found prairie vegetation on all types of topography and geological formations. He favors a climatic cause for the prairies, especially exposure to excessive evaporation and the drying effects of the "two o'clock sun." Forests, are, therefore, limited largely to the more rugged areas of the state and along streams where there is some protection from these extremes of drying. Even in the more heavily forested portions of northeastern Iowa, forests are found chiefly on the northern and eastern slopes.

Several papers deal with the general topic of grassland openings in the forest (Vestal, 1918, Shimek, 1910, and Hanson, 1922) and stress the local xeric conditions of these prairie sites, relating them to topography, slope, and exposure.

Two papers, Loomis and McComb (1944) and McComb and Loomis (1944), give the prairies of Iowa a subclimax status in the hierarchy of plant succession, dating their origin back to xerothermic periods in postglacial time and the beginning of the current forest climax to the end of the last dry cycle, "which was probably 1100 A.D."

Moyer (1910), in his discussion of the prairie vegetation of southwestern Minnesota, describes the bluff flora, "where the soil is dry and where xerophytic plants abound," and which appear to be similar to the dry lime prairies studied here. Bluff prairies of the Mississippi Valley in Iowa and Wisconsin were studied by Shimek (1924). He found that these grasslands tend to be on the southwest-facing bluffs and that the other faces are likely to be heavily wooded. Factors responsible for this distribution are: the afternoon sun, the drying southwesterly winds of summer, the rapid runoff of water from steep slopes, and a very porous soil. Regarding fires as a factor, Shimek says that "the once prevalent and still current belief that the treelessness of the prairies was due to prairie fires obviously will not apply to the prairies of the bluffs. . . . In fact the existence of these detached prairie tracts in many places is strong proof that the prairies were not caused by fires." In his writings of the vegetation of the upper Mississippi Pammel (1890) states that even the sunny side of some of the treeless slopes are "becoming rapidly covered with a forest growth when fenced and protected from fires."

The bur oak openings of southern Wisconsin have been studied by Stout (1944), and he considers them to be remnants of an earlier and more dense marginal forest in which the older of the bur and white oaks withstood the destruction of fires. In his study of the phytosociology of an oak woods in southern Wisconsin, Cottam (1949) has shown that the cessation of the fires at the time of settlement enabled the oak openings to grow into oak woods and, further, that the trend in these is now toward a climax maple-basswood forest.

The thin-soil bluff prairies of southwestern Wisconsin have been called relics by Chavannes (1940). She noted that nearly all of these steep prairies have a south to southwesterly exposure and that parts of some are being invaded by forest. Relic prairies on the sandy soils of central Wisconsin have been studied by Thomson (1940).

The first quantitative work on prairies in this region was done on the deep-soil prairies of Rock County by Green

(1950). She found the dominant grasses on these prairies to be Stipa spartea, Panicum sp., Sporobolus heterolepis, Andropogon gerardi, and Andropogon scoparius. Wagner (1951), who also worked with deep-soil prairies, studied their species composition and emphasized the relationships between their soils and that of adjacent fields.

The publication of a survey study of 65 prairie stands by Curtis and Greene (1949), who used a species-presence method to describe them floristically, should serve as a basis for a more thorough investigation of each of the types enumerated. These types--low prairie, high prairie, sand prairie, and high lime prairie--undoubtedly represent the whole gradient of wet to dry physiographic sites upon which the prairie was found prior to settlement. A somewhat similar gradient on the rough topography of northwestern Iowa has been indicated by Kelley (1931). He distinguishes the true prairie on the slope from both the prairie-meadow transition in the draw and the steppe plant community on the hilltops. The latter type is distinguished from the true prairie by the bunched nature of the grasses in the steppe contrasted with the dense sod of the true prairie.

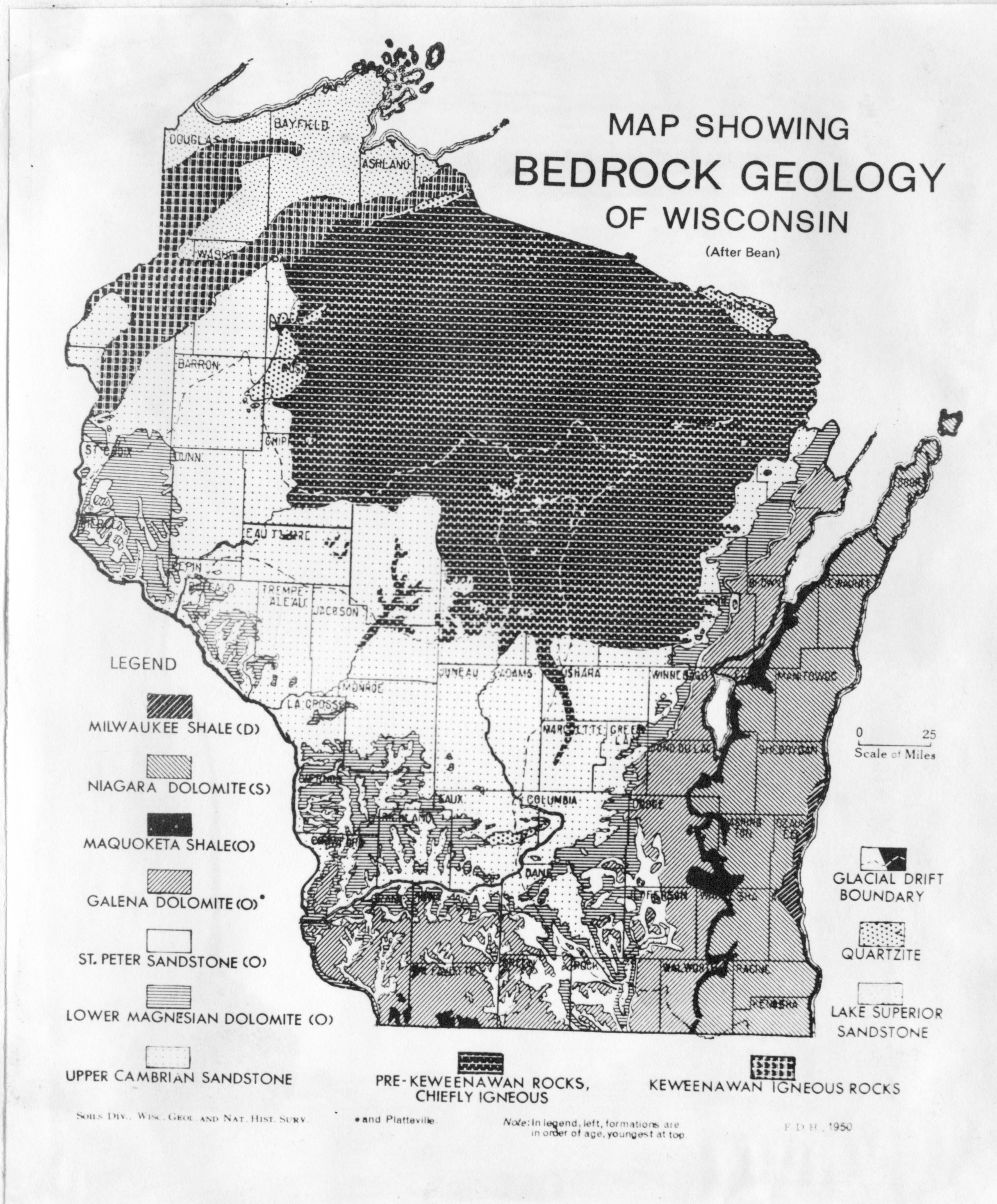
Figure 14

Five physiographic features of Wisconsin (after Martin).

Fig. 10. The five geographical provinces of Wisconsin.

Figure 15

Bedrock geology of Wisconsin


MAP SHOWING
BEDROCK GEOLOGY
OF WISCONSIN
(After Bean)
DOUGLAS
BAYFIELD
ASHLAND
BARRON
ST. CROIX
DUNN
TREMPEALEAU
JACKSON
MONROE
LA CROSSE
JUNEAU
ADAMS
WINNEBAGO
MANITOWOC
COLUMBIA
DANE
JEFFERSON
WALWORTH
RACINE
KENOSHA
0 25
Scale of Miles
LEGEND
MILWAUKEE SHALE (D)
NIAGARA DOLOMITE (S)
MAQUOKETA SHALE (O)
GALENA DOLOMITE (O)*
ST. PETER SANDSTONE (O)
LOWER MAGNESIAN DOLOMITE (O)
UPPER CAMBRIAN SANDSTONE
PRE-KEWEENAWAN ROCKS, CHIEFLY IGNEOUS
KEWEENAWAN IGNEOUS ROCKS
GLACIAL DRIFT BOUNDARY
QUARTZITE
LAKE SUPERIOR SANDSTONE
SOILS DIV., WISC. GEOL. AND NAT. HIST. SURV.
* and Platteville.
Note: In legend, left, formations are in order of age, youngest at top
F. D. H., 1950

DESCRIPTION OF THE AREA

The prairie remnants of southwestern Wisconsin are today a very small part of the vegetation of this region. The general area under consideration in this study, referred to as either southwestern Wisconsin or the prairie-forest province, is located south of a line running diagonally across the state from St. Croix County in the northwest to Lake Michigan in the extreme southeastern corner. It is, in general, the area in which oak forests rather than pine occupy the intermediate stages in the forest succession toward a maple-basswood climax.

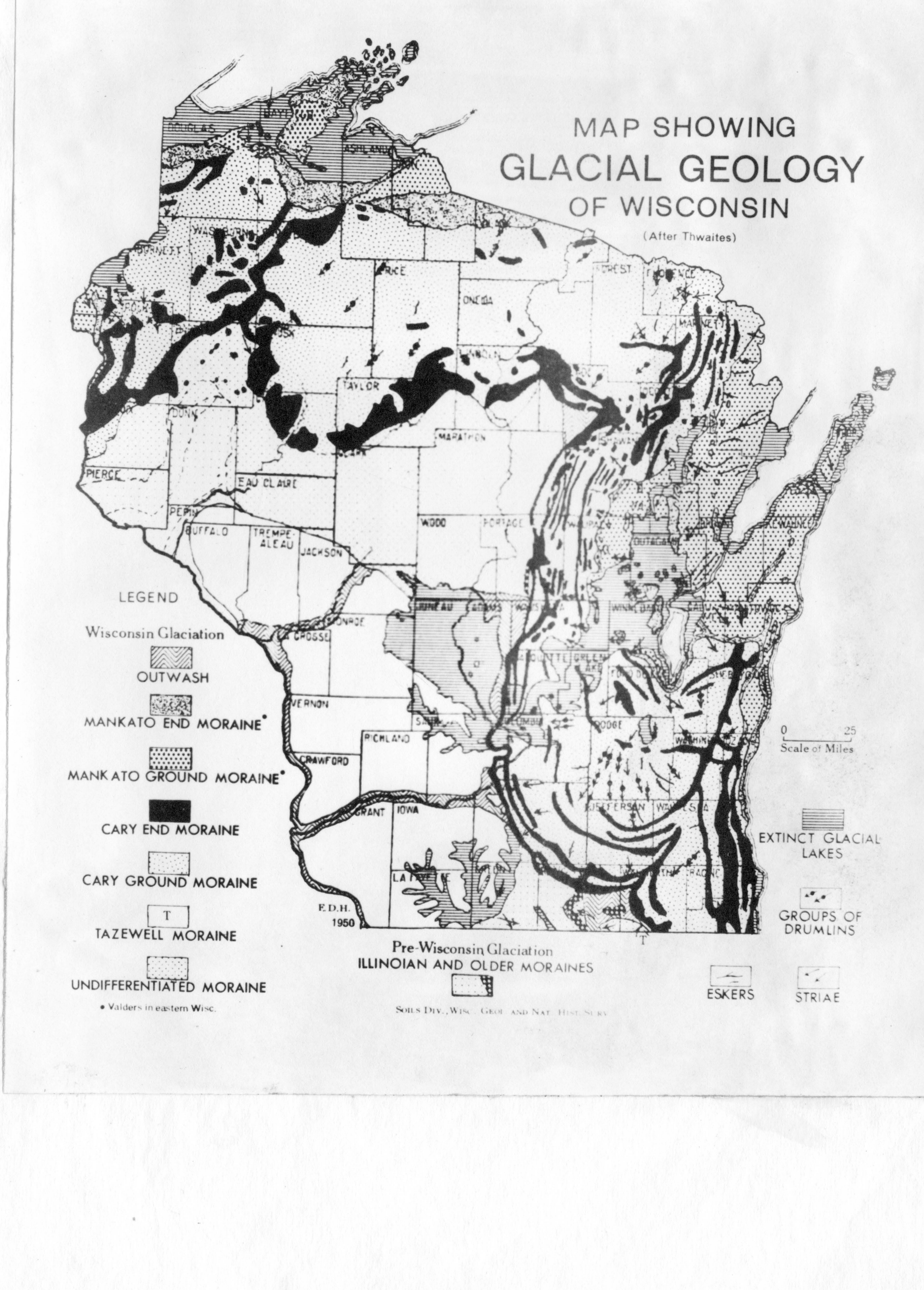
Geology and Physiography

Various geological features of the state of Wisconsin are shown in Figures 14, 15, and 16. Any attempt to cover the geology or physiography of the prairies as they existed in pre-settlement times would involve a discussion of the geology of the entire region, since the prairies were not confined to any few physiographic features. Such a general discussion is well covered by Martin (1932).

Since the dry lime prairies are characterized by having a very thin calcareous soil, the location of these prairie remnants is somewhat limited. Also, because of the location in the state with respect to the larger areas of prairie to

Figure 16

Glacial geology of Wisconsin


MAP SHOWING
GLACIAL GEOLOGY
OF WISCONSIN
(After Thwaites)
LEGEND
Wisconsin Glaciation
OUTWASH
MANKATO END MORAINE*
MANKATO GROUND MORAINE*
CARY END MORAINE
CARY GROUND MORAINE
T
TAZEWELL MORAINE
UNDIFFERENTIATED MORAINE
* Valders in eastern Wisc.
Pre-Wisconsin Glaciation
ILLINOIAN AND OLDER MORAINES
Soils Div., Wisc. Geol. and Nat. Hist. Surv.
EXTINCT GLACIAL LAKES
GROUPS OF DRUMLINS
ESKERS
STRIAE
0 25
Scale of Miles
E.D.H.
1950
DOUGLAS
ASHLAND
WASHBURN
PRICE
ONEIDA
FOREST
TAYLOR
MARATHON
DUNN
PIERCE
EAU CLAIRE
PEPIN
BUFFALO
TREMPE-ALEAU
JACKSON
WOOD
PORTAGE
OUTAGAMIE
JUNEAU
ADAMS
MONROE
LA CROSSE
VERNON
RICHLAND
CRAWFORD
GRANT
IOWA
DODGE
JEFFERSON
T

Figures 17 and 18

Two views of the flat to gently rolling country of southern Dane and northern Green counties on the Galena-Platteville dolomites.

the south and west, most of the prairies studied are in the Driftless Area or very close to this province. In the rugged and deeply dissected uplands of southwestern Wisconsin the steeply sloping dolomite-capped hills offer the ideal habitat for this kind of plant community.

In the Driftless Area dry lime prairies are found mainly on two kinds of bedrock. South of the Wisconsin River on the gently sloping, southward-facing upland of the Galena-Platteville dolomites (Ordovician age) are a number of prairies, in southern Dane and northern Green counties (Figs. 17 and 18). These thin-soil prairies are on the eastern margin of the once-extensive prairie areas of the mineral lands of southwestern Wisconsin and are much less steep than the prairies on the bluffs along the Wisconsin and Mississippi rivers. That this back slope of the cuesta was originally prairie and the roughly dissected escarpment more or less timbered has been shown by references to historical data.

North of the Wisconsin River the extensive Prairie du Chien dolomites (Lower Magnesian), also of Ordovician age, account for most of the steep bluffs (Figs. 19 and 20). These bluff prairies cut across various rocks of Cambrian age. The Prairie du Chien dolomites extend beyond the Driftless Area into Pepin, Pierce, and St. Croix counties, where, in an area of very old and thin drift, the dry lime prairies occur on the rocky slopes as they did farther to the south.

The numerous sand prairies located on the terraces along

Figure 19

A steep, south-facing prairie on the Lower Magnesian dolomites along the Wisconsin River valley.

Figure 20

A view of the prairie above (Fig. 19) showing its relation to the surrounding wooded areas.

Figure 21

A small roadside prairie remnant on a thin-soil hilltop surrounded by lush, cultivated fields. A part of the Dane prairie, in northern Dane County.

Figure 22

A view of the rolling, glaciated Arlington prairie in southern Columbia County. Native prairie plants have almost entirely disappeared from this extensive, highly cultivated area.

the Wisconsin, Mississippi, Black, and Chippewa rivers and on the extensive areas of Cambrian sandstones and glacial lake beds in the central part of the state are not included in this study.

In the glaciated areas of Wisconsin, dry lime prairies are found on the gravelly soil of the steep kettle moraine of Waukesha County and on limestone outcrops in regions of very thin drift, such as southeastern Green County and the counties north of the Driftless Area. The extensive prairies, which were on the deep drift of Wisconsin age, for instance, the Arlington prairie of Dane and Columbia counties (Figs. 21 and 22), are now entirely in cultivation, and very little of the original prairie vegetation can be found along the road-sides of this area. At the edge of this prairie, however, in the hilly country near the Wisconsin River, a number of remnant prairies are found. Several excellent remnants of the extensive deep-soil prairies on the flat outwash plains of southern Rock County can be found along railroads (Figs. 23 and 24).

Most of the prairies included in this study of dry lime prairies are located on rather steep, southwest-facing slopes. Eighty-nine per cent of the 64 stands included in this study have an exposure that is either south, west, or southwest. The few (7) with exposures other than these have a very slight slope. Half of the 89 per cent have a southwest exposure, while southern and western exposures are divided evenly among

Figure 23

A deep-soil, mesic prairie on the gravelly outwash plains of Rock County. A railroad-side remnant.

Figure 24

Most of this area (Figure 23) is in cultivation.

the other half. The average slope of the prairies, measured with an Abney level, can be used to divide the stands into the following classes: 34 per cent have a slope of from 0 to 6 degrees (level to gently sloping), 36 per cent have a slope of from 7 to 15 degrees (sloping to steep), and 30 per cent have a slope of over 15 degrees (steep to very steep).

Figure 25 shows the appearance of two slopes of an east-west valley in northern Dane County. The slope of each is approximately 27 degrees. The north-facing slope is heavily wooded, while the south-facing slope is treeless.

Figure 26 pictures a dry lime prairie which in many respects is a typical one. It occupies the top and south-facing slope of a limestone-capped hill just within the Driftless Area in northwestern Dane County, a few miles outside the terminal moraine of the Cary ice sheet. It is surrounded by woods: a rather thick oak forest having many open grown white and bur oaks is on the north-facing slope, a narrow band of oak-hickory forest occupies the base of the slope near the road, and on the level top, back from the open prairie, is a pastured oak opening. The topography of the prairie varies from the flat, thin-soiled top of the hill to the very steep south-facing slope of 27 degrees.

That much of southwestern Wisconsin has been covered with blankets of silt of aeolian origin of varying depth is shown by Figure 27. This is undoubtedly an important factor in determining the depth and fertility of the soils of this

Figure 25

Two opposite sides of an east-west valley in northern Dane County. The north-facing slope (background) is heavily forested, while the south-facing slope (foreground) is in grassland.

Figure 26

A view of prairie #19 in northern Dane County. Southwest slope in prairie vegetation surrounded by oak openings, oak-hickory, and oak forests.

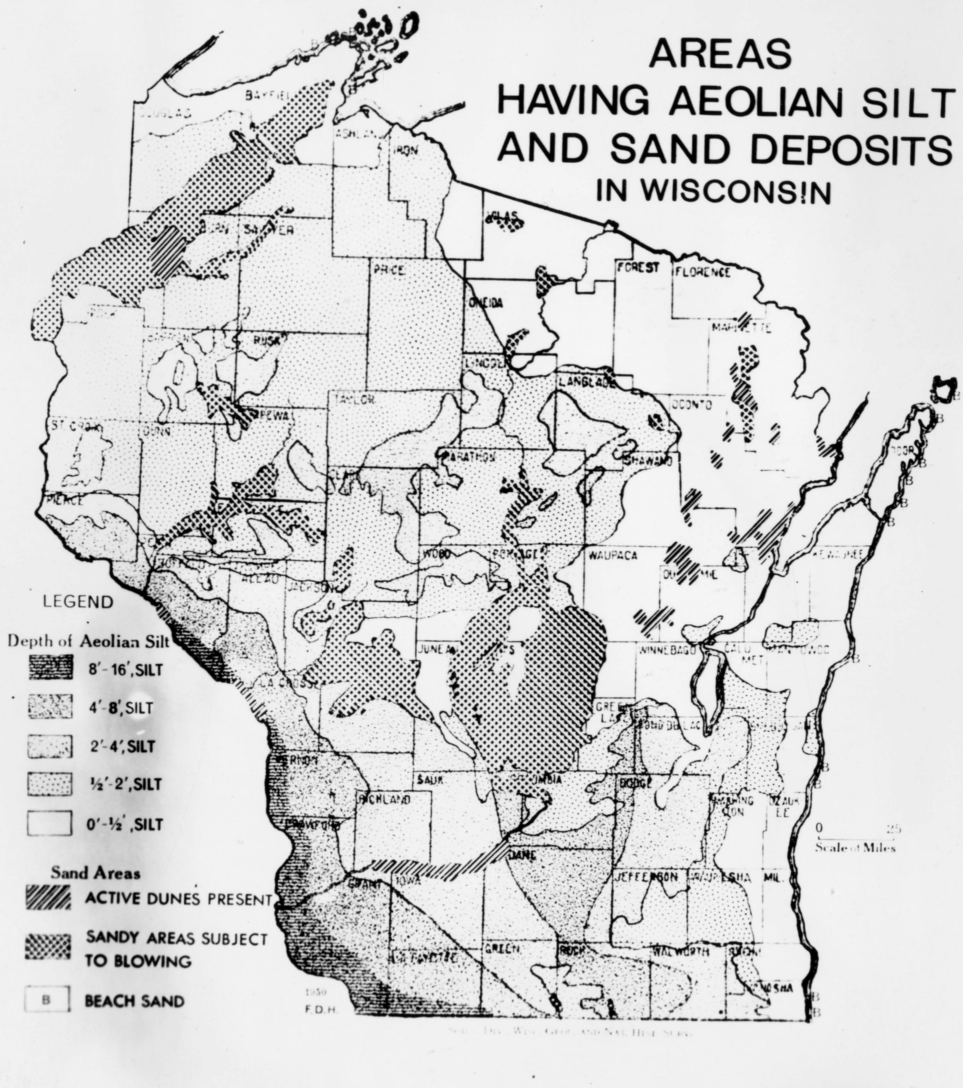
area, but it is probably less important regarding the soil of the dry lime prairies, since the agent which deposited the loess, the strong southwesterly winds, was responsible also for removing most of what would accumulate from time to time on the exposed ridges and slopes facing the southwest. Nevertheless, some of the soil on these dry lime prairies, particularly that in small depressions, is a fine powdery silt.

Soils

Certain aspects of the soils of the dry lime prairies have already been mentioned; namely, their thinness and their calcareous nature. Certain other characteristics are rather obvious. Because of the shallow nature of these soils, the slope and exposure of the habitats to excessive drainage and to prevailing winds, their instability and immaturity can be understood. They are, thus, azonal or immature soils. The shallow top layer in which the bulk of the roots are located can be designated as the A horizon and the substrate upon which this layer rests called either the C or D horizons. The D horizon is the dolomite bedrock itself or the weathering sandstone with many broken fragments of dolomite lying on it, and the C horizon consists of whatever loess or other unconsolidated material has accumulated. These soils are, then, largely lithosols, or, in the case of the soils on the unconsolidated calcareous gravels of the kettle moraine, regosols. It is conceivable that in the case of a number of instances where loess is found in a part of the particular prairie being

Figure 27

Map showing extent and depth of wind-deposited materials in Wisconsin.


AREAS
HAVING AEOLIAN SILT
AND SAND DEPOSITS
IN WISCONSIN
LEGEND
Depth of Aeolian Silt
8'-16', SILT
4'-8', SILT
2'-4', SILT
½'-2', SILT
0'-½', SILT
Sand Areas
ACTIVE DUNES PRESENT
SANDY AREAS SUBJECT TO BLOWING
B BEACH SAND
0 25
Scale of Miles
1950
F.D.H.

studied the soil be regarded a rego-lithosol.

In the older soil-survey bulletins these shallow-soiled areas are classed simply as "rough, stony land-including rock exposures, cliffs, and land too steep and rough to plow or cultivate profitably." Since this is not good agricultural land, these soils apparently have not been studied very intensively. Most of these dry rocky exposures in Wisconsin are now grazed; the dry lime prairies included in this study exist because by accident some of this poor agricultural land has escaped disturbance.

Modern soil categorizing would include most of these dry lime prairie soils of southwestern Wisconsin in the Sogn-Dolomitic Rock Outcrop complex, in which the A horizon is 9 inches or less to a dolomitic bedrock. This could be either the level or steep phase of the Fayette-Dubuque series.

A soil sample from the A horizon has been collected for each of 44 of the stands and analyzed by the state soils-testing laboratory for the following factors: pH, available calcium, magnesium, phosphorus, potassium, NO_3 and NH_4 nitrogen. In addition a water-retaining capacity determination has been made. Although the results of these tests are shown and discussed later, a few general statements by way of description are made here. Field determinations and results from the soils-testing laboratory showed the pH's to be almost consistently 8.0. In checking the pH's with a Beckman potentiometer, using the method suggested by Peech and others (1947), it was found that the pH's were not greatly lower, but ranged from 7.3 to 7.9. This would place these soils in the mildly alkaline class (pH 7.4-7.8). The amounts of available calcium and magnesium were very high, which is expected since these soils have developed on dolomitic rock. The amount of calcium ranged from 3000 to 6000 ppm. (average 4800), and the amount of magnesium ranged from 300 to 600 ppm. (average 495).

Climate

The areas of prairie in the Midwest have been described by Borchert (1950) as occupying a wedge extending across southwestern Wisconsin and Illinois into Indiana and as being a transition zone between the more continental area to the south and west and the more maritime and forested area to the north and east. This transition zone, further, is between an area of heavy winter snowfall and reliable summer rains and an area of relatively dry winters and occasional low summer rainfall. Such a region, the prairie-forest province, is said to be able to support prairie, forest, and oak savanna, the predominating type of community which succeeds depending on the emphasis the area feels due to any east or west shift of this general climatic pattern.

Transeau (1935) has shown that the eastward extension of the prairie, the prairie peninsula, occupies an area which does differ from the heavily forested regions to the north and south. The ratio of the precipitation to the evaporation (P/E) is lower in the prairie peninsula. Transeau also emphasized the importance of extremes of environmental factors--that "an extreme drought . . . can change the vegetation more in a few years than a century of favorable weather." Winter drought caused by the freezing of the soil in the prairie area of Iowa as an important factor in preventing the survival of tree seedlings has been suggested by McComb and Loomis (1944), although they state that the drought years of the 1930's did not affect the forests as a whole in this area.

Shimek (1911), though referring to the prairie areas of Iowa in general, states that the prairies are uniformly so situated that they are fully exposed to the factors which cause rapid evaporation--the sun and the wind. He also stressed the importance of extremes, that "any period, no matter how short, which is fatal to trees is sufficient to prevent the development of a forest, even though the greater part of each season is favorable to tree growth."

Willett (1949) has discussed world patterns of climate during geological time and, in particular, postglacial time. According to him and other students of climate variations, there have been since the recession of the last ice sheet two periods of climatic optima, in which the climate has been significantly warmer and drier than at present. These are estimated to have occurred from about 5000 to about 1000 B.C. and from 400 to 1000 A.D. These periods become all important in accounting for the eastward march of the prairie in the warmer and presumably drier years and the encroachment of the forest during the cooler and wetter years. A region that is ecotonal between grassland and forest would be very sensitive to such climatic shifts.

The mechanism whereby the wedge-shaped prairie peninsula can shift, moving in a general east-to-west direction in periods of strong mean westerly circulation patterns, has been suggested by Willett (1949) as due to long-period climatic fluctuations caused by solar variations in ultraviolet. Results of such shifts can be demonstrated within the era of recorded history elsewhere: the expansion of Viking civilization into Greenland during the second climatic optimum followed by a destruction of these colonies in a period of climatic stress when the glaciers of Greenland advanced, and the closing by glaciers of certain passes in the Alps which had been routes of migration during the same climatic optimum. These dates (about 1000 A.D.) agree with the conclusion by McComb and Loomis (1944) that in Iowa a general dry cycle ended about 1100 A.D.

That the climate today may be undergoing certain changes which will affect the prairie vegetation of southwestern Wisconsin is suggested by Willett (1951), who, by the extrapolation of sunspot-climate relationships, predicts that the temperature over much of the world will fall during the next 15 years, reaching a first minimum level during the 1960-65 period. Significant cooling will occur in northern Europe and eastern United States, and the rainfall in the lower middle latitudes south of 50 degrees N will be substantially higher. Further prediction is made by Willett that the general recent recession of glaciers in all regions is due to be reversed in the near future, being most pronounced during the next 20 years. Field botanists working in southern Wisconsin during the past several summers will concur with these predictions.

That there have been climatic shifts and cycles in postglacial times and that the mechanism for these shifts exists have been demonstrated (Willett, 1949, 1951, Borchert, 1950). However, the magnitude of these changes and the manner in which climatic changes alone have affected the vegetation of the prairie-forest border are not very clear. One wonders, for instance, how long a time and how great a drought are necessary to change a heavily wooded region into prairie.

The dry lime prairies under consideration here have been described as having excessive surface drainage and thereby subject to severe droughts during the drier summer months. This factor is a useful one in explaining the persistence of these remnant prairies and the physiognomy of their vegetation. No detailed study of the microclimate of these prairies has been made.

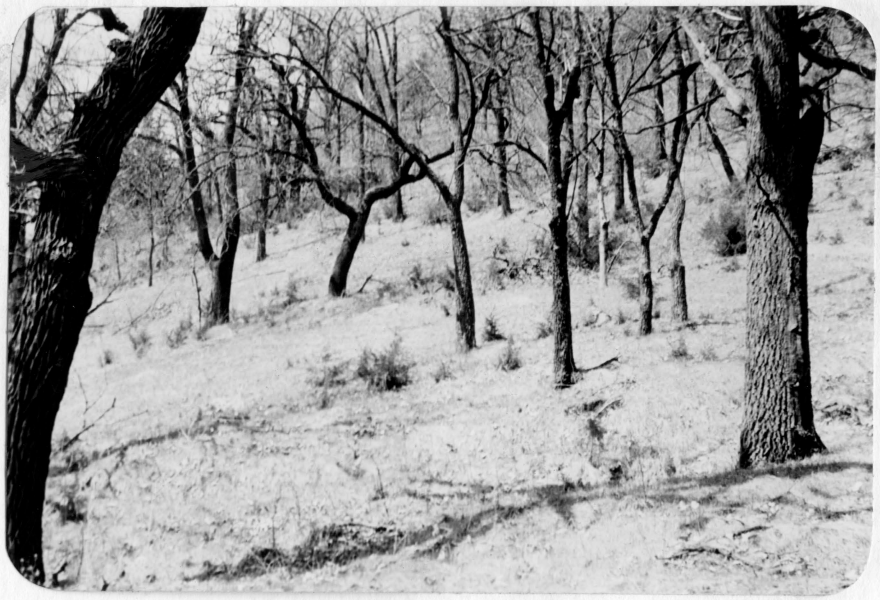
The predominating south and southwest exposure of these prairies has already been mentioned. Geiger (1950) discusses

Figure 28

View of widely spaced trees on a south-facing hillside in a coulee in upper Mississippi Valley.

Figure 29

View of more heavily forested north-facing hillside of same coulee (Fig. 28).



very thoroughly the microclimatic effects of various exposures and degrees of slope. He has shown that the coldest direction of slope is the northern and the warmest varies from the southwest (in January until spring) to the northeast (June) and back to the southwest (summer and autumn). Further, he points out that the morning sun, which finds a moist ground, uses up a great part of the solar energy in drying out the soil and can concentrate its greatest work in the afternoon on the southwest exposures in actually raising the temperature of the soil. Shimek has expressed the same idea by the use of the term "two o'clock sun." Opportunities for detailed microclimatic studies are especially numerous in the many coulees along the Mississippi, where, within very small areas, exist fragments of prairie and forest, ranging from oak openings to dense forests, on opposite slopes (Figs. 28 and 29).

Biotic Influences

It has been said that plant associations are "contemporary expressions of historical events and processes, involving changes in environment and biota over a long period of geologic time" (Sauer, 1950). The main biotic forces considered here as they have probably affected the vegetation of the prairie-forest region include the use of fire by the natives, their dependence on such large mammals as the bison, and their reliance on agriculture for a substantial part of their subsistence.

The historical references quoted earlier attempted to demonstrate the probable role of the Indian fires in the maintenance and spread of the grasslands in the Midwest: when these fires were stopped, many of the prairies and oak openings grew up into oak woods. These dramatic changes were undoubtedly obscured by the rather rapid and complete settlement of the Midwest in the nineteenth century.

A century is a very short time geologically and ecologically speaking. In this short period of time European man has profoundly changed the appearance of the grasslands of the Midwest. A drive through the rich, rolling fields of the Arlington prairie of Dane and Columbia counties will reveal few if any remnants of native prairie. In fact, very few scattered prairie plants will be seen along the roadsides of this once-extensive grassland. The common roadside plants today are largely European importations, most of them exhibiting a decided weedy habit. Thus within a relatively short time the native American biota has been almost entirely supplanted by the intensely cultivated and pastured lands of the midwestern farm.

Stewart (1941) has stressed the need for botanists to consider vegetation in the light of history and ethnology. Historical references to the Indian of the Midwest as a hunter and agriculturist have already been used. Waugh (1916) has described the girdling of trees and then the burning of them by the Iroquois Indians of the East. This reference also states that despite the hunting activities of these Indians, a greater part of their food supply came from the maize fields. The Huron Indians, again in an area east of the prairie-forest region, were even more agricultural than the Iroquois and stored up surplus corn enough for 3 or 4 years. This reference also notes that here, in the East, "large tracts of lands, as in the prairie regions, were frequently burned over to furnish clearings for fields and villages. The explorer Galinee, in 1669, on his way to the west by way of the Seneca country found . . . beautiful broad meadows on which grass grew as tall as himself. . . . Treeless meadows more than a hundred leagues in length were reported from the south where great quantities of corn and fruit were grown."

Beyers (1946), in discussing the environment of the northeastern United States, has shown that even this forested part of the country was not an unbroken wilderness but had considerable areas cleared by fires and maintained by annual fires. This paper has many early historical references from the seventeenth century which show the widespread use of fires in keeping the land open.

Specific references to the occurrence of prairies and open savannas in the prairie-forest region have already been given. From Hibbard (1904) we learn that some of the cornfields of the Sacs and Foxes in southwestern Wisconsin were over 400 acres in size and that there were very many extremely large cornfields along the Mississippi Valley. In addition to corn, beans, squashes, and tobacco were grown in considerable quantities. This reference shows also that early military expeditions were for the most part dependent on food supplies furnished by the Indians and that some of the early travellers soon became adept at finding and seizing the caches of corn the provident Indians had stored away. Early settlers also seized the small cultivated plots of the Indians for their fields and used native-grown seed in their plantings.

Perhaps a thorough understanding of the environment of the Indian of pre-white settlement times is a subject away from the realm of orthodox plant ecology. However, since the Indian lived close to nature and probably understood in his wisdom much of the dynamics of vegetational changes, it may be profitable to think of him as a practical ecologist who had learned that he could in a number of ways manipulate his environment for the betterment of both hunting and agricultural pursuits. According to Collier (1948), at the time of the arrival of the white man there was no square mile unoccupied or unused. Something of the intimate relationship of the Indian to his physical and biotic environment is indicated in this work: "The Indian made it his business to have fullness of life within material meagerness and within a deep insecurity which his wisdom did not even want to see exterminated. . . . The abode of this insecurity was not within his own soul or within his group life but was with the world of war, drought, flood, storm, and pestilence. . . . These

Figure 30

Map taken from Allen (1876) showing eastward range of bison and its coincidence with prairie peninsula.


COLUMBIA
SASKATCHEWAN
RUPERT RIVER
ALBANY
MANITOBA
MOOSE ABBITIBBE
DAKOTA
WYOMING
NEBRASKA
IOWA
WISCONSIN
ILLINOIS
INDIANA
OHIO
NEVADA
UTAH
CALIFORNIA
INDIAN TERR
MISSOURI
KENTUCKY
TENNESSEE
ARKANSAS
NEW MEXICO
TEXAS
LOUISIANA
MISSISSIPPI
ALABAMA
GEORGIA
NORTH CAROLINA
CHIHUAHUA
Detroit
Springfield
Indianapolis
Columbus
Frankfort
Nashville
Little Rock
Jackson
Austin
Charleston
Savannah
Montreal
Ottawa
Boston
Providence
Philadelphia

societies existed in perfect ecological balance with the forest, the plain, the desert, the waters, and the animal life."

A recent and exhaustive study of the bison (Roe, 1951) has shown the former ranges and the importance of this large mammal to the economy of the Indian. An earlier work by Allen (1876) has also demonstrated this and has shown also the gradual westward migration of the bison with the settlement of the interior of the continent. Figure 30, which is taken from Allen, shows the original range of the bison east of the Mississippi prior to 1800. The coincidence of this range with the prairie peninsula is notably interesting.

Although we have no written record for the sweep of historical events in postglacial North America as we have for Europe and Asia, we can be certain that the entire central part of the continent of North America and in particular the Mississippi, Ohio, and Missouri river valleys have long been populated. Shaler (1899) has commented on these prehistoric peoples: "The Ohio and Upper Mississippi valleys abound in the tumuli and fortifications, which indicate that the people had been more numerous . . . and that they depended more upon agriculture and less on the chase than their successors who met the white man when he first came to this country." An early map from Thomas (1891), Figure 31, is used because of its coincidence with the prairie peninsula.

A number of the various mound builders, especially the

Hopewellian, were largely agricultural (Shetrone, 1941). This particular culture, which was centered along the Ohio River and is apparently well represented along the upper Mississippi, probably represents the highest development in aboriginal culture north of Mexico. Both the actual number of mounds and the number of remains within the larger burial mounds indicate high densities of population, urbanization, and, in general, a rather high level of civilization. Hernando De Soto, in 1541, apparently found one of the last phases of this mound-building civilization in the lower Mississippi Valley (Ford, 1952).

Whether these peoples lived in a relatively treeless region or actually used fire to clear land of trees is not known. Students of early man in America stress the use of fire by all primitive people. Stewart (1941) cites the finding of a number of Folsom points on the prairies as evidence that the burning of the grasslands may have started early in postglacial times before trees had become established. Sauer (1944) is of a like opinion: that early man became a predator on the large animals, hunted in organized bands, and used fire drives as a chief and effective weapon. It seems logical to assume that fire was used very early in postglacial times in the prairie-forest border region, that the various mound builders used fire to keep the forest from encroaching, and that the later hunting people used fire to clear their fields and to increase the pasturage for the bison and other game. Further, there must have been close relationships among a

Figure 31

Map from Thomas (1891) showing distribution of Indian mounds. The numbers along the Ohio River in prairie peninsula and the prairie-forest region of Wisconsin are particularly striking.

DISTRIBUTION OF MOUNDS IN THE EASTERN UNITED STATES number of events: the spread of prairie eastward by fire alone and by fire and drought, eastward migrations of the bison as a result of droughts and because of the eastward expanse of the prairie, the hunting of the bison by the Indians, population pressures of both the Indian and the bison as a result of any extension of grassland. The Indian-bison-grassland biome was well adapted to expand into a normally forested region if aided by fire and drought.

PHYTOSOCIOLOGICAL STUDIES ON DRY LIME PRAIRIES

Criteria

The chief criteria employed in choosing suitable stands for study have been discussed in both the Introduction and the Description of the Area. In general, areas of undisturbed prairie vegetation having a very thin soil over consolidated bedrock (chiefly dolomites) or coarse gravel with a pH of 7.5 and over were included in this study.

The prairies of this type studied first, when this work was begun in the summer of 1949, were the numerous ones in Perry and Primrose townships in southern Dane County. These remnant prairies are on the edge of the once-extensive prairie areas of the mineral lands of southwestern Wisconsin and exist on areas with soil too thin for cultivation on the southward-sloping cuesta of the Galena-Platteville dolomites. These prairies are further characterized by having a flat to very gently sloping topography. Most of the other stands studied were found by systematically searching the entire southern and western parts of the state. Collection sites from various herbarium specimens gave many hints regarding locations of prairies. While many of the prairies found elsewhere were much steeper than the Perry-Primrose stands, the general aspect of all the dry lime prairies was very similar. Several of the best prairies were those on southwest-facing bluffs in several state parks in western Wisconsin.

Most of the criteria mentioned are objective enough; however, the factor of disturbance became a somewhat confusing one on at least several occasions. Usually, however, there is no question regarding this. For instance, a pastured hillside having a great deal of Kentucky blue grass and only a very few prairie plants will look very different from an ungrazed hillside prairie with its taller prairie grasses and clones of yellow Coreopsis and Helianthus. In the autumn these ungrazed prairies present a very striking picture, with the tawny color of little blue stem visible for long distances.

There is no problem in distinguishing a heavily grazed prairie from an undisturbed one; however, there may be a question regarding a very slightly grazed prairie or one once grazed but now coming back to native prairie vegetation. The presence of old and often broken fences around an area indicates a former pasture as does the presence of small steplike terraces around the steeper hills. A certain amount of subjective judgment probably always enters into decisions concerning the choice of a suitable stand for an ecological study. Until enough grazed prairies in various degrees of disturbance are studied and certain objective criteria thereof established, a certain amount of subjectivity will probably have to be tolerated. Certainly the original prairie of the Midwest was subject to a great deal of disturbance, including grazing; however, this was probably of a more discontinuous nature than the intensive grazing of the modern pasture.

Although there is a certain amount of variation in soil depth in the dry lime prairies, in general, the very shallow nature of the soil is one of the best and easiest of the criteria to apply. Soil depth may vary from less than one inch to over nine inches in spots; however, a rather constant depth of from slightly less than one to two or three inches is by far the commonest. Bare rock ledges and extremely sparse vegetation in the thinner-soil areas are common features of the steep prairies especially. Characteristic also is the bunched nature of the grasses in these areas of very thin soil. This is in marked contrast with the dense sod of the deep-soil prairies.

A particular stand to be included in this study should consist of undisturbed native prairie vegetation growing in a very shallow soil over either a dolomitic bedrock, sandstone with dolomitic rubble on its surface, or, in the glaciated regions of southeastern Wisconsin, a calcareous gravel. Field determinations of the soil pH should be over 7.5; actually they were, in nearly all cases, 8.0.

Methods of Study

As stated before, a total of 64 stands of undisturbed dry lime prairies, scattered from southeastern Wisconsin to eastern Minnesota, are included in this study. These stands are found in 13 counties of Wisconsin. Six stands occur outside the state. The Wisconsin stands seem to be somewhat grouped. For example, 23 prairies are found in Dane County, and 8 and 7 stands are found in nearby Green and Columbia counties. The bluffs of the Mississippi Valley seem to constitute another group, although a more scattered one.

Because it is felt that a survey study of many stands of a particular kind of plant community should precede detailed studies of any one or few stands, this work is concerned primarily with such an over-all view. This application of the mass-collection technique should supply information leading to detailed studies of some of the best typical stands and those stands which, although they satisfy the criteria, are somehow atypical.

Any detailed study of grassland vegetation is time-consuming and tedious. Many of the studies made previously elsewhere have involved such procedures as counting the aerial stems of grasses and forbs, charting growth habits and locations within study plots, and digging trenches to study roots. Such information was not obtained for the stands studied here for obvious reasons involving time.

The chief methods of studying the many stands involved here are the presence list of species in each stand and the quadrat method of sampling populations. Actually there are three levels of information involving species presence available. First, there are presence lists for all the 64 stands studied; second, there are available presence lists for 20 square meters (20 scattered quadrats each measuring one meter on each side) for a total of 41 stands; and third, for 20 of the 41 stands studied with quadrats information regarding boxed quadrats is available. This latter method involves the use of a special meter quadrat having wires stretched from side to side in two directions, dividing the square meter into 16 quadrats, each measuring 25 cm. on edge. From these 16 contiguous quadrats within the larger quadrat, information concerning the distribution of certain plants is obtained.

While the meter quadrat may not necessarily prove to be the best size for analyzing all species in a prairie, it was used in this study for convenience and uniformity, since this size is so widely used in studying herbaceous vegetation.

The specific location of each stand and its number used in discussing the stand in this report can be found in the Appendix. Certain other data, besides presence lists and quadrat figures, are also available. These are the degree of slope, direction of exposure, and the results from the various soil analyses.

An area which satisfied the criteria established for a dry lime prairie was studied in the following manner. The prairie was first walked over, its size, location, exposure, slope, and any other peculiarity of topography and soil noted. A presence list of species was made at this time. The 20 quadrats were laid at regular intervals along several lines which varied in number and length with the size and shape of the stand. A prairie roughly rectangular in shape, for instance, might be sampled by placing the quadrats on two parallel lines along the long axis of the prairie and perhaps 25 paces apart. The distances between quadrats vary with the size of the stand being sampled; however, 15, 20, and 25 paces were distances commonly used. In establishing the lines on which the quadrats were placed, it was customary to sight a tree or some object on the distant horizon to avoid unconsciously walking toward any particular spot on the prairie. To avoid the condition of disturbance at the edge of the prairie, all quadrats were located at least 10 feet within the prairie itself.

The nomenclature used is that of the eighth edition of Gray's Manual of Botany (Fernald, 1950). Since many of the plants examined in the quadrats especially were in vegetative or even in seedling stages, problems in identification were rather common. Usually the first several weeks of each summer were devoted to a careful comparison of the more difficult plants with herbarium specimens. Questionable plants were collected and tagged in the field and later identified in the herbarium. It is hoped that there are a minimum number of identification errors in the study. Several plants presented problems which resulted in a lumping of these in the final data. For example, although it is very easy to distinguish *Viola pedata* and *Viola pedatifida* while they are in flower, it is extremely difficult and in many cases impossible to separate the two in late summer. The data for

Figure 32

Example of punch card used in recording data for each stand. Numbers below notched holes indicate per cent frequency of species.

#40

Brady's Bluff, Perrot State Park

Trempealeau County, Wisconsin

T 18 N R 9 W Sec. 20

West exposure, 30 degree slope

Soil data:

pH	8.0	K.	50.
WRC	64.8	NO_3	15.
Ca.	6000.	NH_3	7.5
Mg.	550.		
P.	50.		

these two species are confusing: in some there is a separation of these two species, and in others they are not separated. In the final data they are listed simply as Viola. The genus Carex is treated thus also.

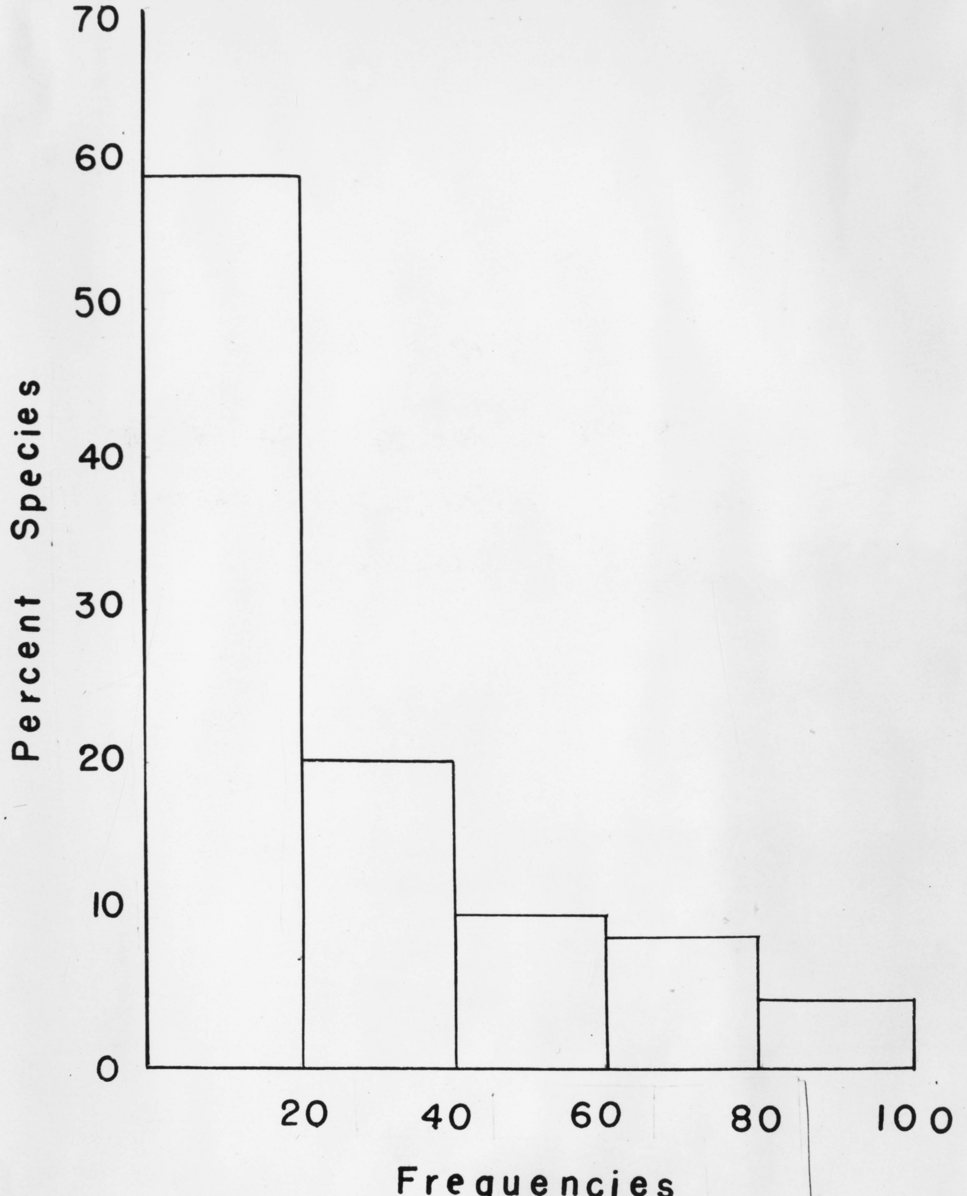
Data from rough field notes were recorded on special prairie-survey sheets (see Appendix), but it soon became apparent that these sheets would be too bulky and awkward when various comparisons among stands were to be made. To overcome this difficulty the data were transferred to punch cards, made by drilling holes around the edges of 5 x 8 inch filing cards and allowing each hole to represent a particular species. To indicate that a species was present in a stand, the edge of the card above the hole representing that species was cut out, and if the species occurred in one or more of the quadrats, its frequency value was written directly below the hole. It becomes simple, therefore, to separate all stands in which any species is found from the stands where that species is not present. Also, by placing two cards representing two stands side by side, it is easy to note how many and which species the two stands have in common. All the data from each stand were reduced to two cards per stand (Fig. 32), making manipulation of the data simple and time saving.

Concepts

With the data available it is possible to deal with three common phytosociological concepts. These are fre-

Figure 33

The distribution of species frequencies of all stands in Raunkiaer's frequency size classes.



70
60
50
40
30
20
10
0
Percent Species
20
40
60
80
100
Frequencies

quency, presence, and constancy. The first of these, frequency, is an analytical or intrastand characteristic which is commonly defined as the number of samples (quadrats) in which a species occurs expressed as a percentage of the total number of samples examined (Curtis and McIntosh, 1950). Since 20 quadrats were used in each stand, the frequency values range from 5 to 100 per cent. Frequency is, in a sense, a measure of the ubiquity of a species within a stand provided the quadrat size used is not too large. Only 4 species have frequency values of 100 per cent, and these species, Andropogon scoparius, Bouteloua curtipendula, Andropogon Gerardi, and Euphorbia corollata, occur with such a high frequency in only 7 different stands. The distribution of the high-frequency ranges (70-100 per cent) are shown in Tables 1 and 2, while the distribution of the frequencies of all stands, according to Raunkiaer's frequency size classes, is shown in Figure 33.

Two lists of 50 species each follow (Tables 3 and 4) which rank the individual species according to their average frequencies. This term has a different meaning in each case. In Table 3, average frequency is obtained by dividing the sum of the frequencies of each species by the number of stands in which it occurs. This list favors those species which may occur in only a few stands but where, for some particular reason, they have high frequencies. In this listing such species would rank as high as, or higher than, those species occurring in a large number of stands with relatively high

TABLE 1

Distribution of species and stands in frequency classes of 70 per cent and over

	Frequency values 70-75%	80-85%	90-95%	100%
Number of species within frequency class	15	18	9	4
Number of stands having species within frequency class	47	34	21	7

TABLE 2

Numbers of stands having species with frequencies of 70 per cent and over

Species	70-75%	80-85%	90-95%	100%
Andropogon scoparius	9	7	7	3
Bouteloua curtipendula	8	5	2	2
Andropogon Gerardi	5	2	4	1
Aster sericeus	7	2	2	--
Euphorbia corollata	2	1	2	1
Amorpha canescens	3	3	--	--
Asclepias verticillata	2	1	1	--
Solidago nemoralis	1	2	1	--
Helianthus laetiflorus	1	1	1	--
Helianthus occidentalis	1	1	--	--
Liatris aspera	--	2	--	--
Liatris cylindracea	3	--	--	--
Muhlenbergia cuspidata	1	1	--	--
Aster ericoides	--	1	--	--
Aster laevis	--	1	--	--
Coreopsis palmata	1	--	1	--
Castelleja sessiliflora	1	--	--	--
Viola	2	1	--	--
Bouteloua hirsuta	--	1	--	--
Geum triflorum	--	1	--	--
Sporobolus heterolepis	--	1	--	--

TABLE 3

A list of species ranked according to average frequency

i.e., $\frac{\text{sum of frequencies of a species}}{\text{number of stands in which it occurs}}$

Andropogon scoparius	71.3	Aster laevis	22.8
Bouteloua curtipendula	62.4	Verbena stricta	22.5
Andropogon Gerardi	52.9	Sisyrinchium campestre	22.5
Aster sericeus	52.9	Liatris aspera	22.1
Phlox pilosa	46.7	Aster ericoides	21.5
Bromus Kalmii	45.0	Viola	21.0
Amorpha canescens	40.4	Solidago rigida	20.9
Euphorbia corollata	38.3	Pedicularis canadensis	20.5
Asclepias verticillata	38.2	Stipa spartea	20.4
Solidago nemoralis	37.7	Kuhnia eupatorioides	20.0
Helianthus laetiflorus var. rigidus	35.9	Geum triflorum	19.5
Panicum perlongum	35.7	Poa compressa	19.4
Helianthus occidentalis	34.3	Artemisia caudata	18.8
Liatris cylindracea	33.6	Arabis lyrata	18.8
Bouteloua hirsuta	32.9	Dodecatheon Meadia	18.8
Petalostemum purpureum	32.7	Aster oblongifolius	18.1
Sporobolus vaginiflorus	31.6	Aster linariifolius	17.8
Coreopsis palmata	31.4	Hedeoma hispida	17.8
Arenaria stricta	31.1	Rosa	17.2
Sporobolus heterolepis	29.1	Tradescantia ohiensis	17.0
Muhlenbergia cuspidata	28.9	Commandra umbellata	16.1
Silphium laciniatum	26.5	Sporobolus cryptandrus	16.0
Castelleja sessiliflora	25.0	Ambrosia artemisiifolia	15.2
Aster ptarmicoides	24.5	Silphium integrifolium	15.0
Antennaria	24.4	Helianthemum	15.0

TABLE 4

A list of 50 species ranked according to their average frequency

i.e., $\frac{\text{sum of frequencies of a species}}{41}$

Andropogon scoparius	71.3	Helianthus occidentalis	11.7
Bouteloua curtipendula	62.4	Kuhnia eupatoroides	10.9
Andropogon Gerardi	50.2	Aster oblongifolius	10.6
Aster sericeus	46.5	Ambrosia artemisiifolia	10.4
Euphorbia corollata	43.7	Antennaria	10.1
Amorpha canescens	35.5	Hedeoma hispida	10.0
Solidago nemoralis	34.0	Castelleja sessiliflora	9.8
Panicum perlongum	33.1	Bouteloua hirsuta	9.6
Petalostemum purpureum	30.9	Commandra umbellata	8.7
Sporobolus heterolepis	24.6	Potentilla arguta	8.3
Coreopsis palmata	24.5	Poa compressa	7.6
Liatris cylindracea	22.9	Scutellaria parvula	7.4
Helianthus laetiflorus var. rigidus	22.8	Anemone patens	7.3
Arenaria stricta	20.5	Lithospermum incisum	6.9
Viola	17.9	Panicum oligosanthes var. Scribnerianum	6.9
Aster ericoides	16.9	Silphium laciniatum	6.5
Solidago rigida	16.3	Panicum Leibergii	6.5
Asclepias verticillata	15.8	Lithospermum canescens	6.3
Stipa spartea	15.5	Ratibida pinnata	6.2
Muhlenbergia cuspidata	13.4	Geum triflorum	5.7
Rosa	13.4	Verbena stricta	5.5
Liatris aspera	12.9	Pedicularis canadensis	5.0
Artemisia caudata	12.8	Linum sulcatum	4.6
Aster ptarmicoides	12.6	Sorghastrum nutans	4.6
Sisyrinchium campestre	12.1	Physalis virginiana	4.6

frequencies. Two species, Phlox pilosa and Bromus Kalmii, which rank number 5 and 6 on this list, are notable examples. Both species are unimportant members of dry lime prairies. Although their frequencies are high, Phlox occurs in quadrats in only three stands, while Bromus occurs in quadrats in only one stand.

As used in the second list (Table 4), average frequency is the quotient of the sum of the frequencies of a particular species divided by the number of stands studied by quadrats (41). This list, which does not favor sporadic species with high frequencies, contains neither Phlox nor Bromus among the first 50 species. Several other differences can be seen also. Asclepias verticillata, for instance, ranks ninth on the first list but only eighteenth on the second, and Helianthus occidentalis, which ranks thirteenth on the first, is not among the first 50 species on the second list. Reasons for these differences may involve distribution of species within the general area studied, the "accidental" appearance of a species in one or a few stands, or the fact that the stands involved may be atypical ones and different in some way from the average dry lime prairie. These reasons are further discussed later.

A more interesting fact than the few exceptions already mentioned is the very great similarity between the two lists. This similarity is especially striking among the first ten or twelve species, or dominants, when both Phlox and Bromus are omitted (Table 5).

TABLE 5

A comparison between the rank of the first 12 species of Table 3 (the first number) and the rank given to the same species in Table 4 (the second number) when <u>Bromus Kalmii</u> and <u>Phlox pilosa</u> are omitted

1---1	5---6	9---8
2---2	6---5	10-12
3---3	7---7	11--9
4---4	8--13	12-10

Two synthetic or interstand characteristics, presence and constancy, are easily calculated from the data-containing cards. Of the two terms, presence is the simpler, being defined as the number of stands in which a species occurs expressed as a percentage of the total number of stands examined. Constancy makes use of a certain uniform sample rather than the entire stand and has, therefore, more precision than presence. Constancy, which is a sort of stand frequency, is obtained by dividing the number of samples (one per stand) in which a species occurs by the total number of stands studied (expressed as a per cent). In this study the sample used is the entire group of 20 quadrats in each stand. Constancy thus overcomes any differences in stand size since each sample (20 square meters) is of a uniform size.

Two lists (Tables 6 and 7) rank the first 50 species according to presence and constancy. It can be seen by examining these lists that among the first 50 species there is good

TABLE 6

A list of species ranked according to presence

Andropogon scoparius	100.
Bouteloua curtipendula	100.
Andropogon Gerardi	98.4
Amorpha canescens	98.4
Petalostemum purpureum	98.4
Solidago nemoralis	95.3
Rosa	95.3
Aster sericeus	92.2
Euphorbia corollata	92.2
Sporobolus heterolepis	87.5
Ambrosia artemisiifolia	85.9
Panicum perlongum	85.9
Coreopsis palmata	82.8
Erigeron strigosus	82.8
Anemone patens	82.3
Potentilla arguta	81.3
Aster ericoides	81.3
Kuhnia eupatoroides	79.7
Stipa spartea	79.7
Solidago rigida	77.7
Hedeoma hispida	73.5
Artemisia caudata	73.5
Asclepias verticillata	73.5
Anemone cylindrica	73.5
Ratibida pinnata	71.9
Monarda fistulosa	71.9
Viola	70.3
Lithospermum incisum	70.3
Antennaria	70.3
Helianthus laetiflorus var. rigidus	67.2
Lithospermum canescens	67.2
Oenothera biennis	67.2
Arenaria stricta	66.1
Physalis virginiana	65.6
Commandra umbellata	64.1
Scutellaria parvula	64.1
Panicum Leibergii	64.1
Liatris aspera	64.1
Liatris cylindracea	62.5
Rhus glabra	62.5
Aster oblongifolius	62.5
Aster azureus	60.8
Poa compressa	59.4
Linum sulcatum	56.3
Verbena stricta	56.3
Quercus macrocarpa	51.6
Sorghastrum nutans	50.0
Juniperus virginiana	48.5
Castilleja sessiliflora	45.3
Koeleria cristata	42.2

TABLE 7

A list of the first 50 species ranked according to constancy

Andropogon scoparius	100.	Kuhnia eupatoroides	56.1
Bouteloua curtipendula	100.	Lithospermum canescens	56.1
Andropogon Gerardi	95.2	Commandra umbellata	53.7
Petalostemum purpureum	95.2	Sisyrinchium campestre	53.7
Panicum perlongum	92.7	Aster ptarmicoides	51.2
Solidago nemoralis	90.3	Scutellaria parvula	51.2
Amorpha canescens	87.8	Panicum oligosanthes var. Scribnerianum	48.8
Aster sericeus	87.8		
Euphorbia corollata	87.8	Muhlenbergia cuspidata	46.4
Sporobolus heterolepis	85.4	Panicum Leibergii	46.4
Coreopsis palmata	78.1	Ratibida pinnata	43.9
Rosa	78.1	Linum sulcatum	43.9
Solidago rigida	78.1	Antennaria	41.5
Stipa spartea	75.6	Asclepias verticillata	41.5
Aster ericoides	70.8	Anemone cylindrica	39.0
Ambrosia artemisiifolia	68.3	Castilleja sessiliflora	39.0
Artemisia caudata	68.3	Helianthus laetiflorus var. rigidus	39.0
Liatris cylindracea	68.3		
Arenaria stricta	65.9	Physalis virginiana	39.0
Potentilla arguta	65.9	Poa compressa	39.0
Lithospermum incisum	61.0	Erigeron strigosus	36.6
Anemone patens	58.5	Sorghastrum nutans	36.6
Aster oblongifolius	58.5	Helianthus occidentalis	34.2
Liatris aspera	58.5	Monarda fistulosa	34.2
Viola	58.5	Lobelia spicata	31.7
Hedeoma hispida	56.1	Oenothera biennis	31.7

agreement. In fact, in the list of the first 25 species there are 19 in common, and in the second 25 there are 13 in common.

Table 8 compares the presence, constancy, and rank of the first 20 species.

Presence and constancy diagrams which show the distribution of species in five size classes are shown in Figure 34. Although more species are involved in presence than in constancy (206 as against 149) and the number of species in the first (or smallest) size class is much larger in the presence diagram, the two diagrams are remarkably similar when the percentages of species rather than the total numbers of species are used.

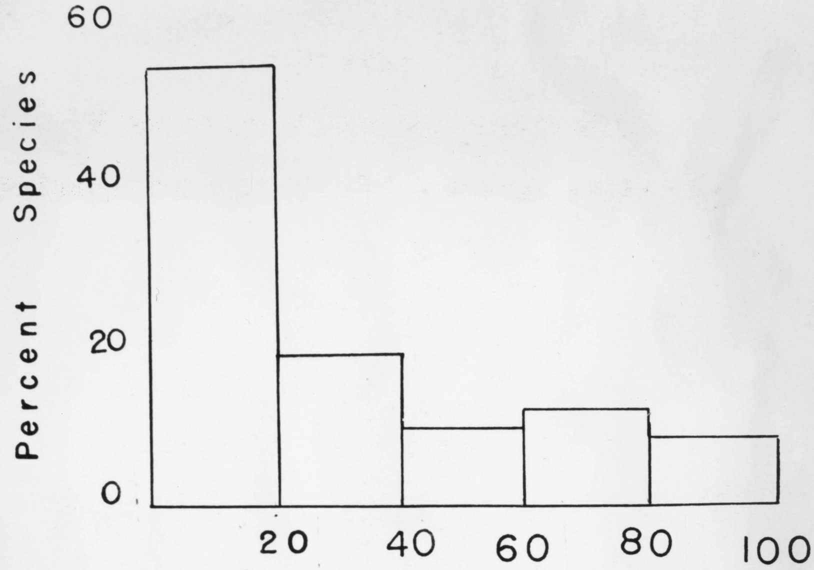
In preparing the final, master list of species of plants found on the dry lime prairies studied in the prairie-forest border region of southwestern Wisconsin, two concepts, frequency and constancy, have been combined. The product of average frequency, i.e., $\frac{\text{summation of frequencies}}{41}$ and constancy attempts to combine intrastand and interstand values and to rank each species accordingly. Table 9 is based on this two-value idea, and its general similarity with the previously discussed lists is perhaps indicative of the high level of homogeneity among all the stands of this rather distinctive plant community. This is especially noteworthy among the commonest species.

Figure 34a

Distribution of species in 5 presence classes (based on 206 species).

Figure 34b

Distribution of species in 5 constancy classes (based on 149 species).


Percent Species
60
40
20
0
20
40
60
80
100

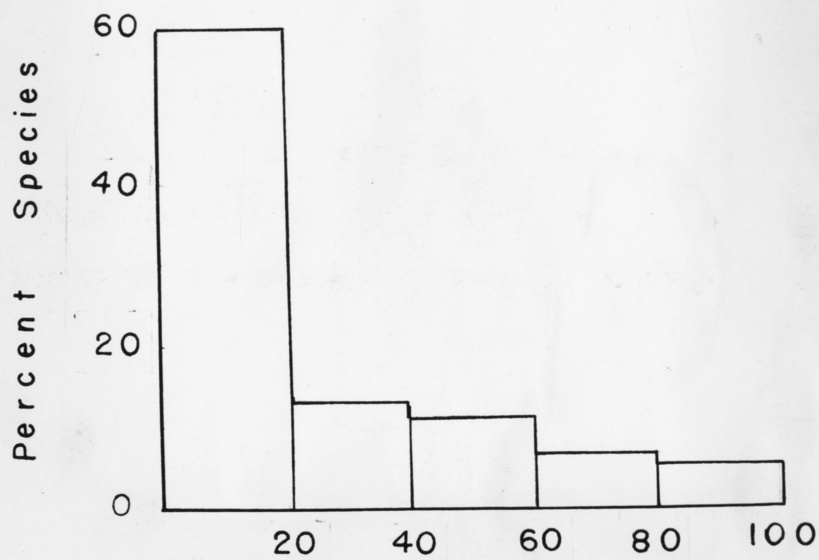

Percent Species
60
40
20
0
20
40
60
80
100

TABLE 8

A comparison of the first 20 species ranked according to presence with the same species ranked according to constancy

	Presence		Constancy	
	Presence	Rank	Constancy	Rank
Andropogon scoparius	100.	1	100.	1
Bouteloua curtipendula	100.	1	100.	1
Andropogon Gerardi	98.4	2	95.2	2
Petalostemum purpureum	98.4	2	95.2	2
Amorpha canescens	98.4	2	87.8	5
Solidago nemoralis	95.3	3	90.3	4
Rosa	95.3	3	78.1	7
Aster sericeus	92.2	4	87.8	5
Euphorbia corollata	92.2	4	87.8	5
Sporobolus heterolepis	87.5	5	85.4	6
Ambrosia artemisiifolia	85.9	6	68.3	10
Panicum perlongum	85.9	6	92.7	3
Coreopsis palmata	82.8	7	78.1	7
Erigeron strigosus	82.8	7	36.6	22
Anemone patens	82.3	8	58.5	13
Potentilla arguta	81.3	9	65.9	11
Aster ericoides	81.3	9	70.8	9
Kuhnia eupatorioides	79.7	10	56.1	14
Stipa spartea	79.7	10	75.6	8
Solidago rigida	79.7	11	78.1	7

TABLE 9

Master List of Species

Ranked according to product of constancy and average frequency and, for those species which do not occur in any quadrats, according to presence

Andropogon scoparius Michx.	7130.
Bouteloua curtipendula (Michx.) Torr.	6240.
Andropogon Gerardi Vitman	4779.
Aster sericeus Vent.	4100.
Euphorbia corollata L.	3360.
Amorpha canescens Pursh	3117.
Solidago nemoralis Ait.	3072.
Panicum perlongum Nash	3064.
Petalostemum purpureum (Vent.) Rydb.	2949.
Sporobolus heterolepis Gray	2103.
Coreopsis palmata Nutt.	1914.
Liatris cylindracea Michx.	1567.
Arenaria stricta Michx.	1351.
Solidago rigida L.	1276.
Aster ericoides L.	1200.
Stipa spartea Trin.	1170.
Viola	1050.
Rosa	1047.
Helianthus laetiflorus var. rigidus (Cass.) Fern.	889.
Artemisia caudata Michx.	874.
Liatris aspera Michx.	758.
Ambrosia artemisiifolia L.	710.
Asclepias verticillata L.	656.
Sisyrinchium campestre Bickn.	648.
Aster ptarmicoides (Nees) T. & G.	643.
Muhlenbergia cuspidata (Nutt.) Rydb.	622.
Aster oblongifolius Nutt.	622.
Kuhnia eupatorioides L.	616.
Hedeoma hispida Pursh	561.
Potentilla arguta Pursh	545.
Poa pratensis L.	513.
Aster azureus Lindl.	484.
Commandra umbellata (L.) Nutt.	465.
Anemone patens L. var. Wolfgangiana (Bess.) Koch	427.
Lithospermum incisum Lehm.	424.
Antennaria sp.	419.
Helianthus occidentalis Riddell	401.
Castilleja sessiliflora Pursh	381.
Scutellaria parvula Michx.	380.
Lithospermum canescens (Michx.) Lehm.	356.
Panicum oligosanthes var. Scribnerianum (Nash) Fern.	339.

Master List of Species (cont'd.)

Panicum Leibergii (Vasey) Scribn.	300.
Poa compressa L.	295.
Bouteloua hirsuta Lag.	282.
Ratibida pinnata (Vent.) Barnh.	273.
Linum sulcatum Riddell	203.
Physalis virginiana Mill.	181.
Sorghastrum nutans (L.) Nash	169.
Geum triflorum Pursh	168.
Silphium laciniatum L.	157.
Anemone cylindrica Gray	144.
Erigeron strigosus Muhl.	138.
Verbena stricta Vent.	134.
Prunus pumila L.	127.
Pedicularis canadensis L.	122.
Koeleria cristata (L.) Pers.	118.
Monarda fistulosa L.	96.
Arabis lyrata L.	91.
Dodecatheon Meadia L.	91.
Oenothera biennis L.	69.
Aster laevis L.	67.
Aster linariifolius L.	52.
Rhus glabra L.	45.
Solidago missouriensis Nutt.	35.
Campanula rotundifolia L.	32.
Phlox pilosa L.	25.
Tradescantia ohiensis Raf.	25.
Sporobolus cryptandrus (Torr.) Gray	24.
Sporobolus vaginiflorus (Torr.) Wood	24.
Carex sp.	23.
Petalostemum candidum (Willd.) Michx.	20.
Heuchera Richardsonii R. Br.	19.
Smilacina stellata (L.) Desf.	18.
Salix humilis Marsh.	13.
Asclepias lanuginosa Nutt.	13.
Equisetum hyemale L.	12.
Opuntia humifusa Raf.	11.
Rudbeckia hirta L.	10.
Polygala Senega L.	10.
Lobelia spicata Lam.	9.
Silphium integrifolium Michx.	8.
Eryngium yuccifolium Michx.	7.
Convolvulus sepium L.	6.
Vitis aestivalis Michx.	6.
Elymus canadensis L.	6.
Apocynum androsaemifolium L.	6.
Selaginella rupestris L.	5.2
Psoralea esculenta Pursh	4.8
Juniperus virginiana L.	4.5
Quercus macrocarpa Michx.	4.5
Gentiana puberula Michx.	4.4
Zizia aptera (Gray) Fern.	4.1

Master List of Species (cont'd.)

Asclepias viridiflora Raf.	3.7
Liatris punctata Hook.	3.5
Cyperus Schweinitzii Torr.	3.2
Heliopsis helianthoides (L.) var. scabra (Dunal) Fern.	2.9
Lactuca canadensis L.	2.7
Bromus Kalmii Gray	2.6
Cornus racemosa Lam.	2.6
Solidago juncea Ait.	2.4
Populus tremuloides Michx.	2.4
Ceanothus americanus L.	1.8
Lilium philadelphicum L.	1.8
Monarda punctata L.	1.8
Celastrus scandens L.	1.8
Artemisia ludoviciana Nutt.	1.8
Rubus (blackberry)	1.8
Polygala verticillata L.	1.7
Tragopogon pratensis L.	1.7
Penstemon sp.	1.5
Gentiana quinquefolia L.	1.4
Oxalis stricta L.	1.2
Asclepias tuberosa L.	1.2
Desmodium illinoense Gray	1.2
Cirsium discolor (Muhl.) Spreng.	1.1
Onosmodium hispidissimum Mackenz.	0.9
Helianthemum sp.	0.9
Astragalus caryocarpus Ker.	0.9
Juniperus communis L.	0.6
Draba reptans (Lam.) Fern.	0.6
Ambrosia psilostachya DC.	0.6
Achillea Millefolium L.	0.6
Lespedeza capitata Michx.	0.6
Aquilegia canadensis L.	0.6
Pycnanthemum virginianum L.	0.3
Galium boreale L.	0.3
Polygonatum canaliculatum (Muhl.) Pursh	0.3
Solidago speciosa Nutt.	0.3
Rhus radicans L.	0.3
Quercus velutina Lam.	0.3
Asclepias syriaca L.	0.3
Artemisia frigida Willd.	0.3
Aster pilosus Willd.	0.3
Baptisia leucantha T. & G.	0.3
Cirsium Hillii (Canby) Fern.	0.3
Lactuca ludoviciana (Nutt.) Riddell	0.3
Lechea sp.	0.3
Liatris pycnostachya Michx.	0.3
Tephrosia virginiana (L.) Pers.	0.3
Pyrus ioensis (Wood) Bailey	0.3
Solidago altissima L.	0.3
Astragalus canadensis L.	0.3
Panicum virgatum L.	0.3
Physalis heterophylla Nees.	0.3

Master List of Species (cont'd.)

Silene antirrhina L.	0.3
Rubus (raspberry)	0.3

The following species, which did not occur in any quadrats, are listed according to their presence

Prunus serotina Ehrh.	17.
Betula papyrifera Marsh.	14.
Carya ovata (Mill.) K. Koch	12.5
Acer Negundo L.	12.5
Xanthoxylum americanum Mill.	12.5
Prunus virginiana L.	11.
Panicum praecocius Hitchc. & Chase	11.
Parthenocissus quinquefolia (L.) Planch.	10.
Gnaphalium obtusifolium L.	10.
Celtis occidentalis L.	8.
Physalis subglabrata Mackenz. & Bush	8.
Physocarpus opulifolius (L.) Maxim.	8.
Crataegus sp.	6.
Corylus americana Walt.	6.
Populus grandidentata Michx.	6.
Quercus alba L.	6.
Krigia biflora (Walt.) Blake	5.
Prunus pensylvanica L.	5.
Smilacina racemosa (L.) Desf.	5.
Zigadenus elegans Pursh	5.
Cacalia tuberosa Nutt.	3.
Fragaria virginiana Duchesne	3.
Hieracium longipilum Torr.	3.
Hypoxis hirsuta (L.) Coville	3.
Muhlenbergia racemosa (Michx.) BSP.	3.
Oxalis violacea L.	3.
Potentilla simplex Michx.	3.
Robinia Pseudo-Acacia L.	3.
Silphium terebinthinaceum Jacq.	3.
Spiranthes sp.	3.
Tilia americana L.	3.
Triosteum perfoliatum L.	3.
Verbascum Thapsus L.	3.
Veronicastrum virginicum (L.) Farw.	3.
Agoseris cuspidata (Pursh) Raf.	1.6
Aster sagittifolius Wedemeyer	1.6
Cassia fasciculata Michx.	1.6
Cenchrus longispinus (Hack.) Fern.	1.6
Chenopodium album L.	1.6
Hypericum perforatum L.	1.6
Linaria vulgaris Hill	1.6
Lithospermum croceum Fern.	1.6
Lupinus perennis L.	1.6
Mirabilis nyctaginea (Michx.) MacM.	1.6

Master List of Species (cont'd.)

Orobanche uniflora L.	1.6
Oxalis europaea Jord.	1.6
Plantago Purshii R. & S.	1.6
Polygala sanguinea L.	1.6
Prenanthes aspera Michx.	1.6
Prenanthes racemosa Michx.	1.6
Prunus americana Marsh.	1.6
Quercus Muehlenbergii Engelm.	1.6
Smilax herbacea L.	1.6
Solidago graminifolia (L.) Salisb.	1.6
Sporobolus asper (Michx.) Kunth	1.6
Symphoricarpos albus (L.) Blake	1.6
Teucrium canadense L.	1,6
Ulmus rubra L.	1.6
Valeriana ciliata T. & G.	1.6

Of the total of 56 families of angiosperms represented in this list, 62 per cent of the species are found in the following families: Compositae (23 per cent), Gramineae (14 per cent), Rosaceae (8 per cent), Leguminosae (7 per cent), Liliaceae (4 per cent), Scrophulariaceae (3 per cent), and Asclepiadaceae (2.8 per cent). Thirty families were represented by a single species each. In their survey study of 65 relic prairies of all types (low, deep-soil, dry lime, and sand prairies), Curtis and Greene (1949) found the following five families to be the best represented: Compositae (27 per cent), Gramineae (9.7 per cent), Leguminosae (7.2 per cent), Asclepiadaceae (4.2 per cent), and Umbelliferae (3.8 per cent).

Characteristic Species

Upon examination of the master list of species, it is noticed that most of the dominant species are rather common prairie plants not exclusively confined to dry lime prairies. It can be readily assumed, however, that the particular order of these dominants in Table 9 is characteristic of the dry, thin-soil part of the entire gradient from wet to extremely dry prairie. Since the data obtained in the present study deal with only one extreme end of this gradient, it cannot be used to separate those species which are almost entirely confined to the dry lime prairies.

The following list of species is given as characteristic ones--species largely confined to the dry lime prairie. The list was arrived at by the pooling of field experiences of Drs. J. T. Curtis, H. C. Greene, and the writer. These are listed according to their rank as given in Table 9:

Aster sericeus (4100)
Liatris cylindracea (1567)
Arenaria stricta (1351)
Aster ericoides (1200)
Artemisia caudata (874)
Aster oblongifolius (622)
Muhlenbergia cuspidata (622)
Kuhnia eupatorioides (616)
Lithospermum incisum (424)
Castelleja sessiliflora (381)

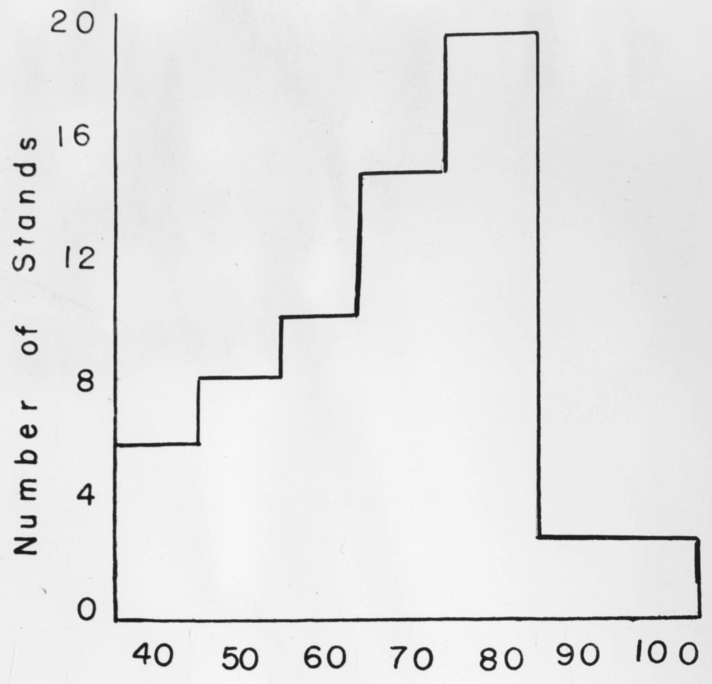
Only 3 stands contained all 10 characteristic species; as many as 4 stands had as few as 4. Nineteen stands contained 8 species. The over-all average for all the stands was 67 per cent (6.7 species). The distribution of various percentages of the characteristic species among the stands is shown in Figure 35a. Figure 35b shows the distribution of numbers of stands having increasing numbers of characteristic species, beginning with 59 stands having *Aster sericeus*, 39 stands having *Aster sericeus* and *Liatris cylindracea*, and ending with only 3 stands having all 10 species.

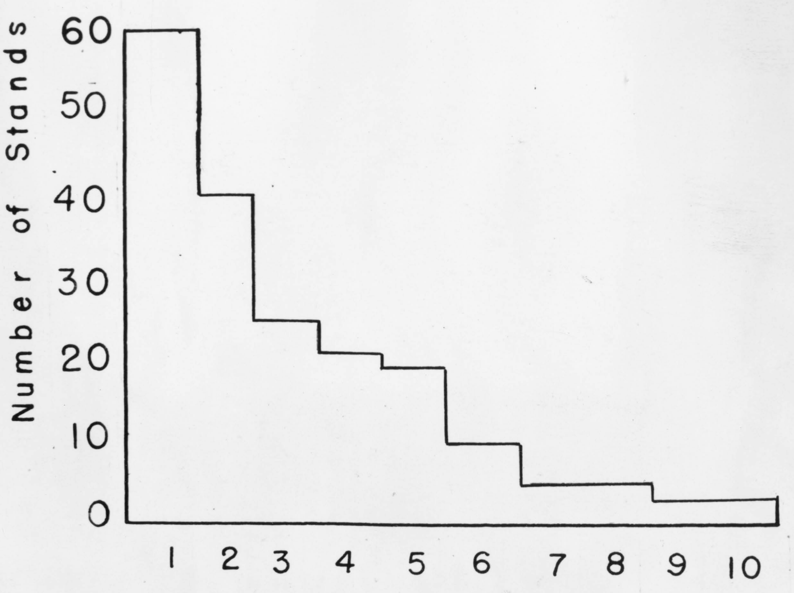
Figure 35a

Distribution of stands having increasing percentages of characteristic species.

Figure 35b

Numbers of stands having an increasing number of characteristic species. Species arranged according to decreasing products of constancy and average frequency. Group 1 has species 1, group 2 has species 1 and 2, etc.


Number of Stands
20
16
12
8
4
0
40
50
60
70
80
90
100


Number of Stands
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10

A Gradient of Stands Based on Frequency Data

Attention has already been called to the apparent uniformity among the lists of important species, based on both frequency and presence data. The following discussion is an attempt to investigate further this apparent uniformity among the various stands by using frequency data. The data have been placed on individual cards in accordance with an order established for each species (Table 9), making comparisons among the stands relatively simple. The sums of frequencies of all the species in a stand, and of the first 10 and 20 species, have also been written on each card. Most of what follows is based on several assumptions: that similar stands will have many more species in common than dissimilar ones, that the sum of frequencies of species of similar stands will be very nearly the same, and that the sum of differences of frequencies of species will be lower in similar stands than in highly different ones.

All stands studied in this section were placed along a gradient based on the sum of frequencies of the first 20 species in the order based on the product of the constancy and average frequency. Altogether, several gradients were tried, but the one based on the first 20 species seemed to give more meaningful results than a gradient based on the sum of all the species, for instance. Undue importance is placed on many of the unimportant species when all the species are used. The two extremes of the gradient obtained by using the first 20 species are 915 and 440, and the average of this range (648) is very close to the median (640). For convenience in handling many stands, groups of 6 stands each were used. Results are given in Table 10 where it can be seen that, except for the last group of 6 stands, the number of species per stand and the number of species found within quadrats vary but little from group to group. This applies to the number of species each group has in common also. The last group contains all of the extremely small and depauperate stands, differing more in the numbers of species than do the rest. The last column of Table 10 contains a ratio found by dividing the sum of frequencies of the species in common in any group by the sum of frequencies of all the species in that group. This ratio, using groups of 6 stands along the gradient based on the sum of frequencies of the first 20 species, varies from 45.0 to 62.2. The distribution of these ratios is in the form of a smooth, rather flat curve, with the lowest ratio for the last group of stands.

Such a ratio could vary from zero, where there are no species in common, to 100, where all the species are in common. Other ratios which would also demonstrate uniformity among the stands can be used. For instance, when the ratios of the sum of frequencies of the first 10 species to the sum of frequencies of the first 20 species are calculated, the results are: 67.2, 66.9, 70.5, 68.9, 73.1, and 72.2, and when

TABLE 10

Groups of 6 stands along gradient	Average number of species per stand	Average number of species found in quadrats	Number of species group has in common	Sum of frequencies of first 10 species	Sum of frequencies of first 20 species	Sum of frequencies of all species	Sum of frequencies of species in common in group	Sum of freq. of species in common / Sum of frequencies of all species
1	66.	45.	20.	3415.	5082.	8120.	4704.	57.9
2	64.	41.	19.	2990.	4468.	6750.	4199.	62.2
3	65.	46.	21.	2827.	3991.	6150.	3676.	59.7
4	71.	42.	17.	2531.	3672.	6135.	3182.	51.8
5	57.	39.	18.	2418.	3306.	5675.	2828.	49.8
6	47.	36.	11.	2040.	2824.	4790.	2153.	45.0

the ratios of the sum of frequencies of the first 20 species to the sum of frequencies of all species in the group are obtained, the results are: 62.5, 64.7, 64.8, 59.8, 58.2, and 58.9.

The ratio, given in Table 10, which is used to demonstrate a degree of uniformity among the various stands, can be seen to be a function of the number of stands used in any grouping by examining Table 11. The manner in which this ratio decreases with an increase in the number of stands used is shown by using the same order and grouping of stands but having each new group include the stands of the previous groups. Thus, group 6 in Table 11 which includes all the stands has only 7 species in common and has a ratio of only 30.1. It would be expected that these 7 very common species would very likely remain in common as the number of stands were increased. Also, the fact that the ratio decreases very slowly after the first 3 groups of stands is undoubtedly explained by the importance of the 7 or 8 top-ranking species in making up the greater part of the sum of frequencies of the species in common in the groups. Table 11, further, establishes different levels of uniformity which might be obtained if groups of stands greater than 6 are used.

If, instead of using groups of 6 stands, pairs of stands are used, higher ratios can be expected, and more species in common among pairs than among groups of 6 or more stands will be found. When pairs of stands within each group of 6 stands

TABLE 11

Stands along gradient—cumulative in groups of six	Number of species group has in common	Sum of frequencies of species in common	Sum of frequencies of all species in group	Sum of freq. of species in common / Sum of freq. of all species
1 6 stands	20	4694.	8120.	57.9
2 12 stands	14	6591.	14870.	44.3
3 18 stands	11	7992.	21025.	38.0
4 24 stands	10	9354.	27160.	34.4
5 30 stands	8	11667.	33590.	34.5
6 36 stands	7	11332.	37625.	30.1

are treated and results averaged, the following are the numbers of species in common among the pairs of stands in each group of 6: 40, 34, 33, 40, 34, and 25. Ratios, based on average sums of frequencies for the paired stands are as follows: 90.4, 78.8, 80.7, 77.2, 74.2, and 70.6.

The distribution of the number of species in common in the pairs of stands and the ratios for these individual pairs is shown in Figure 36. This graph shows, in addition to the general trend, that any increase in numbers of species in common among the pairs will be, most likely, among the dominant species which contribute most to the sums of frequencies.

The ratios mentioned above also indicate a very uniform population of the stands near the center of the group and a greater variation of the stands at the two extremes of the gradient. If, instead of using all the species in common, only those among the first 10 are used in calculating the ratio which shows the relationship between the sum of frequencies of species in common (among the first 10) and the sum of frequencies of all species, an extremely uniform, smoothly distributed series of ratios results: 41.8, 45.1, 45.2, 41.2, 41.5, 41.0.

This last series of ratios can be employed to advantage when two rather different kinds of prairies are compared. For instance, it can be shown that dry lime prairies are a group distinct from deep-soil prairies and that the order of the first 10 species can be used diagnostically for this pur-

Figure 36

Relationship between numbers of species in common in pairs of stands along sum of frequency gradient and the ratios of the sum of frequencies of species common to pairs to the sum of frequencies of all species in pairs.


50
48
46
44
42
40
38
36
34
32
30
28
26
24
22
20
Numbers of Species Common to Pairs of Stands
60
62
64
66
68
72
74
76
78
80
82
84
86
88
90
92
94
96
98
100
Sum of Frequencies of Species Common to Pairs/ Sum of Frequencies of all Species in Pair

pose. The range of the ratios mentioned above when dry lime prairies were compared among themselves is from 41.0 to 45.2. Table 12 attempts to show the wider range in this kind of ratio when 15 dry lime prairies are each compared with 3 deep-soil prairies. The specific location of the dry lime prairies can be found in the Appendix, whereas the locations of the 3 deep-soil prairies used are as follows: number 15, Rock County (T 2N R13 E sec. 28); number 49, Grant County (T 2N R1 W sec. 36); and number 61, Iowa County (T 5N R3 E sec. 5).

The range of these ratios (Table 12) is a very wide one--from 12.3 to 35.8. This information is used here because it emphasizes the great lack of uniformity between deep-soil and dry lime prairies when the same technique which has demonstrated a great deal of uniformity among dry lime prairies is used. Although many of the first 10 species found in dry lime prairies are also found in deep-soil prairies, their relative importance in the prairie is different.

Uniformity among the stands of dry lime prairies has been demonstrated when stands are placed along a gradient based on the sum of frequencies of the dominant species. This uniformity has been expressed in several ways: by numbers of species per stand, by numbers of species in quadrats, by numbers of species in common, and finally by numerical relationships between sums of frequencies of species in common and sums of frequencies of all species in any grouping.

A very brief consideration of another convenient method

Table 12

Results of comparing 3 deep-soil prairies
(numbers 15, 49, and 61)
with 15 dry lime prairies, using the ratio
of the sum of frequencies of the first 10
species in common to the sum of frequencies
of all species

Dry Lime Prairies	Deep-Soil Prairies		
	15	49	61
1	20.0	30.8	29.4
6	19.2	29.2	24.7
14	22.6	31.7	33.0
12	16.5	22.1	23.3
33	20.0	29.6	30.0
36	21.4	31.6	34.1
40	20.2	37.0	33.0
63	19.6	32.2	35.8
71	22.0	32.9	34.2
35	12.3	22.2	24.2
11	19.0	29.6	31.1
28	19.5	27.4	27.0
42	22.8	31.8	31.5
5	20.4	31.1	35.8
9	14.1	28.9	20.9

of demonstrating uniformity among stands is given next. It is assumed that stands which are very similar will have a much lower sum of difference of frequencies than stands which are highly different. This is a modification of a method of Gleason (1920) which McIntosh (1950) used. The latter used the sum of the differences of the D F D (the sum of the density, frequency, and dominance) of the major trees of two forest stands. In the table given below the sum of the differences of the frequencies of the first 30 species of two stands is used.

Table 13

Uniformity demonstrated by the use of the sum of differences of frequencies of the first 30 species. Averages based on groups of 6 stands arranged along the gradient (15 combinations are involved in each average). Group 7 includes 6 stands chosen at random.

Group	Average Sum of Differences of Frequencies
1	592.2
2	613.3
3	634.2
4	612.2
5	583.2
6	567.0
7	617.0

The results given are averages of a total of 15 comparisons or combinations among the 6 stands of each group. The order of stands is the same as before (Table 10). The distribution of these average sums of differences of frequencies is a normal one, having a pattern very similar to the ratios given earlier. Since not the same attributes are being measured, it is doubtful that the results between the two methods are directly comparable. The last group given in Table 13 consists of 6 prairies chosen at random from the group regardless of their order on the gradient.

It is concluded that frequency can be used as a further indication of homogeneity among the dry lime prairies. A gradient based on the sums of frequencies of the dominant species of the various stands gives a series of rather uniform ratios expressing relationships between the sums of frequencies of species in common and all species in any pairs or groupings of stands. For a general treatment of stands of dry lime prairies in the prairie-forest province of southwestern Wisconsin the above-discussed methods offer a good measurement of homogeneity.

A Treatment of Stands on a Geographic Basis

In the preceding section it has been demonstrated that there exists a relatively high degree of homogeneity among the dry lime prairies of southwestern Wisconsin when the factor of frequency is used as the variable. A convenient gradient based on the sum of frequencies of the dominant species has been utilized in demonstrating this uniformity. When ratios of the sum of frequencies of species in common to any group of stands along this gradient to the sum of frequencies of all the species of the particular group are used, it is seen that the variations in these variables are slight and distributed along very smooth curves. The above-mentioned facts do not, however, preclude the possibility of demonstrating different levels of homogeneity if the stands are treated in some other way than the gradient used.

The prairies studied are found on a variety of physiographic sites: the gravelly moraines of southeastern Wisconsin, relatively flat-topped prairies on the Galena-Platteville dolomites, and very steep south-southwest-facing bluffs along the Mississippi River. The chief criteria used in picking sites for study were the very thin soil, the undisturbed nature of the prairie vegetation, and the high soil pH. Because of the striking uniformity of these criteria, there seems to be little reason for trying to subdivide the prairies into any groups. However, due to the fact that a great many of the prairies seem to be somewhat clustered in some areas, it is decided toplace most of them into 3 more or less distinct geographic divisions. These groups of adjacent prairies include a group of very similar stands in southern Dane and northern Green counties, a group of prairies on somewhat more diverse topography in northern Dane and southern Columbia counties, and a third group of more widely scattered stands on the Mississippi bluffs.

Six stands from each of these three regions have been treated in the same manner as were the groups of 6 stands along the gradient. These stands were chosen so that all in each group were as closely clustered as possible. The occasional scattered stands on the edge of these areas were not used. Table 14 gives the results of these treatments, where, in part A, numbers of species per unit and ratios based on sums of frequencies are compared, and in part B, average sums of differences of frequencies of the first 30 species are used.

Although this particular treatment does show several deviations from results obtained when stands were treated in a non-geographical way, it should be at the same time emphasized that these differences are not especially great. In part A of Table 14, for instance, only the Mississippi bluffs have a much higher ratio than any found in Table 10. This can be related to the larger number of species the group has in

Table 14

A comparison of 18 prairies from three geographic areas in southwestern Wisconsin

	Southern Dane Co.	Northern Dane Co.	Mississippi Valley
A. Sum of frequency of all species	5800	7035	6015
Number of species per stand	48	71	71
Number of species in quadrats	36	44	41
Number of species common to group	20	27	31
Ratio of sum of frequency of common species to sum of frequency of all species	65.7	65.7	74.1

B.

Average of the sum of differences of frequencies of first 30 species (15 comparisons in each group of 6 stands)

1. Southern Dane County	558.9
2. Northern Dane County	517.0
3. Mississippi Valley	535.6
4. Six stands chosen at random	617.0

common. It can be seen that the Northern Dane County group, which has a high number of species in common also, has a much higher sum of frequencies of all species than the Mississippi bluff prairies.

In contrasting part B of Table 14 with Table 13, it can be seen that the average sums of differences of frequencies are lower when stands are grouped in geographic areas. Perhaps a surprising fact is the relatively low average sum for the Northern Dane County group of prairies. The average sum of differences of frequencies for the geographically grouped prairies is 537., which is lower than any average for groups when stands are arranged along a gradient based on sums of frequencies of the dominant species and much lower than the average of these averages (600.3).

Two general points regarding levels of homogeneity are emphasized: that when near-by stands are treated as groups, their levels of homogeneity are higher than those obtained by the same methods used in treating the entire group of prairies without regard to their locations, and that apparently certain differences exist among the 3 geographic groups treated. In an effort to find out what some of these differences may be, the floristic composition of the various groups as related to certain environmental factors must be next considered.

A STUDY OF ENVIRONMENTAL FACTORS

Introduction

No single prairie has been studied intensively as far as the environment is concerned. The following attempts to relate certain floristic factors with those aspects of the environment studied. Most of these are soil characteristics. A single, pooled sample was collected from the top or A horizon of most of the stands and analyzed by the State Soils Testing Laboratory.

The most obvious differences in floral composition concern relatively minor species. Liatris punctata and Artemisia frigida, for instance, occur only in the westernmost prairies studied. Although the area of the study includes the entire southern part of a state, a much larger geographic area will have to be covered to show that these two species increase in importance as the prairies to the west are considered. Muhlenbergia cuspidata also presents a problem. Although this grass is common and relatively important on the Mississippi bluffs and rather common though less important on the prairies of southern Dane County, it is missing from the prairies of northern Dane County.

The fact that it is possible to increase the level of homogeneity to a certain degree when vicinal stands are considered as units will be applied to the environmental data also.

Soil Nutrients and Vegetation

The soil calcium, magnesium, and pH values of the stands were extremely uniform. In addition to these, potassium, phosphorus, and nitrogen contents were determined. The water-retaining capacity is also considered here. When these factors are considered for groups of 6 stands along a gradient based on the sum of frequencies of the first 20 species (Table 15), no particular trends are shown. Table 16 shows the variations among several factors when stands are arranged according to several variables. Of these only the phosphorus seems to vary with the potassium in a significant way, and this variation remains essentially the same when size classes of phosphorus instead of groups of 6 stands along this gradient are used. A correlation between location of stands and phosphorus content is evident, for all the stands in the first group and over half of the second are located in southern Dane and northern Green counties.

TABLE 15

The variation of certain soil characteristics and other factors along a gradient based on the sum of frequency of the first 20 species

Groups of 6 stands along gradient	Water-retaining capacity (%)	Ca (ppm.)	Mg (ppm.)	P (ppm.)	K (ppm.)	NO_3 (ppm.)	NH_3 (ppm.)	Average number of species in stands	Average number of species in quadrats
1	89.0	4500.	542.	30.	145.	7.1	7.5	66.	45.
2	71.4	5000.	525.	55.	86.	4.5	4.2	64.	41.
3	69.4	4910.	558.	67.	100.	10.9	7.9	65.	46.
4	72.7	4100.	475.	45.	91.	7.1	6.0	71.	42.
5	67.5	4910.	475.	67.	84.	7.1	5.4	57.	39.
6	70.5	4500.	487.	81.	92.	7.0	6.2	47.	36.

TABLE 16

Variations among several soil factors

(results are averages of groups of 6 stands)

A. Arranged according to water-retaining capacity

Water-retaining capacity (%)	P (ppm.)	K (ppm.)	# species per stand
93.8	28	118	68
83.7	61	80	55
76.1	47	94	64
70.9	60	103	48
67.3	31	96	69
61.0	92	116	40

B. Arranged according to phosphorus

P (ppm.)	K (ppm.)
143	82
92	89
57	103
38	112
31	112
15	111

The stands in the other 4 groups are about evenly divided between the northern Dane County and the Mississippi Valley prairies. Those stands having the highest amount of phosphorus, therefore, are located on the Galena-Platteville dolomites.

Whitson (1927) gives some substantiating information regarding this variation in phosphorus content. For the Dodgeville silt-loam soils of Dane County, which are of residual origin and thus reflect the nature of the bedrock, a total phosphorus of 0.144 per cent is given. The Carrington silt-loam soils of Columbia County, on glacial drift, have a total phosphorus content of 0.069 per cent, while the Marshall silt-loam soils, of loessal origin, have a total phosphorus content of 0.068 per cent. These latter two soils probably compare well with the prairie soils of northern Dane County and the Mississippi Valley bluffs, and the former, with the higher phosphorus content, correspond with the soils on the Galena-Platteville dolomites of southern Dane County.

That other differences occur in the general environmental complex is shown in Table 17. These differences, in addition to the soil phosphorus variation, include average slope, glacial geology, average number of species per stand, and number and importance of "rare" species. The prairies of southern Dane County are flat to slightly sloping and therefore more uniform in relation to the bedrock. This is

TABLE 17

Variations in certain environmental and vegetational factors among 3 geographical areas

	Southern Dane Co.	Northern Dane Co.	Mississippi Valley
water-retaining capacity (%)	69.2	74.6	75.9
soil Ca (ppm.)	5000	4200	4430
soil Mg (ppm.)	540	545	436
soil P (ppm.)	106	26	30
soil K (ppm.)	87	109	98
# of species per stand	48	71	71
average slope (degrees)	2	8	20
bedrock	Galena-Platteville dolomites	Lower Magnesian dolomites	Lower Magnesian dolomites
glacial geology	Driftless Area (mostly) a few on Illinoian drift	glaciated (Cary ice of Wisconsin)	Driftless Area & pre-Wisconsin drift
exposure (%)	southwest-70 west------20 east------10	southwest-60 west------10 south-----10 north-northwest-20	southwest-80 west------20
sum of freq. of first 80 species	5549	6316	5560
# species beyond first 80	31	55	58
sum of freq. of these "rare" species	241	719	455

a marked contrast with the steep prairies of the Mississippi Valley bluffs. Although these prairies cut across several strata of rock, the dominating bedrock of these and northern Dane County is the Lower Magnesian dolomite. The species referred to as "rare" ones are those which rank below the eightieth on the master list, an arbitrary division based on convenience of handling the data.

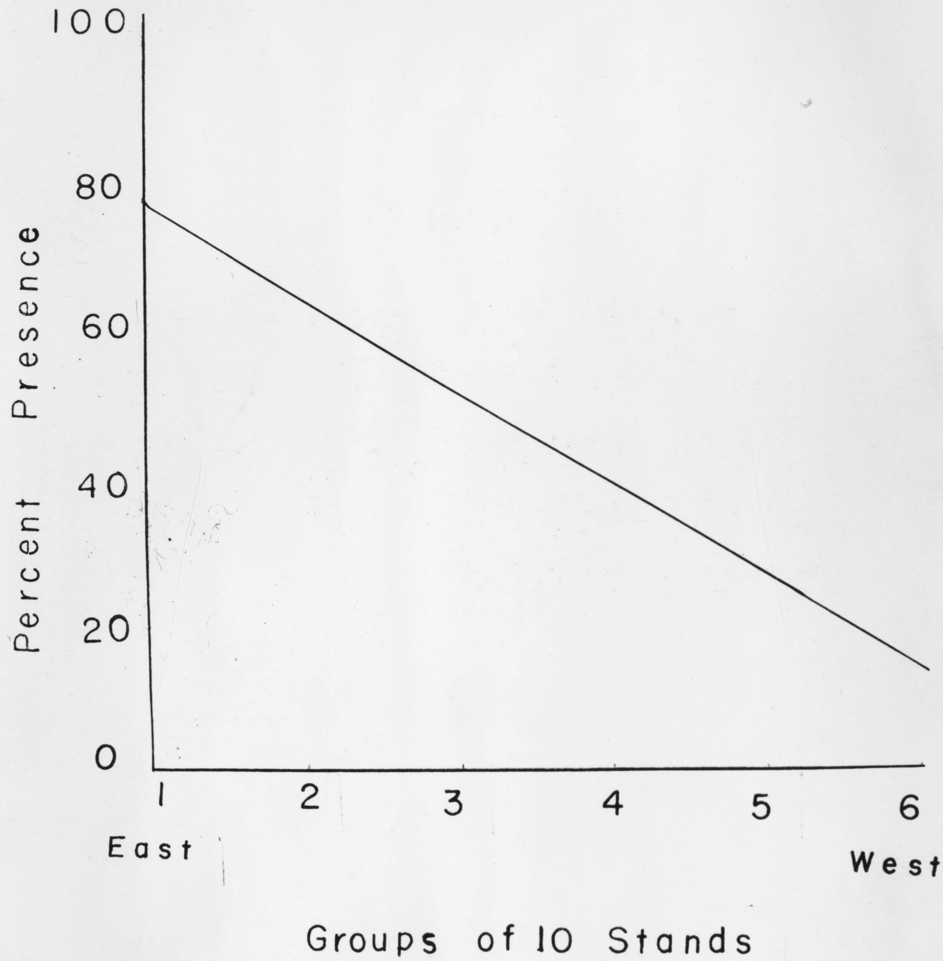
Several of the differences noted in Table 17 may be related to several factors not recorded. For instance, the less steep and generally smaller prairies of southern Dane County have undoubtedly suffered from a greater amount of disturbance in the past than have the steeper and less accessible stands elsewhere. More of the prairies of northern Dane County and the Mississippi Valley bluffs are surrounded by forests.

Superimposed on the recorded variables is another factor which probably plays a role in determining some of the variations in species in the 3 groups. This is the east-to-west orientation of the stands within the area covered by this study. Although this seems hardly of any importance in distinguishing the southern Dane County stands from the northern Dane County ones, it is probably important in explaining some of the differences between the farther-removed Mississippi Valley prairies and the Dane County stands.

Table 18 lists the relatively few species which demon-

Figure 37

Decrease in per cent presence along an east-to-west gradient of Arenaria stricta, Asclepias verticillata, Geum triflorum, Verbena stricta, and Psoralea esculenta.



100
80
60
40
20
0
Percent Presence
1
2
3
4
5
6
East
West
Groups of 10 Stands

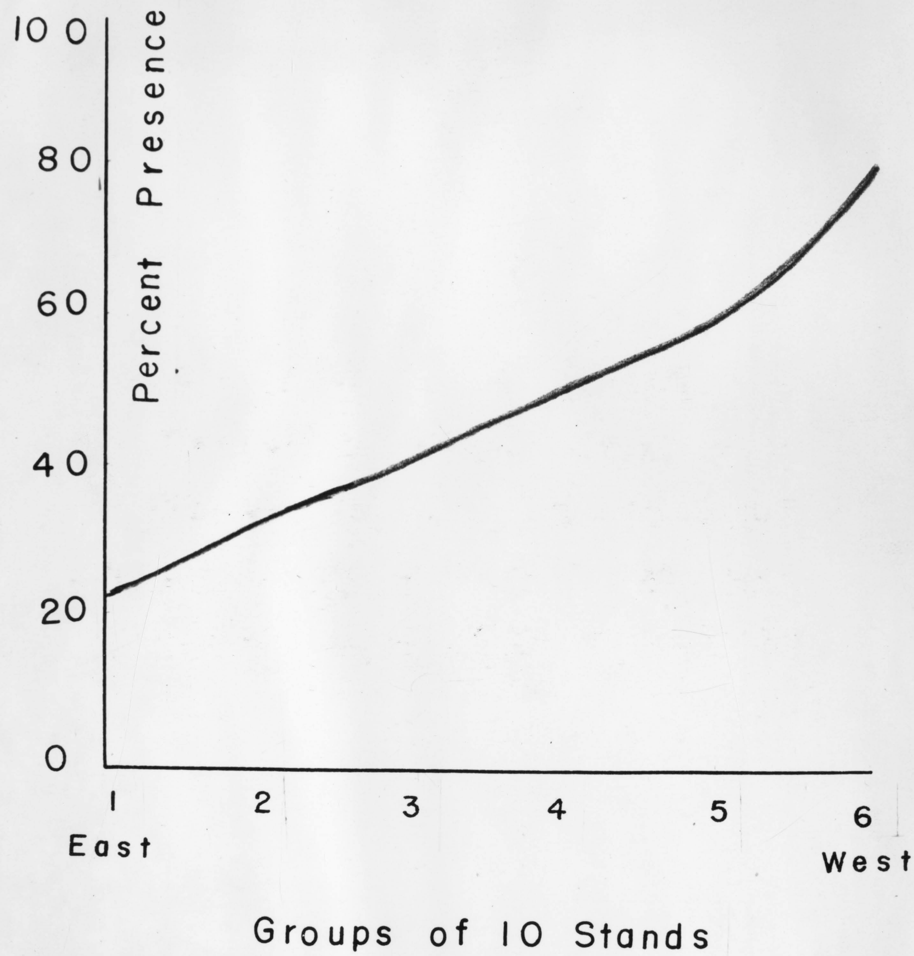
strate rather well-marked variations in constancy and average frequency when the southern Dane, northern Dane, and Mississippi Valley prairies order is considered. The important species do not show such increasing or decreasing tendencies, and when average values for the first 60 species are examined, a high level of homogeneity for these values is indicated.

Essentially the same results as shown in Table 18 can be obtained in a slightly different way. Instead of using the 3 geographical areas as a means of grouping the stands, a total of 60 stands were considered along an east-to-west gradient. Figures 37 and 38 show results for the same species when these 60 stands are divided into 6 groups of 10 stands each. Presence is used here instead of constancy and average frequency, since more stands than quadrat data are available for were used. These curves would suggest even more than Table 18 results that an east-to-west distribution is the factor involved. To test this idea further a much larger area should be considered--the entire prairie peninsula or the area from Wisconsin into the Dakotas.

Table 19 offers more information about variations of certain species among the 3 groups. The southern Dane County prairies are, generally, less rich and lush in growth than the others. Several of the species relatively more important in northern Dane County, as Eryngium yuccifolium and Phlox pilosa, are more characteristic of mesic prairies

Figure 38

Increase in per cent presence along an east-to-west gradient of *Bouteloua hirsuta*, *Aster oblongifolius*, *Apocynum androsaemifolium*, *Scutellaria parvula*, and *Sorghastrum nutans*.



100
80
60
40
20
0
Percent Presence
1
East
2
3
4
5
6
West
Groups of 10 Stands

TABLE 18

Variations of certain species among geographic areas I.

	S. Dane Co.		N. Dane Co.		Mississ. bluffs	
	C.	av. f.	C.	av. f.	C.	av. f.
A. Species showing a decrease in importance when this order is concerned						
Arenaria stricta	90	36	90	31	10	5
Asclepias verticillata	100	53	80	2	60	3
Geum triflorum	90	7	30	32	10	1
Verbena stricta	90	8	70	2	40	2
Psoralea esculenta	60	3	20	1	0	0
Average	86	21	58	14	24	2
B. Species showing an increase in importance when this order is concerned						
Scutellaria parvula	50	6	80	12	100	68
Bouteloua hirsuta	10	5	20	13	70	22
Sorghastrum nutans	10	5	70	5	100	12
Aster oblongifolius	50	4	40	15	100	18
Apocynum androsaemifolium	10	1	30	4	80	2
Average	26	4	48	10	90	13

TABLE 18 (continued)

	S. Dane Co.		N. Dane Co.		Mississ. bluffs	
	C.	av. f.	C.	av. f.	C.	av. f.
C. Species arranged in order of C. and av. f. (averages of 10 species)						
Species 1-10	96	45	100	48	100	44
Species 11-20	78	21	90	26	85	17
Species 21-30	62	20	71	14	80	16
Species 31-40	55	9	78	18	79	11
Species 41-50	48	12	63	13	67	7
Species 51-60	47	5	55	5	37	2
Average of all 60	65	19	76	21	75	17

than of dry ones. The greater variation in soil depth in the glaciated northern Dane County stands and in the steep bluff prairies of the Mississippi Valley has already been noted.

In conclusion it can be stated that the high level of homogeneity demonstrated by the major species can be extended to include the various soil nutrients. Only soil phosphorus shows any great variation. This can be related to the difference in bedrock: the southern Dane County group of stands which has a much higher phosphorus content is located on the Galena-Platteville dolomites. However, such other differences as average slope, glacial geology, and degree of past disturbances have to be considered also. A much more detailed study of the relation between prairie species and high phosphorus content of soils on these bedrocks needs to be undertaken.

TABLE 19

Variations of species among geographic areas II

A. Species which show no apparent change in either presence or average frequency. Seventy per cent of these are among the first 25 species in importance

Andropogon scoparius	Helianthus laetiflorus
Andropogon Gerardi	Kuhnia eupatorioides
Amorpha canescens	Liatris cylindracea
Anemone patens	Panicum perlongum
Artemisia caudata	Panicum oligosanthes
Aster ericoides	Physalis virginiana
Aster sericeus	Oenothera biennis
Bouteloua curtipendula	Petalostemum purpureum
Coreopsis palmata	Solidago nemoralis
Erigeron strigosus	Rosa
Hedeoma hispida	

B. Species which decrease in importance from southern Dane County to the Mississippi bluffs

Psoralea esculenta	Arenaria stricta
Verbena stricta	Geum triflorum
Asclepias verticillata	Lithospermum incisum

C. Species which increase in importance from southern Dane County to the Mississippi bluffs

Apocynum androsaemifolium	Panicum leibergii
Aster oblongifolius	Petalostemum candidum
Bouteloua hirsuta	Ratibida pinnata
Castelleja sessiliflora	Salix humilis
Commandra umbellata	Scutellaria parvula
Lithospermum canescens	Sorghastrum nutans
Liatris aspera	Stipa spartea

TABLE 19 (2)

D. Species which are absent or very much lower in importance in southern Dane County, although about equal in importance in northern Dane County and on the Mississippi bluffs

Anemone cylindrica	Silphium laciniatum
Heuchera Richardsoni	Smilacina stellata
Linum sulcatum	Sporobolus heterolepis
Potentilla arguta	Rudbeckia hirta

E. Species of lower importance in northern Dane County than elsewhere

Ambrosia artemisiifolia	Muhlenbergia cuspidata (absent)
Elymus canadensis	Solidago rigida

F. Species of higher importance in northern Dane County than elsewhere

Antennaria	Eryngium yuccifolium
Aster linariifolius	Pedicularis canadensis
Aster ptarmicoides	Phlox pilosa

Some Possible Effects of Glaciation

The location of many stands just within and without the terminal moraine of the Cary ice offers an excellent opportunity for studying any possible effect of glaciation on the vegetation of these stands. Earlier Gould (1937) made a study of prairie vegetation in glaciated and unglaciated areas and found a number of differences; however, since he did not confine his study to any one particular kind of prairie, it is doubtful if his findings can be applied here.

For this particular study 18 stands were chosen from the following locations: (1) within the terminal moraine (stands number 28, 12, 32, 33, 35, and 36), (2) just outside the moraine, in an area undoubtedly affected by drainage from the ice sheet (stands number 10, 11, 13, 19, 42, and 47), and (3) farther removed from the moraine and probably not directly affected by the drainage (stands number 1, 6, 7, 14, 17, and 18).

A modification of Jaccard's coefficient of community (Jaccard, 1928) was used in making comparisons between pairs of stands. This ratio, expressed as a per cent, is obtained by dividing the number of species any two stands have in common by the total number of species found in the two stands. Within any group of 6 stands it is possible to make 15 comparisons. Results given here are averages of these various combinations, as indicated. When members of the above groups are compared with each other, the following average coefficients are obtained: group 1, 55.8 per cent; group 2, 50.0 per cent; and group 3, 52.8 per cent. The results given in Table 20 were gotten by comparing each of the 6 stands within the terminal moraine with each of the stands of the other groups. These results show an interesting and consistent change as one compares the averages of stands within the moraine with themselves (55.8 per cent), with stands just without the moraine (45.4 per cent), and with the farther-removed stands (42.4 per cent).

These findings lead one to ponder postglacial migrations of prairie floras--whether these differences reflect variations in habitats which act as selecting agents or whether the prairie actually persisted during the ice age in the Driftless Area and the differences noted above reflect migration problems of certain species from a prairie refugium south of the moraine. In either case the results probably reflect certain differences between areas variously affected by the ice and its drainage.

TABLE 20

Variations in Jaccard's coefficient of community when stands within, near by, and more removed from the terminal moraine of the Cary ice are compared

stand numbers within the moraine	average with others in same group	averages with 6 stands near moraine	averages with 6 stands more distant from moraine
28	54.6	45.1	41.3
12	55.5	44.9	41.8
32	57.3	45.7	42.8
33	53.4	46.1	46.2
35	59.8	44.6	40.0
36	54.1	46.0	42.2
averages	55.8	45.4	42.4

The interesting problem of the distribution of Muhlenbergia cuspidata has relevance here, since it is entirely absent from the areas covered by the ice and affected by its drainage, although it is present in the southern Dane County group of stands which include those farthest from the ice.

Further, this species is more important in the stands along the Mississippi River, a region still farther from the Cary ice. Certainly suitable sites for this species exist within the glaciated area. Among the common species, only Psoralea esculenta exhibits a similar distribution pattern. It is interesting to note that differences between glaciated and non-glaciated prairies have also been reported in Ohio by De Selm (1953), including a similar pattern for Muhlenbergia. With the present information it does not seem possible to explain the strange distribution of this species except to relate it to glaciation.

Mechanical Analysis of Soils

The air-dried soils which had been sifted through a 2-mm. sieve in preparation for the chemical analyses were run through a series of sieves which separated the following size particles: 2.0-1.0 mm., 1.0-0.5 mm., 0.5-0.25 mm., 0.25-0.10 mm., 0.10-0.06 mm., and below 0.06 mm. Results are given in Table 21. The most obvious and striking characteristics of these soils are their great uniformity and fineness. When soils from 8 deep-soil, mesic prairies are analyzed also, the differences of the various size particles are very notable. The soils of the dry lime prairies are immature and lack a crumb structure; the dominant sizes are 0.25-0.1 mm. and 0.1-0.06 mm., making these a very fine sandy soil.

TABLE 21

Results of mechanical analysis of soils

Averages of stands, as indicated	Size particles, ranges in millimeters (results expressed in per cent)					
	1 2.0-1.0	2 1.0-0.5	3 0.5-0.25	4 0.25-0.1	5 0.1-0.06	6 less than 0.06
36 dry lime prairies	6.4	13.4	15.1	35.4	25.4	4.3
10 s. Dane Co. prairies	3.7	9.8	16.0	45.5	20.7	4.5
10 n. Dane Co. prairies	8.9	16.4	16.4	27.5	26.7	4.2
10 Miss. Valley prairies	6.2	15.6	12.8	29.0	32.0	4.4
first 6 stands on sum of freq. gradient	12.3	19.7	15.1	24.7	23.7	4.5
last 6 stands on sum of freq. gradient	3.8	13.0	13.8	39.5	25.3	4.6
center 12 stands on sum of freq. gradient	6.8	12.8	15.7	36.5	23.9	4.3
8 deep-soil, mesic prairies	35.3	20.7	11.5	13.4	15.0	4.1

Of interest also are the differences found when the soils of the 3 geographic areas and of groups of stands along the sum of frequencies gradient are considered. The soils of the stands near the center of this gradient compare very well with the overall average for all stands. The stands at the high end of this gradient are here because of the more varied flora of these prairies, and this, in turn, is because of the variation in the soil. These stands show the beginnings of a true prairie soil in the areas of deeper soil. A greater number of soil samples taken would undoubtedly refine the relationships between soil depth, structure, and a variability in vegetation, expressed by both numbers of species per stand and sums of frequencies.

The significant differences between the particle-size distribution of dry lime and mesic prairies include aspects of soil structure as well as mere particle size. The crumb structure of the latter accounts for the unusually high per cent of the first two classes. It would appear that certain of the stands at the upper end of the frequency gradient are actually transitional in nature as far as these soil characteristics are concerned.

Variations in Soil Depth and Vegetation

The criterion of soil depth as a means of delimiting areas for inclusion was, perhaps, the simplest of all used. The variation in soil depth in the stands has already been mentioned. Some had small pockets of somewhat deeper soil in depressions in the rocky substrate; these often had, in addition to a dense sod, clones of such plants as Panicum Leibergii.

In making quadrat studies it was customary to note those which fell on unusually thin or deep soil. Only these extreme situations were noted. Deep soil here means anything over 4 inches to bedrock or gravel, while thin soil means extremely bare and rocky areas. For this particular study a total of 40 such quadrats, 20 from the deep-soil phase and 20 from the shallow, were removed from the field data. These represent a random selection of quadrats from the entire area studied.

Table 22 lists species which seem to be affected by variations in soil depth. These results should be interpreted to express trends rather than absolute preferences to any particular soil depth.

TABLE 22

The occurrence of certain plants in quadrats from extremely shallow and deep-soil phases of dry lime prairies

A. Species found in quadrats on very thin-soil but not in quadrats in deep soil

Arenaria stricta	Hedeoma hispida
Artemisia caudata	Castelleja sessifolia
Ambrosia artemisiifolia	Scutellaria parvula
Asclepias verticellata	Prunus pumila
Aster ptarmicoides	Arabis lyrata
Aster oblongifolius	Potentilla arguta

TABLE 22 (2)

B. Species confined to quadrats in deep-soil phase

Rosa	Heuchera Richardsonii
Kuhnia eupatorioides	Salix humilis
Panicum oligosanthes var. Scribnerianum	Eryngium yuccifolium
Panicum Leibergii	Gentiana puberula
Sorghastrum nutans	Hieracium longipilum
Anemone cylindrica	Liatris pychnostachya
Erigeron ramosus	Monarda fistulosa

C. Species found in both shallow and deep-soil phases but with a frequency of 25 per cent or higher in shallow-soil phase

Andropogon scoparius	Panicum perlongum
Bouteloua curtipendula	Liatris cylindracea
Solidago nemoralis	Muhlenbergia cuspidata

D. Species found in both phases but with a frequency of 25 per cent or higher in deep-soil phase

Andropogon Gerardi	Aster ericoides
Euphorbia corollata	Stipa spartea
Amorpha canescens	Phlox pilosus

E. Species found in both phases but with a frequency of from 10 to 25 per cent higher in shallow-soil phase

Antennaria	Aster laevis
Viola	Aster linariifolius
Helianthus laetiflorus var. rigidus	Aster azureus

F. Species found in both phases but with a frequency of from 10 to 25 per cent higher in deep-soil phase

Liatris aspera	Lithospermum canescens
Commandra umbellata	Bromus Kalmii

G. Species having equal frequencies (± 5 per cent) in both phases

Sporobolus heterolepis	Poa compressa
Lobelia spicata	Ratibida pinnata
Coreopsis palmata	Silphium laciniatum
Solidago rigida	Verbena stricta
Anemone patens	Koeleria cristata
Helianthus occidentalis	Pedicularis canadensis

In addition to demonstrating this preference to variations in soil depth, an attempt was made to use the data from these quadrats as a standard with which all the stands could be compared. Three hypothetical stands were constructed from the 40 quadrats, and frequencies of species were placed on punch cards in the same way as was frequencies from all the stands. Prairie "A" consists of all 40 quadrats and represents, therefore, a stand having samples from equal areas of thin and deep soil. Prairie "B" was made up of only the 20 quadrats on the thin-soil phase, while "C" consisted of the 20 deep-soil quadrats. It is assumed that a stand consisting entirely of shallow soil will resemble prairie B more than either A or C and a stand having a great variation in soil depth will resemble A the most. A dry lime prairie included in this study should be more like A or B. The particular method used in comparing the various stands with the 3 hypothetical prairies was that of comparing the sum of differences of frequencies of the first 30 species, as used previously.

Three mesic prairies (stands number 15, 49, and 61) resembled C most and B the least as expected. When the dry lime prairies were compared, it was found that they could be divided into 2 groups: those resembling A most, and those resembling B most. The averages of the sums of differences of these groups of stands are given in Table 23.

TABLE 23

A comparison of 3 hypothetical prairies with mesic and dry lime prairies. Results given in average sums of differences of frequencies.

	A (composite-thin and deep-soil phase)	B (thin-soil phase)	C (deep-soil phase)
3 mesic prairies	616	831	448
10 dry lime prairies	450	531	551
12 dry lime prairies	584	495	757

A very few of the dry lime prairies which resemble A the most actually are least like B, although the differences between the resemblances of B and C are very slight. These can be thought of as transitional between mesic and thin-soil stands. A very slight correlation between this order and sum of frequencies of the first 20 species can be demonstrated. This latter figure is 714 for the first group of dry lime prairies (Table 23) and 675 for the second group and is only 440 for the 3 mesic stands. This difference between the 2 groups of dry lime prairies is slight and can be used as a further demonstration of their homogeneity. In fact, if the stands are considered in 4 groups along this gradient (Table 23) and the averages of the sums of differences are converted to a percentage basis, an extremely interesting series of comparisons results. These are shown in Table 24. It seems doubtful that such results would occur with any but a very uniform group of stands.

TABLE 24

Dry lime prairies compared with 3 hypothetical prairies. Five stands are included in each group. Average sums of differences for each group expressed as per cents.

	A	B	C
group 1	28.3	36.0	35.6
group 2	30.3	33.3	36.3
group 3	31.1	28.5	40.4
group 4	32.1	25.5	42.4

Of special interest are those stands which are found in group 1, which can be thought of being somewhat transitional in nature. By the test applied in Table 24 it can be seen that although these stands resemble hypothetical prairie A most, their resemblances to both prairies B and C are about equal. Of the stands in this group, one, number 35, has a relatively large area with soil depths of 14 inches and over. This prairie has a number of species not typical of dry lime stands occurring with quite high frequencies. For instance, the frequency of _Aster laevis_ is 35 per cent, _Phlox pilosa_ is 40 per cent, _Salix humilis_ is 25 per cent, _Bromus Kalmii_ is 45 per cent, _Gentiana puberula_ is 10 per cent, and _Liatris pychnostachya_ is 5 per cent. This stand is located in northern Dane County. Of the 10 stands resembling prairie A in Table 23, 4 are from northern Dane County, 4 are from the Mississippi bluffs, and only 2 are from southern Dane County. This difference, based on a floristic variation with soil depth, can be added to those enumerated in Table 17.

The peculiar position of stand 35 can be seen by examining Table 25. Here it is compared with shallow-soil stands (1, 32, and B) and with deep-soil stands (C and 15). It can be seen that this stand occupies a position between the shallow and deep-soil prairies, although it is more like the thin-soil stands.

TABLE 25

A comparison of stand 35 with certain shallow and deep-soil prairies, expressed in sums of differences of frequencies of the first 30 species.

B and 32 - 435	1 and B - 450	32 and B - 435
1 - 450	32 - 515	1 - 515
35 - 469	35 - 589	35 - 565
C - 650	C - 760	C - 765
15 - 928	15 - 928	15 - 1003

In the following study of prairie number 35, results are based on 100 quadrats measuring 25 cm. on an edge. These quadrats were located along two parallel lines placed on the long axis of this prairie, and the soil depth in the center of each quadrat was recorded. The depth varies from 0 to slightly over 14 inches, the average being 5.4 inches. If 4 inches is used as a dividing point, it is possible to divide the quadrats into two groups, with 52 quadrats in the 0-4 inch class and 48 quadrats in the 4.1-14 inch class. On this basis, the average number of species per quadrat is 6.6 for the first group and 6.1 for the second.

This stand undoubtedly has a greater proportion of its area with soil deeper than that typical for dry lime prairies than any other stand in this study and comes as close to being a transitional prairie as any. Relations between distribution of species and soil depth is shown in Table 26. The frequencies in this table are based on two divisions of the quadrats: the first at 3.5 and 7.5 inches in depth and the second at 4 inches.

When comparisons between Tables 22 and 26 are made, the differences in methods should be remembered. In the one case only two extremes of soil depth are used, while in the other the depth varies gradually from 0 to 14 inches. The first table is made from 40 meter quadrats chosen out of all stands, while the second represents findings from a single stand using 100 small quadrats. In general, however, the results are amazingly similar, lending support to the importance of soil depth as a factor selecting species for this kind of community. Only Sporobolus heterolepis, Coreopsis palmata, and Liatris aspera show discrepancies.

TABLE 26

Variation in species frequencies and soil depth classes in transitional prairie 35.

	Soil depth classes (in inches)				
	0-3.5	4-7.5	8-14	0-4	4-14
Andropogon scoparius	83	52	23	80	40
Anemone patens	4	4	--	4	2
Antennaria sp.	34	22	4	32	14
Arenaria stricta	4	4	--	4	2
Aster ericoides	19	11	15	22	14
Aster linariifolius	34	15	8	32	12
Aster sericeus	40	19	8	40	12
Bouteloua curtipendula	70	40	4	68	22
Carex pennsylvanica	19	26	4	22	12
Liatris aspera	21	7	11	22	8
Liatris cylindracea	21	7	--	20	4
Poa compressa	47	26	8	46	16
Aster azureus	8	--	4	4	2
Petalostemum purpureum	6	--	--	6	--
Potentilla arguta	2	--	--	2	--
Prunus pumila	6	4	--	6	2
Solidago nemoralis	2	--	--	2	--
Viola pedata	11	7	--	8	4
Asclepias verticillata	2	4	--	2	2
Amorpha canescens	17	26	30	18	28
Andropogon Gerardi	23	44	46	24	44

TABLE 26 (continued)

Anemone cylindrica	2	19	11	6	12
Bromus Kalmii	6	44	80	10	62
Cirsium discolor	--	4	4	--	4
Coreopsis palmata	6	33	42	10	36
Lithospermum canescens	--	7	4	--	6
Monarda fistulosa	--	4	4	--	4
Panicum Leibergii	--	4	11	--	8
Panicum oligosanthes var. Scribnerianum	4	11	8	6	8
Petalostemum candidum	--	4	23	2	12
Phlox pilosa	2	11	30	6	20
Salix humilis	4	11	23	4	18
Solidago missouriensis	2	22	27	2	28
Solidago rigida	2	--	8	2	4
Aster laevis	2	--	11	2	6
Sporobolus heterolepis	11	22	53	12	36
Stipa spartea	17	11	11	16	12
Euphorbia corollata	15	15	23	16	18
Panicum perlongum	9	4	8	8	6
Ratibida pinnata	23	19	23	24	20
Pedicularis canadensis	6	11	4	6	8
Ambrosia artemisiifolia	2	4	--	2	2

A further illustration of vegetational consonance with soil depth can be demonstrated by using the same order of stands as used in Table 23 (but omitting the deep-soil stands) and comparing the average sum of differences of frequencies of the first 30 species. An average of 541 is obtained when the first 6 stands are compared with each other, and averages of 542 and 543 are gotten for the following groups of 6 stands. When the first 6 stands of this gradient are compared with the last 6 stands an average sum of differences of 648 is obtained.

The striking similarity shown among both the floristics and environmental factors examined has been the main theme of this section. It should also be emphasized that there is a need for a great deal of further study of the environment of these prairie remnants. The study of the edge of the prairies needs particular attention. Table 27 gives some information regarding actual moisture content of the A horizon of 2 prairies and surrounding woods over a period of 10 days.

The stands used in Table 27 (numbers 19 and 11) offer an excellent opportunity for a more detailed study of moisture conditions throughout the growing season and particularly during the critical periods of drier weather. Aspens have invaded the ridge-top prairie in one case and are invading a part of the steep prairie in the other. On these sites are nearly all the vegetation types of the entire area -- dry lime prairie, mesic prairie, oak opening (pastured), oak and oak-

TABLE 27

Moisture content of A horizon of 2 prairies and adjacent areas over a period of 10 days (results in average percentages)

1.	Dry prairie (southwest-facing slope)	15.0 per cent
2.	Oak woods (north-facing slope)	29.4 per cent
3.	Oak-Hickory woods (at base of prairie)	18.8 per cent
4.	Dry prairie (top of ridge)	13.9 per cent
5.	Aspen woods (adjacent to dry prairie)	14.1 per cent
6.	Mesic prairie (bottom of catena)	24.6 per cent

hickory forest. Results given in Table 27 would indicate that soil moisture is not the critical factor in the distribution of prairie and forest in the more moist part of the growing season. However, this factor is probably of great importance in the drier parts of the season. Work needs to be done on the effect of the critical dry periods on tree seedlings which start growing on the relatively sod-free dry prairies. The distribution of dry prairie and woodland seems to be based on more complex factors than the single one of moisture.

A final factor which this study has not included except as a criterion in choosing sites for inclusion is that of disturbance. It would seem that the nature, intensity, and duration of the disturbance are all very important in determining the prairie-forest distribution. This is certainly a most important factor in determining the persistence of the prairie, although in the case of the dry, thin-soil prairies, this relationship is not so obvious.

Further, glaciation as a factor of disturbance, determining some of the differences between prairies on glaciated and non-glaciated areas, is suggested by this study. This idea implies that the prairie in the Midwest is not of recent origin but actually existed in the Driftless Area during the Cary stage of the Wisconsin ice sheets. The importance of this is discussed later.

Figure 39

Clone of *Helianthus laetiflorus* showing aggregated type of areal distribution.

Figure 40

Quadrat used in determining areal distribution of species. The meter quadrat was subdivided into 16 quadrats by means of piano wire.

A STUDY OF THE AREAL DISTRIBUTION OF SPECIES

One of the important problems concerning grassland vegetation is that regarding the distribution of the component species. The general problem of random versus non-random distribution has been studied and reviewed rather thoroughly by Curtis and McIntosh (1950) and Goodall (1952).

Upon inspecting many stands of prairies it becomes rather evident that many species seem to be quite aggregated in their distribution (Fig. 39). Such species as *Helianthus occidentalis*, *Asclepias verticillata*, and *Geum triflorum* illustrate this tendency to occur in discrete clones quite well. The tendency of *Panicum Leibergii* to be associated with small pockets of deeper soil has been mentioned previously. On the other hand, such species as *Erigeron strigosus*, *Lithospermum incisum*, and *Verbena stricta* appear usually as scattered individuals.

The following discussion attempts to demonstrate the relative nature of the distribution of a number of prairie species. Results were obtained from the use of a specially constructed quadrat in which the square meter was divided into 16 smaller quadrats, each measuring 25 centimeters on an edge. This quadrat (Fig. 40) was used in a total of 20 stands, and the results of this use are here summarized. Frequency can be calculated for the two size quadrats, for 20 of the large meter quadrats and for 320 of the smaller ones. The two frequencies for the two size quadrats will here be referred to as Frequency (F) for the meter and as frequency (f) for the small quadrats. In the following the ratio of the Frequency to the frequency (the F/f) will be used as an indicator of dispersion. Values for this ratio range from 1 to 16. A species which is highly clumped will occur in many more of the smaller quadrats in relation to the occurrence in the large quadrats than will a species which is widely scattered. The former will have a much lower F/f ratio than the latter.

Admittedly this is not a perfect or even a highly sensitive test for the determination of the kind of dispersion of all the species in a stand. One of its obvious faults lies in its combining the factor of commonness and rareness with dispersion. It is doubtful that the ratio has any significant meaning regarding dispersion when the Frequency is over 65 or below 10 per cent. Actually, however, the Frequencies of most of the species fall between these extremes, and in the results which follow only values between these extremes are used. The rare species and the extremely common ones are not included. The method as used is a fairly rapid one, giving information on many species, and the amazingly consistent results in the values of the ratio would indicate that attributes of growth and dispersion are indeed being measured.

Before the method was used extensively in the field, it was tried in the laboratory on an artificial population, made by placing a number of variously colored dots on a large sheet of paper which had been marked into small numbered squares. Some of the "species" were located by means of a random numbers table (Snedecor, 1946), while others were placed in small clustered groups. In each case the numbers of each "species" was recorded. Quadrats used were small, clear plastic squares divided into 16 small squares and placed on the population sheet in a grid system comparable to the location of quadrats in the field. Quadrats of several sizes were used, and it was found that when the size of the small quadrats was equal to the population mean area, the range of Frequencies obtained was from 10 to 85 per cent.

Table 29 summarizes results from the use of the artificial population in which 7 "species" are involved. Of these, the 5 which were located by means of random numbers (A, B, D, F, and G) have ratios ranging from 7.0 to 15.9, and the 2 aggregated ones (C and E) have ratios of 1.3 and 1.2. Two additional species with low Frequencies (10 per cent) illustrate the same pattern -- the randomly located one having a ratio of 11.1 and the aggregated one a ratio of 3.2. In any actual population of plants it should be possible to demonstrate the entire range of the ratios. The gradation of these ratios is shown in Table 29 which has been prepared from all the stands in which the boxed quadrats have been used (20) and for species whose Frequencies ranged from 10 to 65 per cent.

TABLE 28

Results of ratio F/f on an artificial population, using 20 quadrats each of which was divided into 16 square quadrats. The size of the smaller quadrats was equal to that of the population mean area of the "species".

"species"	F (per cent)	density	f (per cent)	F/f
A	85	40	12.2	7.0
B	35	7	2.2	15.9
C	45	238	29.7	1.5
D	75	25	7.5	10.0
E	35	228	26.9	1.3
F	80	26	8.1	9.8
G	55	17	4.0	13.7

TABLE 29

Relative randomness and aggregation of prairie species, based on ratio, F/f, from 2 size quadrats.

A. Species highly random in distribution

Psoralea esculenta	16.0
Erigeron strigosus	15.1
Solidago missouriensis	12.0
Lithospermum incisum	11.8
Ambrosia artemisiifolia	10.8
Anemone patens	10.4
Lobelia spicata	9.8
Verbena stricta	9.3

B. Species relatively random in distribution

Lithospermum canescens	8.4
Rudbeckia hirta	8.4
Potentilla arguta	8.3
Euphorbia corollata	8.0
Linum sulcatum	8.0
Kuhnia eupatorioides	7.3
Physalis virginiana	7.1
Monarda fistulosa	7.0
Heuchera Richardsonii	7.0
Koeleria cristata	6.8
Castelleja sessiliflora	6.8
Aster laevis	6.8

TABLE 29 (continued)

Aster azureus	6.8
Arabis lyrata	6.8
Anemone cylindrica	6.6
Hedeoma hispida	6.5
Solidago rigida	6.1
Artemisia caudata	6.0
C. Species relatively aggregated in their distribution	
Silphium laciniatum	5.7
Petalostemum purpureum	5.4
Dodecatheon Meadia	5.2
Rosa	5.1
Panicum perlongum	4.9
Aster ericoides	4.8
Scutellaria parvula	4.8
Amorpha canescens	4.7
Liatris aspera	4.7
Liatris cylindracea	4.7
Aster ptarmicoides	4.6
Ratibida pinnata	4.6
Sisyrinchium campestre	4.6
Campanula rotundifolia	4.2
Panicum oligosanthes	4.2
Aster sericeus	4.1
Viola	4.0

TABLE 29 (continued)

D. Species aggregated in their distribution

Sorghastrum nutans	3.9
Antennaria	3.9
Arenaria stricta	3.8
Bromus Kalmii	3.7
Phlox pilosa	3.7
Solidago nemoralis	3.6
Sporobolus heterolepis	3.3
Muhlenbergia cuspidata	3.1
Commandra umbellata	3.1
Coreopsis palmata	2.7
Geum triflorum	2.7
Helianthus laetiflorus var. rigidus	2.4
Panicum Leibergii	2.4
Stipa spartea	2.4
Prunus pumila	2.3
Helianthus occidentalis	2.2
Bouteloua hirsuta	2.0
Poa compressa	2.1
Pedicularis canadensis	1.8
Aster oblongifolius	1.7
Asclepias verticillata	1.2

The average ratios for the somewhat arbitrary divisions in this table are: 11.9, 7.2, 4.7, and 2.7. According to this ranking more species of this kind of prairie are aggregated than are randomly distributed. The distribution of the numbers of species in the two extreme groups is highly different; only 8 are classed as highly random, while 21 are in the aggregated group.

Although this study includes no detailed examination of individual species, several factors involved in the tendency toward aggregation can be mentioned. The extreme habitat of these thin-soil areas offers less than favorable sites for most plants. Variations in soil depth in these prairies have been noted, and several of the species which are clumped, such as Bromus Kalmii, Salix humilis, and Panicum Leibergii, seem very definitely to be correlated with small areas of deeper soil. Undoubtedly most of the clumped species are thus distributed because of the prevalence of vegetative reproduction; however, other factors are probably involved also. Such information should be discovered in a careful study of the autecology of these plants. It is hoped that the above pattern of distribution will serve as a base for such an autecological study.

DISCUSSION

This study is concerned with a phytosociological study of numerous dry lime prairie remnants in the prairie-forest region of southwestern Wisconsin. It has been shown that the vegetation of these very similar habitats is remarkably homogeneous.

Because of the highly fragmented nature of undisturbed native plant communities in the area studied, it is difficult to view these often widely separated stands as a part of a once-continuous mass. One of the aims of this portion of the discussion is to point out the necessity of employing such an over-all view. That a plant community must be interpreted in terms of past geology, climates, and biology as well as in terms of present climate, physiography, and land use is, of course, a basic concept in plant sociology.

The fact that a number of workers in forest ecology in this area (Cottam 1949, Curtis and McIntosh 1951) have stated that the climax vegetation is a form of a maple-basswood forest makes the position of the prairie in this region a more complex one than is ordinarily implied by the term ecotone.

The microclimates of the sites studied are among the most xeric ones of the entire region. This fact simplifies the explanation of the dry lime prairies, but it must be remembered that the entire prairie occurred on sites varying from extreme dryness to high moisture content. Furthermore, the facts that even the most xeric of the sites studied have been in an undisturbed condition and that any disturbance tends to alter the composition of the vegetation add complications to the usual harmonious relationship between the environment and a plant community. That the prairie was so well established on such a variety of sites and that the stands studied were so homogeneous lend credibility to the idea that they have existed in the Midwest for a long time. The occurrence of so much prairie in southwestern Wisconsin 100 years ago poses two problems regarding the genesis of the prairie in this area: the original arrival, and the maintenance and spread in the interval of time since its beginnings.

Students of post-glacial climates generally agree that there have been two periods during which the climate has been warmer and drier than the present and that these xerothermic periods occurred from about 5,000 to 1,000 B. C. and from 400 - 1,000 A. D. It was during these periods that the prairies spread eastward and the deciduous forests waned in the prairie-forest region.

The art of pollen analysis has furnished us with much information regarding the stratigraphy of pollen deposits in peat bogs. There seem to be many gaps in the ecological pictures presented and the extent to which the local ecology of the bog is emphasized is not always clear. The role of prehistoric man as an agent in effecting vegetational changes has been largely neglected, due, no doubt, to the difficulty of finding good evidence. This paper has mentioned the possible part man has played in extending the prairie by the use of fire during the times just prior to European man's arrival. However, the very early arrival of man in the Midwest has also been emphasized. In a region as rich in flora and fauna as this it seems unlikely that population pressures did not exist among early peoples. Such population increases would have greatly heightened the amount of burning, which would have produced the same sort of prairie-forest competition as a prolonged drought. The great numbers of tumuli in this region have been mentioned earlier. Vegetational changes indicated by pollen analysis cannot be interpreted by only climatic changes; the activities of prehistoric peoples must also be considered. The use of fire having an accelerated effect in times of moderately dry weather and population pressures complicates the usually accepted single factor, climate, as the controlling force of vegetational change. The presence of numerous relic communities of white pine and maple-basswood within the area of prairies and oak savannahs indicates that the climatic changes could not have exceeded the tolerance ranges of these.

It is not the aim of this discussion to review the results of numerous pollen analysis studies. The general pattern suggested by these will be used in trying to answer the two questions about the prairie. The fact that the climates in the Driftless Area at the height of the ice and during its retreat are not known makes difficult the interpretation of early events in the revegetation picture. The idea that the entire area was revegetated by a series of plant communities in a phalanx-like order ignores the wide variety of habitats made available and the fact that the region was open to plants coming from several directions. The melting of the Cary ice sheet in Wisconsin favored the ingress of plants from the southwest.

Gleason (1923) has expressed the differential invasion of habitats and the very early entrance of the prairie with its short-lived dominants along the exposed, continuous ridges, uplands, and moraines. The extent of a spruce-fir community at the margin of the ice is not clear; however, that this community spread out on the newly exposed lands is evident from pollen analysis studies made throughout the area once covered by Wisconsin ice sheets. The suggestion is made here that both the prairie and the boreal forest spread out from the Driftless Area and ice margins and early established a mosaic pattern. The role that the rivers had in forming a pathway for the entrance of hardwood species even at the early stages of revegetation has also been emphasized by Gleason. An interesting relationship probably exists between the duration of the waning ice with its extensive glacial lakes and the boreal forest.

That pines followed the spruce-fir in a cool but drier climate and that these, in turn, migrated north and gave way to the establishment of an oak complex in the first xerothermic period is not difficult to visualize. The presence of prairies in both the pine and oak periods is easily accounted for by the dry climate. The amoeba-like spread of the prairie at the expense of the forest was accomplished by both droughts and fires, and the early-established mosaic pattern made this change relatively simple, since the prairie did not have to come from hundreds of miles distance but from many local areas.

The following period, a cooler and wetter one, favored the spread of a maple-basswood type of forest from locally favorable sites along waterways onto the prairies and oak forests. Again, it is doubtful that the prairie disappeared. Instead, it contracted, and its existence was aided by physiography and fire. A second xerothermic period followed from about 400 to 1,000 A. D. Again the prairies and oaks were favored and the maple forests reduced in size. In the cooler and wetter period following this dry era, the use of fire as a means of keeping the country open seems to have been a recognized necessity by the native peoples. It was thus that the first European men found the country.

The above sequence is suggested as the probable pattern of vegetational changes in post-glacial times for the Midwest. The presence of the prairie as a part of a vegetational mosaic throughout the post-glacial period and its relation to the over-all climatic changes, physiography and exposure of local sites, and recurring fires have been the main ideas expressed. The two questions regarding origin and maintenance of the prairie have been answered in a very general way. The occurrence of dry lime prairies on the xeric sites extends back into pre-Cary times. These could have acted as a reservoir of prairie flora during cool and wet cycles. This thought brings up the interesting but unanswered question of how the composition of these prairies varied from one climatic extreme to the other.

The dry lime prairies are a part of a flora of a moist to very dry gradient extending over a very large geographic area. Such dry areas with shallow soil can be found throughout the prairie peninsula. Here they extend in an interfingering manner throughout the tall grass prairie and oak complex. One would expect that the site requirements become less important as the mixed grass communities of farther west are approached. Here the tall grass elements appear dispersed in the continuous phase of mixed grass prairies.

That the thin-soil prairies of the prairie peninsula are quite similar in composition and physiognomy can be demonstrated by comparing lists of species from prairies in different parts of this entire area. Such lists are not very numerous. Harvey (1908) lists species from two kinds of prairies, rolling uplands and flood plains, in southeastern South Dakota.

Upon comparing the species of the upland prairie with those of the dry lime prairies in Wisconsin, it is found that 41 species are common to the two areas. Six of the 10 so-called characteristic species are among this list. Jones (1944) lists species found on limestone cliff tops in Adams County, Ohio. He mentions that on these over-drained and over-exposed habitats the vegetation frequently grows as a bunch grass community instead of the closed type of growth on the flat areas. A total of 56 of the Ohio plants are found growing on similar sites in Wisconsin, and these include 5 of the characteristic species. Only 3 characteristic species are common to the 3 widely separated areas: Muhlenbergia cuspidata, Aster oblongifolius, and Kuhnia eupatorioides. A total of 20 species are common to the 3 lists. It must be remembered that the list of Wisconsin plants is based on a great many stands; thus it is assumed that if similar lists were available for the other two areas, the degree of similarity would be increased. Among the species common to South Dakota, Wisconsin, and Ohio are such dry-habitat plants as Andropogon scoparius, Bouteloua curtipendula, Hedeoma hispida, Carex pennsylvanica, Koeleria cristata, Lithospermum canescens, Oxalis violacea, Solidago nemoralis, Verbena stricta, and Viola pedatifida.

Differences in species composition between the dry lime prairies and deep-soil mesic prairies have already been demonstrated. When species lists of South Dakota prairies and limestone bluff prairies of Ohio are inspected, it becomes apparent that they resemble the dry lime prairies of this study rather more closely than the latter resemble near-by mesic prairies. The following species occur on dry lime prairies in South Dakota, Wisconsin, and Ohio, but are entirely absent from 6 deep-soil prairies of southwestern Wisconsin: Bouteloua curtipendula, Muhlenbergia cuspidata, Aster oblongifolius, Kuhnia eupatorioides, Koeleria cristata, Hedeoma hispida, and Verbena stricta. The following, which are absent from the mesic prairies also, are found in 2 out of 3 of the locations for the dry lime stands: Liatris cylindracea, Linum sulcatum, Castelleja sessiliflora, Bouteloua hirsuta, and Lithospermum incisum.

The particular physiography of the sites studied has served as a selecting and unifying agent in determining the homogeneity of the dry lime prairies. Such local differences as the distribution of Muhlenbergia cuspidata in the Driftless Area and near-by glaciated prairies do not invalidate this idea. Also, certain east-west differences, as demonstrated even in the limited area of the present study, would be expected. Although dry cycles and recurring Indian fires are used to explain the mosaic pattern of prairie and forest in the entire prairie-forest region, the dry lime prairies can be explained, at least to a large extent, by the selecting action of the xeric habitats.

The discussion which follows attempts to summarize some of the conclusions based on the phytosociological studies of the prairies studied. The criteria used in choosing the stands naturally limited the sites to a group of highly similar ones as far as physical features are concerned. Presence and frequency data have been used in demonstrating floristic homogeneity.

The master list of species (Table 9) ranks them according to the product of the constancy and average frequency. This is an attempt to interpret a species' importance on an over-all geographic basis as well as on an individual stand basis. The particular order of species thus obtained is considered to be characteristic of dry lime prairies. The similarity between the master list and such other lists based on presence or frequency alone has already been mentioned and is interpreted as an indication of the great similarity among the main species of these prairies. The use of the product of constancy and average frequency is, therefore, a method of refining the order of species. Further combinations could have been used; for instance, the product of constancy, average frequency, and frequency based on the smallest, boxed quadrats would have resulted in a series of much higher numbers, but it is doubtful that the order of species would have been changed. Whether this method would yield meaningful results when applied to a community having a wider variation in size of major species is an unanswered question. The problem of a few species, large but important in affecting the growth and distribution of others, is not an important one in dry lime prairies. Among the first 20 species only _Rosa_ and _Amorpha canescens_ are shrub-like.

The stands have been arranged along a gradient based on the sum of frequencies of the first 20 species. This order is more than a matter of convenience, since high levels of homogeneity can be demonstrated with such variables as numbers of species in quadrats, numbers of species in common in groups of stands along this gradient, and especially with a ratio obtained by dividing the sum of frequencies of species in common by the sum of frequencies of all the species in these groups. Uniformity can also be expressed by the use of the average sum of differences of frequencies of the first 30 species. Variables other than frequencies have been used to demonstrate homogeneity also. Soil pH, calcium, and magnesium are especially similar. The fine, calcareous sandy soil is unusually homogeneous when the finer-size particles are considered. An interesting relation exists between the order of stands along the gradient and the coarsest-size particles. The percentage of this size class for the top, middle, and bottom of this gradient is 12.3, 6.8, and 3.8 respectively. The over-all average of all stands for this size is 6.4 per cent.

Obviously no two stands are exactly alike. Any method for demonstrating similarities or differences will have limitations. When the method is employed consistently, however, the levels of similarity or difference established will have meaning and can be used as a basis for making comparisons.

Using identical methods, it was found that the levels of homogeneity can be increased if stands are grouped on a geographic basis. Three more or less naturally grouped areas--southern Dane County, northern Dane County, and the Mississippi Valley bluffs--have been used in these comparisons. The average of the ratios of sums of frequencies of species in common to a group to the sums of frequencies of all species of the group is changed from 54.4 to 68.5 for the stands along the sum of frequency gradient and the geographic groups respectively. The change in the average sums of differences of frequencies of the first 30 species is from 600.3 to 503.5 for the same considerations. High and low values for these two methods mean just the reverse, hence the above changes for the two methods represents a very similar rise in homogeneity levels.

Certain environmental factors show differences among the 3 geographic areas. For instance, the soil phosphorus of the southern Dane County prairies is much higher than in either of the other groups. This fact, in turn, is correlated with the occurrence of these flat to gently rolling prairies on the Galena-Platteville dolomites. Most of the stands in the northern Dane County group are in glaciated territory, although the individual sites are similar to the non-glaciated ones. The Mississippi Valley bluff prairies are very much steeper than the rest. Both of the two latter groups differ from the southern Dane County group in having greater variations in soil depth.

The above demonstrated differences do not explain definitely why the levels of homogeneity rise when vicinal stands are considered. Many of the differences will depend on autecological studies not yet made. Demonstrated differences should serve as a guide for planning such experimental studies. In addition to the apparent relationship to the environment, the factor of history or time is involved. This discussion has presumed the existence of the prairie in the Midwest not only throughout post-glacial times but even in the Driftless Area during the Cary ice sheet. Any plant community existing on such suitable sites would tend, with the passage of time, to more closely resemble adjacent stands than those farther removed.

The results of mechanical analyses and soil-depth studies show a definite trend of those stands with a very high sum of frequencies of all species toward a transitional type of prairie. Such stands, though fitting the field criteria employed, have a more varied flora because they have, usually only in portions of the stand, deeper soil. These stands resemble transitional prairies more than either uniformly typical dry lime or mesic prairies. Only the highly fragmented nature of the prairie remnants prevents one from demonstrating the transition from a dry lime to transitional to deep-soil mesic prairie in any one spot. Although the first of these communities may exist on the top and slope of a hill, the mesic prairie is now invariably a cornfield.

In conclusion, a word about the future of these extremely interesting and beautiful plant communities seems in order. The impending disturbance of every last bit of ground by man and his cattle makes the future of many of these stands very precarious. Since this study was begun several prairies have been destroyed. The fact that the dry lime prairies occur on land largely worthless for pasture should make their preservation rather simple. On the other hand, only the ecologically minded or a very few of the public understand and appreciate the significance of these remnant prairies. To a depressingly large number of people these small "weed patches" are generally worthless.

Actually, these small prairies are museum-pieces of an America that no longer exists. They have witnessed the whole pageant of post-glacial history of the Midwest. They are eminently worthy of preservation. There is still time for the prevention of the last portion of Featherstonhaugh's (1847) prophecy - - - "for the American population will soon drive the Indian after the buffalo, and the cultivated grasses will take the place of the wild ones."

SUMMARY

Sixty-four dry lime prairies in the prairie-forest border region of southern Wisconsin have been studied. Species presence lists have been made for all stands, and for 41 stands frequency data based on 20 meter quadrats per stand are available. Twenty of the latter stands have been studied by means of meter quadrats divided into 16 smaller quadrats.

The stands consist of undisturbed prairie vegetation growing in skeletal soils on gravelly ridges of the kettle moraine of southeastern Wisconsin and on numerous dolomite-capped hills in southern and western Wisconsin. Ninety per cent have a south to southwest exposure, and by field determinations the soil pH is almost consistently 8.0.

A master list has been prepared by ranking the species according to the product of their constancy and average frequency. One hundred sixty-four species have been ranked this way, and an additional 59 have been ranked according to presence. The ten most important species according to this ranking order are: Andropogon scoparius, Bouteloua curtipendula, Andropogon Gerardi, Aster sericeus, Euphorbia corollata, Amorpha canescens, Solidago nemoralis, Panicum perlongum, Petalostemum purpureum, and Sporobolus heterolepis.

A great deal of uniformity is demonstrated by lists of major species ranked according to frequency, presence, and

constancy. The fact that the stands are very homogeneous is further shown by the use of a gradient based on the sum of frequencies of the first 20 species. When groups of stands along this gradient are considered, homogeneity is extended to such variables as numbers of species per stand, number of species per quadrat, and number of species common to the groups. When the ratio of the sum of frequencies of species common to a group of stands to the sum of frequencies of all species in the group is considered along this gradient, the following series is obtained: 57.9, 62.2, 59.7, 51.8, 49.8, and 45.0. A similar measure of homogeneity is demonstrated when the sum of differences of the frequencies of the first 30 species is used.

Uniformity exists also among such soil factors as pH, calcium, magnesium, and potassium. Slope, exposure, bedrock and glacial geology, depth and mechanical analysis of soil have also been studied. Data taken at random from two extremes of soil depth have been used as a standard for comparing stands. The various stands are evenly divided among those resembling the thin-soil phase and the phase having both shallow and deep soil. The latter stands are richer floristically than those having a uniformly thin soil and have the higher sums of frequencies. Although the percentage composition of the finer size soil particles is remarkably uniform, the coarsest size particles show a correlation with the sum of frequency gradient.

It is possible to increase levels of homogeneity when vicinal stands are considered. Average ratios of the sum of frequencies of species in common to the sum of frequencies of all species in a group change from 54.4 to 68.5, while the average sums of differences of frequencies change from 600.3 to 503.5. Only a few and not highly important species show any change in presence or frequency when an east to west direction is considered. In the area studied *Muhlenbergia cuspidata* and *Psoralea esculenta* are absent from areas once covered by Cary ice. Jaccard's coefficient of community has been used in demonstrating differences among stands located within the limits of the Cary ice and progressively farther away. Variations in the average coefficients when this order of stands is considered are 55.8, 45.4, and 42.4. It is postulated that the prairie has existed in the prairie-forest border region not only throughout post-glacial times but actually existed in the Driftless Area during the Third Wisconsin. The mosaic pattern of vegetation, therefore, was established early, and the prairie spread out from physiographically favorable sites during the xerothermic periods. The use of fire as an agent in spreading and maintaining the prairie throughout post-glacial times has been emphasized.

The areal distribution of prairie plants has been studied. A ratio of the frequencies as calculated from 2 size quadrats (20 meter quadrats each containing 16 small contiguous ones) has been used. A high ratio is indicative of a random, non-aggregated distribution, and a low ratio indicates an aggregated type of distribution. Species have been ranked as highly random (only 8 in number), relatively random (18), relatively aggregated (17), and aggregated (21).

The presence of the prairie in southwestern Wisconsin has been used to illustrate the principle that a present-day plant community is the result of many interacting forces. These include past and present climates, geology, physiography, soils, and biotic factors including both prehistoric and present-day man. The voluminous literature of early observations on the prairie, native populations, and the use of Indian fires has been summarized to clarify further the ecological position of the prairie in the Midwest.

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APPENDIX A

Location of stands studied. All counties are in Wisconsin unless otherwise stated.

Stand Number	County	Location	How Studied	Comments
1	Dane	T5NR6E Sec. 13	boxed quadrats	
2	Dane	T5NR6E Sec. 11	quadrats	
3	Dane	T5NR6E Sec. 36	quadrats	
4	Green	T4NR6E Sec. 11	quadrats	
5	Dane	T5NR7E Sec. 30	quadrats	
6	Dane	T5NR6E Sec. 13	quadrats	
7	Dane	T5NR6E Sec. 13	quadrats	
8	Dane	T5NR6E Sec. 23	quadrats	
9	Green	T4NR6E Sec. 4	boxed quadrats	
10	Dane	T8NR6E Sec. 15	boxed quadrats	
11	Dane	T8NR6E Sec. 27 and 28	boxed quadrats	
12	Dane	T8NR8E Sec. 23	boxed quadrats	
13	Iowa	T8NR5E Sec. 19	boxed quadrats	
14	Green	T4NR6E Sec. 10	boxed quadrats	

Stand Number	County	Location	How Studied	Comments
16	Green	T2NR8E Sec. 2	boxed quadrats	
17	Green	T4NR6E Sec. 1	boxed quadrats	
18	Dane	T5NR6E Sec. 24	boxed quadrats	
19	Dane	T8NR7E Sec. 2	boxed quadrats	
20	Green	T3NR8E Sec. 36	boxed quadrats	
21	Columbia	T10NR8E Sec. 8	quadrats	cedar glade and prairie
22	Green	T2NR9E Sec. 33	presence only	
23	Sauk	T9NR5E Sec. 34	quadrats	
25	Dane	T9NR9E Sec. 20	presence only	
26	Columbia	T11NR9E Sec. 17	presence only	
27	Columbia	T11NR8E Sec. 22	presence only	
28	Dane	T9NR9E Sec. 33	boxed quadrats	
29	Dane	T8NR9E Sec. 4	presence only	
30	Dane	T8NR7E Sec. 1	presence only	
31	Dane	T7NR8E Sec. 6	presence only	
32	Columbia	T10NR8E Sec. 27	boxed quadrats	
33	Columbia	T10NR8E Sec. 25	quadrats	

Stand Number	County	Location	How Studied	Comments
34	Dane	T9NR9E Sec. 2	presence only	
35	Columbia	T10NR9E Sec. 31	boxed quadrats	unusually rich--transition between dry lime and mesic
36	Dane	T9NR8E Sec. 5	quadrats	
37	Crawford	T8NR6W Sec. 18	quadrats	extensive, steep prairie
38	Crawford	T10NR6W Sec. 35	presence only	
39	Trempealeau	T18NR9W Sec. 19	presence only	ridge along crest of Trempealeau Mt.
40	Trempealeau	T18NR9W Sec. 20	boxed quadrats	Brady's Bluff unusually rich and extensive
41	Winona, Minnesota	T19NR8W	boxed quadrats	Garvin Heights State Park--extremely rich
42	Dane	T7NR7E Sec. 22	boxed quadrats	
45	Dane	T5NR7E Sec. 19	presence only	edge of lime quarry
46	Green	T4NR6E Sec. 1	presence only	
47	Dane	T8NR7E Sec. 35	presence only	prairie being invaded by <u>Cornus</u> and <u>Rhus</u>.
50	Grant	T6NR3W Sec. 4	presence only	
52	Columbia	T10NR8E Sec. 36	presence only	
53	Dane	T9NR8E Sec. 8	presence only	

Stand Number	County	Location	How Studied	Comments
54	Waukesha	T6NR17E Sec. 35	quadrats	kettle moraine area
55	Waukesha	T6NR17E Sec. 36	presence only	kettle moraine area
57	Dane	T8NR6E Sec. 20	presence only	
58	Richland	T9NR2E Sec. 34	presence only	
60	Sauk	T9NR3E Sec. 36	boxed quadrats	very extensive
62	Grant	T3NR4W Sec. 32	boxed quadrats	
63	Grant	T3NR6W Sec. 13	boxed quadrats	bluffs in Nelson Dewey State Park
64	Palisades Park, Ill.		presence only	prairie openings on bluff top
65	along highway 9, state of Iowa		presence only	
66	Barn Bluff, Red Wing, Minn.		boxed quadrat	unusually rich and extensive
67	Pierce	T25NR18W Sec. 18	presence only	
70	Winona, Minnesota	near Weaver, Minn.	quadrats	
71	Buffalo	T22NR13W Sec. 6	quadrats	
73	Pepin	T23NR15W Sec. 18	quadrats	
74	Pierce	T24NR16W Sec. 23	presence only	
75	Winona, Minnesota	Whitewater Game Refuge	quadrats	extremely extensive

Stand Number	County	Location	How Studied	Comments
76	St. Croix	T28NR19W Sec. 25	quadrats	
77	Pierce	T27NR19W Sec. 18	quadrats	
49	Grant	T2NR1W Sec. 36	quadrats	mesic prairie used for comparative purposes
15	Rock	T2NR13E Sec. 28	quadrats	mesic prairie used for comparative purposes
61	Iowa	T5NR3E Sec. 5	quadrats	mesic prairie used for comparative purposes

APPENDIX B

A. Field sheet on which data were recorded.

B. Sheets on which data were summarized.

Date.........

Prairie survey- field notes
Station no.................

	1	2	3	4	5	6	7	8	9	10
Ambrosia art.										
Amorpha canes.										
Androp. furc.										
Androp. scop.										
Artimes. caud.										
Asclep. vert.										
Aster ericoid										
Aster ptarmic										
Aster seric.										
Boutel. curtip										
Commandra umb.										
Coreopsis pal.										
Euphorbia cor.										
Helianth occid										
Helianth rigid										
Koeleria crist										
Kuhnia eupat.										
Liatris asper										
Liatris cylind										
Lithosp canes.										
Lithosp incis										
Monarda fist.										
Meuhlen. cusp										
Panicum leiber										
Panicum perlong										
Petalost. purpur										
Physalis										
Ratibida pinnat										
Rosa										
Rudbeckia hirt										
Solidag missou										
Solidag nemoral										
Sporobolus het.										
Sorghastrum nut.										
Stipa spartea										
Viola										

PRAIRIE SURVEY TYPE:

STATION NO.																							
Acer negundo																							
Acerates floridana																							
A. lanuginosa																							
A. viridiflora																							
Achillea millefoli																							
Agoseris cuspidata																							
Agropyron subsecun																							
Allium canadense																							
A. cernuum																							
Ambrosia artemisif																							
A. psilostachya																							
Amorpha canescens																							
Amphicarpa monoica																							
Andropogon furcatu																							
A. scoparius																							
Anemone canadensis																							
A. cylindrica																							
A. patens																							
A. quinquefolia																							
A. virginiana																							
Antennaria sp.																							
Apios tuberosa																							
Apocynum androsaem																							
A. cannabinum																							
Aquilegia canadens																							
Arabis lyrata																							
Arenaria stricta																							
Aronia melanocarpa																							
Artemisia caudata																							
A. ludoviciana																							
A. serrata																							
Asclepias amplexic																							
A. incarnata																							
A. ovalifolia																							
A. purpurascens																							
A. sullivantii																							
A. syriaca																							
A. tuberosa																							
A. verticillata																							
Aster azureus																							
A. ericoides																							
A. laevis																							
A. linariifolius																							
A. novae-angliae																							
A. oblongifolius																							
A. pilosus																							
A. ptarmicoides																							
A. sagittifolius																							
A. sericeus																							
A. umbellatus																							
Astragalus candens																							
Aureolaria grandifl																							

PRAIRIE SURVEY TYPE:

STATION NO.																							
Baptisia leucantha																							
B. leucophaea																							
Besseya bullii																							
Blephilia ciliata																							
Bouteloua curtipen																							
B. hirsuta																							
Brauneria pallida																							
Bromus kalmii																							
Cacalia atriplicif																							
Cacalia suaveolens																							
C. tuberosa																							
Calamagrostis cana																							
Callirhoe triangul																							
Calopogon pulchell																							
Carex Muhlenbergii																							
C. pennsylvanica																							
C. vulpinoidea																							
Castilleja coccine																							
C. sessiliflora																							
Ceanothus american																							
Celastrus scandens																							
Cicuta maculata																							
Cirsium discolor																							
C. hillii																							
C. undulatum																							
Comandra umbellata																							
Convolvulus sepium																							
Coreopsis palmata																							
Cornus racemosa																							
Corylus americana																							
Crataegus sp.																							
Cypropedium candiu																							
C. pubescens																							
Desmodium canadens																							
D. illinoense																							
Dodecatheon meadia																							
Draba caroliniana																							
Dryopteris thelypt																							
Elymus canadensis																							
E. virginicus																							
Equisetum arvense																							
E. hyemale																							
E. laevigatum																							
Erigeron philadelp																							
E. pulchellus																							
E. ramosus																							
E. yuccifolium																							
Eupatorium altissi																							
Euphorbia corollat																							
Fragaria virginian																							
Galium boreale																							
G. tinctorium L.																							

PRAIRIE SURVEY TYPE:

STATION NO.																							
Psoralea esculenta																							
Pteridium latiuscu																							
Pycnanthemum virgi																							
Pyrus ioensis																							
Quercus macrocarpa																							
Ratibida pinnata																							
Rhus glabra																							
R. radicans																							
Rosa																							
Rudbeckia hirta																							
R. subtomentosa																							
Salix sp.																							
Sanicula sp.																							
Saxifraga pennsylv																							
Scleria triglomera																							
Scutellaria parvul																							
Selaginella rupest																							
Senecio aureus																							
Silene antirrhina																							
S. stellata																							
Silphium integrifo																							
S. laciniatum																							
S. perfoliatum																							
S. terebinthinaceu																							
Sisyrhincium campe																							
Smilacina stellata																							
S. racemosa																							
Solidago altissima																							
S. graminifolia																							
S. juncea																							
S. missouriensis																							
S. nemoralis																							
S. riddellii																							
S. rigida																							
S. serotina																							
S. speciosa																							
Sorghastrum nutans																							
Spartina pectinata																							
Specularia perfoli																							
Spiraea alba																							
Spiranthes ochrole																							
Sporobolus cryptan																							
S. heterolepis																							
S. vaginiflorus																							
Stachys palustris																							
Steironema ciliatu																							
S. lanceolatum																							
Steironema quadrif																							
Stipa spartea																							
Taenidia integerri																							
Tephrosia virginia																							
Thalictrum dasycar																							

PRAIRIE SURVEY TYPE:

STATION NO.																							
Thaspium aureum																							
Tradescantia ohioe																							
Triosteum perfolia																							
Valeriana edulis																							
Verbena hastata																							
V. stricta																							
Vernonia fascicula																							
Veronicastrum virg																							
Vicia americana																							
V. angustifolia																							
V. villosa																							
Viola pedata																							
V. petatifida																							
V. sagittata																							
Vitis vulpina																							
Zigadenus elegans																							
Zizia aptera																							
Z. aurea																							
Additional sp:																							

PRAIRIE SURVEY

TYPE:

STATION NO.																							
Lupinus perennis																							
Lycopus americanus																							
L. uniflorus																							
Lysimachia quadrif																							
Lythrum alatum																							
Monarda fistulosa																							
Monarda punctata																							
Muhlenbergia racem																							
Napaea dioica																							
Oeonthera biennis																							
O. pumila																							
O. rhombipetala																							
Onoclea sensibilis																							
Orobanche fascicul																							
O. uniflora																							
Oxalis violacea																							
Oxybaphus nyctagin																							
Oxypolis rigidior																							
Panicum leibergii																							
P. perlongum																							
Panicum praecocius																							
P. scribnerianum																							
P. virgatum																							
Parnessia carolini																							
Parthenium integri																							
Pedicularis canade																							
P. lanceolata																							
Pentstemon digital																							
Petalostemum candi																							
P. purpureum																							
Phalaris arundinac																							
Phlox glaberrima																							
P. pilosa																							
Physalis heterophy																							
P. subglabrata																							
P. virginiana																							
Plantago Rugelii																							
Polemonium reptans																							
Polygala polygama																							
P. sanguinea																							
P. senega																							
P. verticillata																							
Polygonatum commut																							
Polytaenia nuttall																							
Populus tremuloide																							
Potentilla arguta																							
Potentilla canaden																							
P. fruticosa																							
Prenanthes alba																							
P. racemosa																							
Prunella vulgaris																							
Psedera vitacea																							

PRAIRIE SURVEY

TYPE:

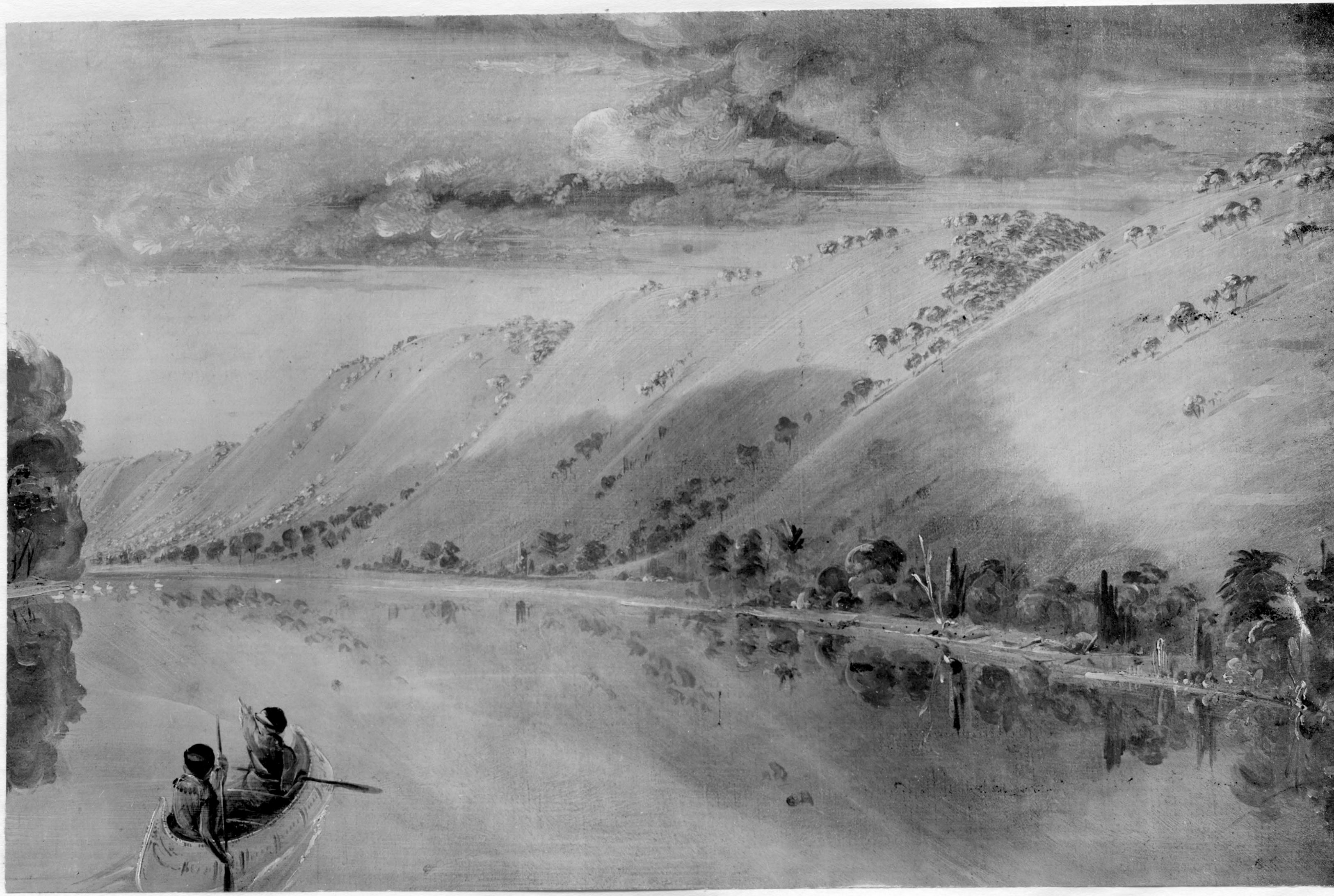
STATION NO.																							
Gaura biennis																							
Gentiana andrewsii																							
G. procera																							
G. puberula																							
G. saponaria																							
Geranium maculatum																							
Gerardia aspera																							
G. gattingeri																							
Geum triflorum																							
Gnaphalium obtusif																							
Grindelia squarros																							
Habenaria leucopha																							
Hedeoma hispida																							
Helianthemum sp.																							
Helianthus grosses																							
H. occidentalis																							
H. rigidus																							
H. strumosus																							
Heliopsis scarbra																							
Heuchera richardso																							
Hieracium canadens																							
H. longipilum																							
Hierochloe odorata																							
Houstonia caerulea																							
H. longifolium																							
Hypoxis hirsuta																							
Hystrix patula																							
Iris virginica																							
Koeleria cristata																							
Krigia biflora																							
Kuhnia eupatorioi																							
Lactuca canadensis																							
L. ludoviciana																							
Lathyrus ochroleuc																							
L. palustris																							
L. venosus																							
Lechea tenuifolia																							
Leptoloma cognatum																							
Lespedeza capitata																							
Liatris aspera																							
L. cylindracea																							
L. liqulostylis																							
L. pycnostachya																							
L. spicata																							
Lilium michiganens																							
L. philadelphicum																							
Linum sulcatum																							
Lithospermum canes																							
L. croceum																							
L. incisum																							
Lobelia Kalmii																							
L. spicata																							

APPENDIX C

Miscellaneous photographs

of prairies

A. An early picture of dry lime prairies, from Catlin's 1848 collection. # 322. Madame Ferrebault's Prairie from the river above; the author and his companion descending the river in a bark canoe, above Prairie du Chien, Upper Mississippi; beautiful grass-covered bluffs.



Two steep bluff prairies. The top one is Brady's Bluff, Perrot State Park, Tremealeau County, along the Mississippi River. The bottom one is near Spring Green, Sauk County, along the Wisconsin River.

The effect of grazing on native prairie vegetation. The top picture is from southern Dane County, and the bottom is from the Dane Prairie, northern Dane County

A "soil profile" of a dry lime prairie showing the skeletal nature of the soil and its relation to the bed rock.

The wooded edge of the prairie is usually very abrupt. Prairie near Cassville, Grant County, along the Mississippi River.

Open grown oak in pasture at the edge of prairie # 19, Dane County. The prairie occupies the thin-soil, exposed area in the foreground.

Aspen invading the south-facing portion of prairie # 19.

Approved John T. Curtis

Date June 3, 1954