Vegetation of Iowa

H. S. Conard

State University of Iowa
Studies in Natural History

G. W. MARTIN, *Editor*

THE VEGETATION OF IOWA

AN APPROACH TOWARD A PHYTOSOCIOLOGIC ACCOUNT

HENRY S. CONARD, Ph.D., Sc.D.

Study Series No. 424

VOLUME XIX NUMBER 4

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THE VEGETATION OF IOWA

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Apologia

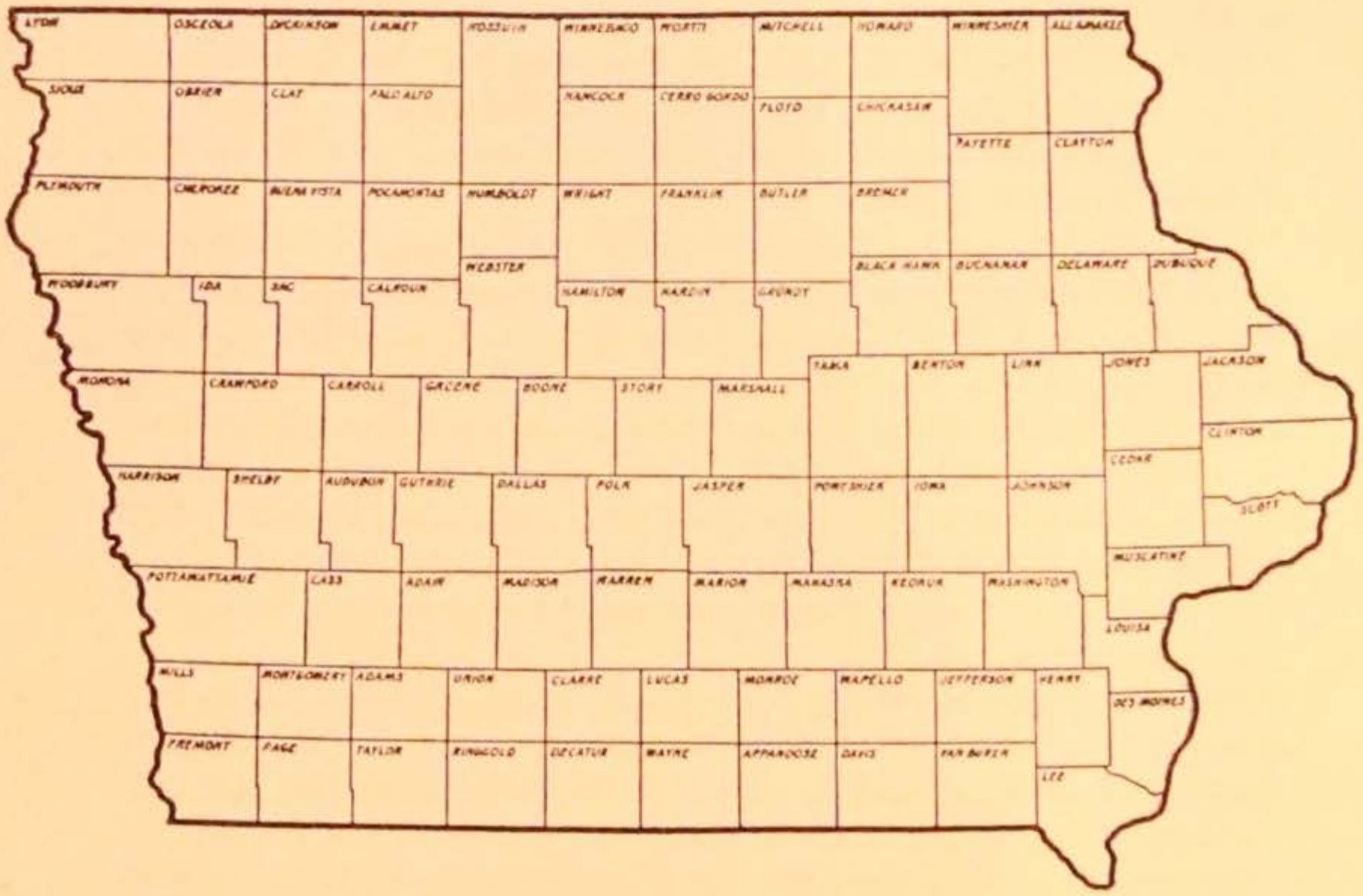
Twenty years ago we hoped that Professor Bohumil Shimek, who knew the vegetation of Iowa as no one has known it before or since, would write down his observations and mature conclusions on the subject. Time caught up with the Professor, and he died in 1937, having completed only the first part of his undertaking. This covers the environmental factors. The paper was published as a Bulletin of the University (Shimek 1948).

From time to time I have been urged to describe the vegetation of Iowa as I have known it since 1906, in lieu of Shimek's unfinished work. Though I have observed topography and plant life in every county of the State, and have collected mosses in 98 of the 99 counties, I feel that my knowledge is gravely inadequate for the task assigned. Nevertheless I could readily agree that a description must be written as soon as possible, and I have yielded to persuasion, especially that of Professor Robert B. Wylie, whose encouragement has really kept the work going. I have insisted that the treatment must be at least quasi-sociological.

Help has been abundantly forthcoming from my wife, Louisa Sargent Conard, from Professor G. W. Martin, Dr. R. F. Thorne, Professor J. M. Aikman, and the late Doctors W. A. Anderson and Ada Hayden. The support of the Graduate College and the Botany Department of the State University of Iowa was essential to the project. To all of these much thanks.

HENRY S. CONARD

January 1952.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CLAY
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HANCOCK
CERRO GORDO
FLOYD
CHICKASAW
PLYMOUTH
CHEROKEE
BUENA VISTA
POCAHONTAS
HUMBOLDT
WRIGHT
FRANKLIN
BUTLER
BREMER
FAYETTE
CLAYTON
WEBSTER
BLACK HAWK
BUCHANAN
DELAWARE
DUBUQUE
WOODBURY
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CALHOUN
HAMILTON
HARDIN
GRUNDY
MONONA
CRAWFORD
CARROLL
GREENE
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MONROE
MARELLO
JEFFERSON
HENRY
DES MOINES
FREMONT
PAGE
TAYLOR
RINGGOLD
DECATUR
WAYNE
APPANOOSE
DAVIS
VAN BUREN
LEE

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Introduction

Environment.—In a posthumous paper by the late Professor Bohumil Shimek, Iowa as a home for plants has been thoroughly described. Abundant data and documentation are provided. Therefore, by way of introduction to the present essay on the vegetation itself it is only necessary to touch upon the topics usually treated in a description of environment.

Topography. Since the lowest point in Iowa is 477 feet above sea level, and the highest is 1675 feet, and these are three hundred miles apart, local relief is always relatively slight. The river valleys are indicated by a map of watersheds (**Fig. 1**). In the northeastern "driftless area," the valleys are abrupt, deep and narrow, and outcrops and ledges of sandstone, limestone and dolomite are very general.

Geology. Aside from the very local influence of cliffs and ledges, bedrock is without effect upon the vegetation of Iowa. On the other hand, the Pleistocene glacial drifts and loesses are of prime importance. They furnish the parent material of nearly all soils, and have much to do with topography and drainage. The glacial map (**Fig. 2**) must be kept constantly in mind.

Soil. While the prairie soils are typical chernozems or prairyerths, and the eastern woodland soils are "gray-brown podzolic" soils, the local conditions have given rise to some hundreds of kinds of soil as recognized by present day pedologists. A recent bulletin from Iowa State College (**1949**) explains that an entirely new classification of Iowa soils is in process of development. This bulletin recognizes a major unit, the Soil Association, made up of many Types. The relations of these may be illustrated by a block diagram from that bulletin (**Fig. 3**). Recent studies have shown a high degree of correlation between vegetation and soils as now understood. The results of these studies are not yet available.

Climate. Iowa has a mid-latitude continental climate with cold winters and hot summers, with no dry season, but with the wettest month in late spring and the driest in late winter, and a relatively dry autumn. Very similar climates, soils (loess) and vegetation (grassland) are found only in southwestern Ukraine and adjacent Bessarabia and Rumania, and southwest of Mukden in Manchuria. Corn (maize) is the dominant crop in the European locality, soy beans in the Manchurian.

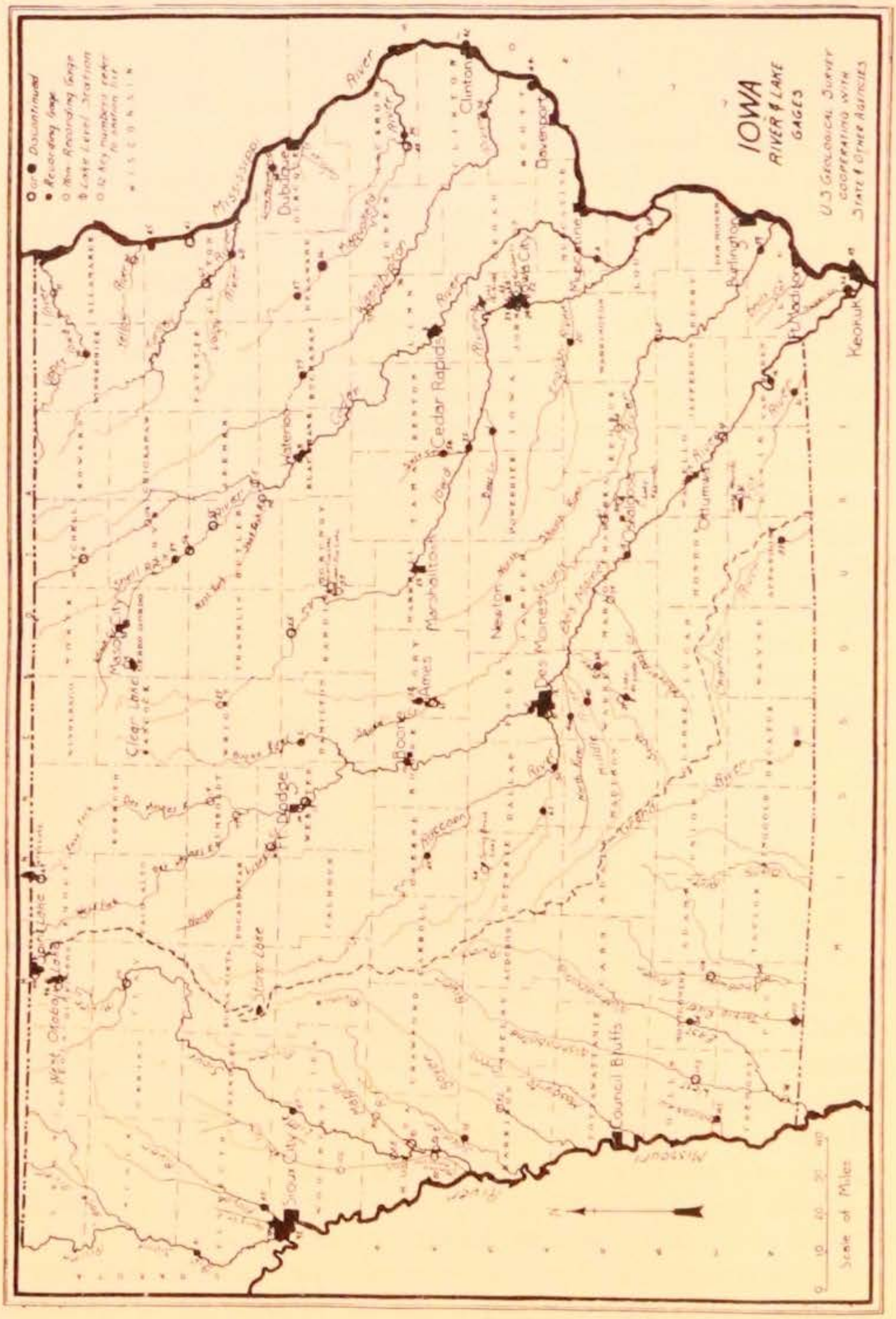


Fig. 1. Drainage basins of Iowa. Courtesy of the Iowa Geological Survey and the U. S. Geological Survey.

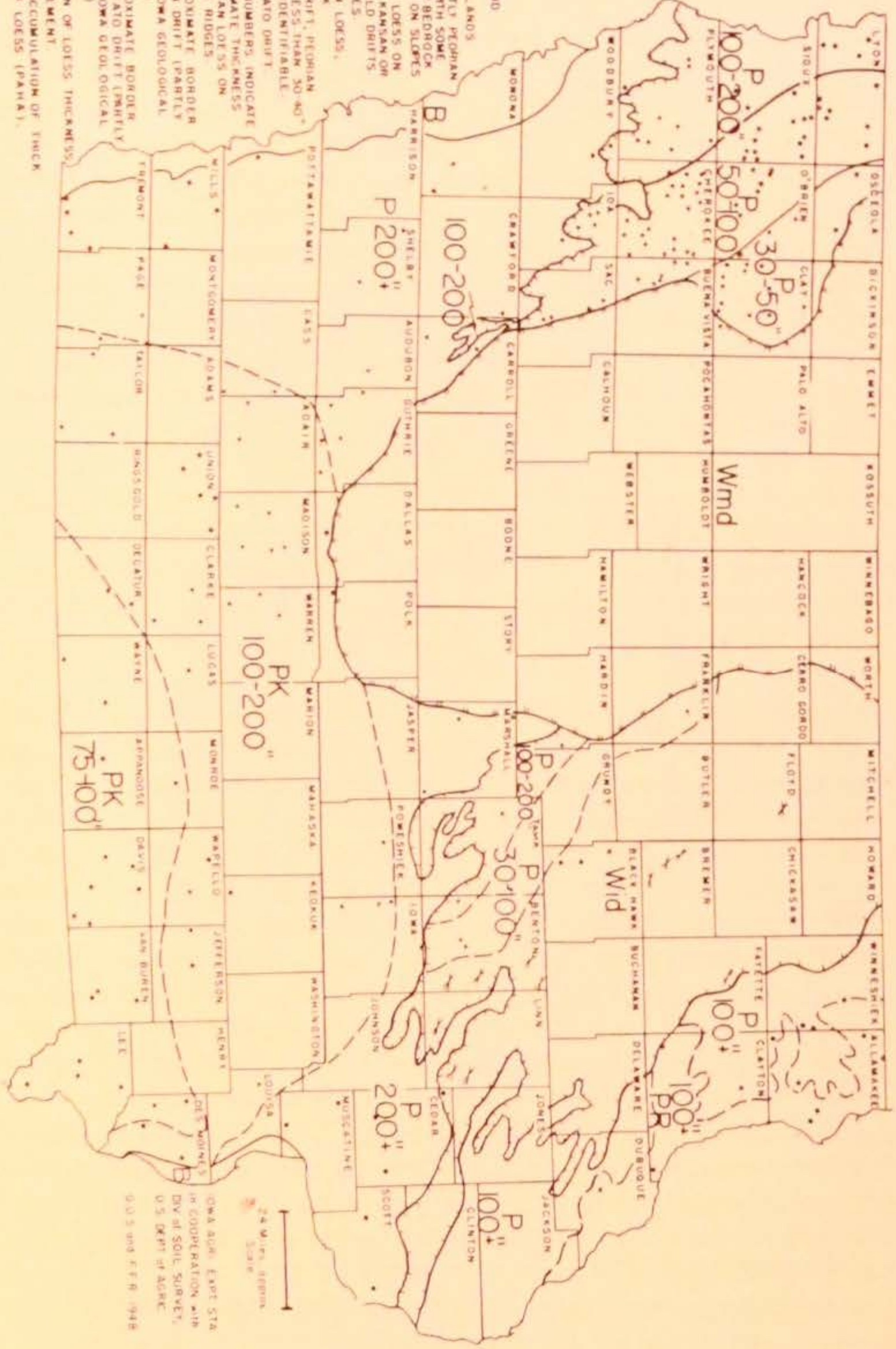


Fig. 2. Glacial drifts and soil materials, after Riecken & Smith 1949.

In brief, Iowa is a grassland with forests along the major streams. Familiarity with the forest map (**Fig.4**), the glacial map (**Fig. 2**) and the drainage map (**Fig. 1**) will be assumed in the following pages.

Floristics. The flora of Iowa has received attention from the time of the first explorers. Parry's list (Owen **1852**; Ellsworth **1922**), based on collections made in 1847 near Davenport, and on a trip to near Des Moines (Parry **1878**), seems to be the first on record. "Complete" lists of the vascular plants have been published by Greene (**1907**), Cratty (**1933**) and Conard (**1951**). The mosses and liverworts were listed by Conard (**1945, 1946**), the algae by Prescott (**1931**), the parasitic fungi by Gilman and Archer (**1929**), the Myxomyeetes by Macbride and Martin (**1934**). Lists of other groups, the floras of several counties and lesser areas, and nearly everything else about the plant life of Iowa will be found in annual reports and special bulletins of the State Geological (and Natural History) Survey, in the proceedings of the Iowa Academy of Science (fifty year index in volume 51; Drexler **1945**), the Natural History publications of the State University, the Iowa State College Journal of Science, and the shelves of theses and dissertations in the libraries of the State College and University. Large herbaria are maintained at the State College and University, by Mr. David L. Savage at Mount Pleasant, and by the Davenport Academy of Science.

Floristics took an ecological slant at about the turn of the century. Plants of limited areas were listed by habitats. Pammel (**1902**) distinguished a number of habitats in western Iowa with the species found in each. He pointed out the changes in flora from one habitat to another, and corresponding differences in topography and soils. He described in similar terms the flora of northern Iowa peat bogs (**1909**). Hayden (**1918**) described communities in a "prairie province" in central Iowa according to habitat, and Tolstead (**1938**) treated similarly the flora of northeastern Iowa. The most exhaustive works of this kind are Shimek's Plant Geography of the Okoboji Region (**1915**) and Hayden's survey of Clay and Palo Alto Counties (**1942**). Aikman and Gilly (**1949**) listed the woody plants at several places along the Des Moines and Missouri Rivers. Shimek envisioned a Plant Geography of Iowa, the first part of which was recently posthumously published (**1948**). His field notebooks are at the State University. From these field notes the lists of plants have been sorted out by counties, and in some cases tabulated as plants of woodlands, prairie, swamps etc., rocks, sand and weeds. These lists have been freely drawn upon for the present study.

We now need to build upon these foundations by the methods of

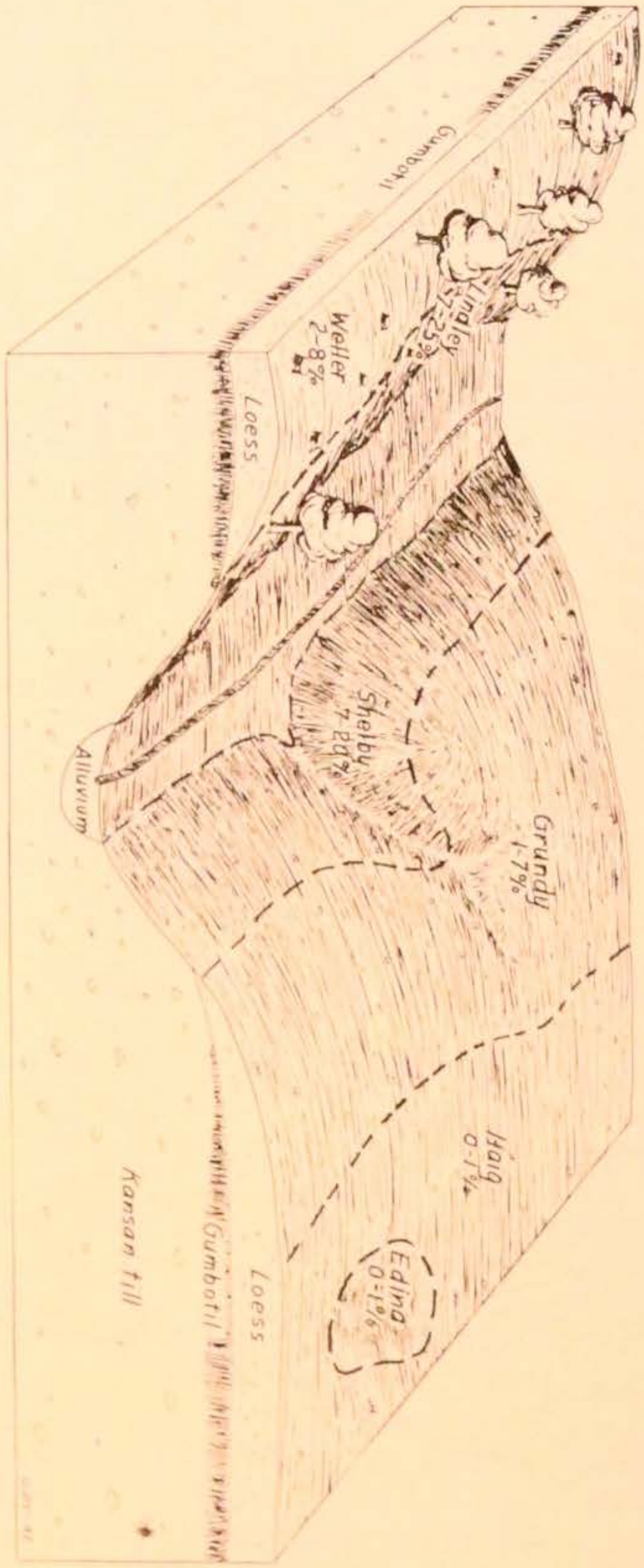


Fig. 3. Relation of soils to topography and parent material, after Riecken & Smith 1949.

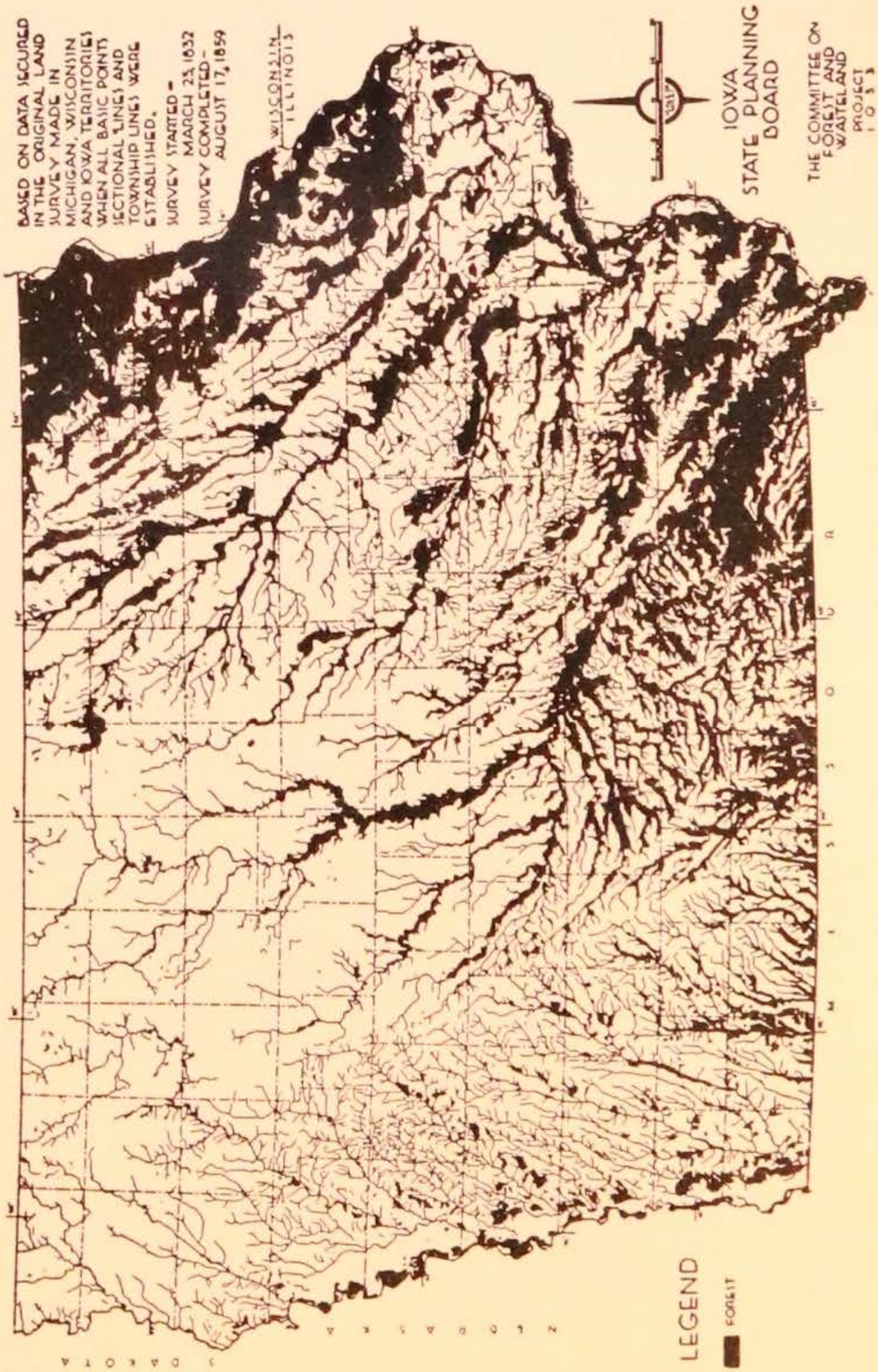


Fig. 4. Original forests (black). Courtesy of Iowa State Planning Board.

plant sociology. It is our aim herein to piece together the available data into a preliminary sociological account of The Vegetation of Iowa,—preliminary and tentative because the studies necessary for an adequate treatment have not been made. This is an outline for such studies.

CHAPTER I

Woodlands

Woodlands and grasslands covered the surface of Iowa in the proportion of about 1 to 7 when the white man came (**Fig. 4**). Bordering the woodlands there was often a strip of shrubland. There are also in Iowa plants that inhabit both still and running waters. And on cliffs and rocks other kinds of plants find foothold. With the advent of agriculture and grazing distinct weed floras have come in. Thus many kinds of vegetation occur within the State.

Wherever plants grow each individual comes into various relations with other individuals. These relations may be designated as social, no matter whether they are helpful or harmful or neutral. Thus plants are found in social groups, societies or communities. According to the floristic composition of the groups we have

Woodland communities
Shrubland communities
Grassland communities
Emersed aquatic communities
Submersed aquatic communities
Moss and lichen communities of rocks, soil or bark
Fern and flower communities of rocks and cliffs
Weed communities
Communities of cultivated plants

WOODLAND COMMUNITIES

Tree communities in Iowa are closely related to rivers and river valleys, so that we nearly always find a gradual transition from the willow associations of river-banks to the bur oak associations on the upper slopes. We find in eastern Iowa a regular series:

Willow association
Elm association; Elmwoods
Red oak association
Bur oak association

THE WILLOW ASSOCIATION (SALICETUM)

The peachleaf willow, (*Salix amygdaloides*),[1] occupies perennially wet margins of waterways, attaining a height of 50 to 60 feet and

[1] Latin names of vascular plants are taken from Gray (**1950**); of bryophytes from MFNA. Names of algae are from various sources. For names of fungi I am indebted to Professor G. W. Martin; but he would not write them without citing authorities. Varieties and forms have mostly been ignored.

a diameter of 12 to 16 inches. Much larger diameters are on record. Beneath these there may be a shrubbery of *Salix interior*, and an herbage of *Polygonum* spp. and *Leersia*. The moss *Aphanorhegma patens* is occasionally found in the moist soil. This grouping may be called the Salicetum amygdaloidis. A variant of this association occurs where *Salix nigra* takes the place of *Salix amygdaloides*. The associated plants are the same.

A Salicetum amygdaloidis with *Crataegus* species and *Polygonum* is marginal on older, drier bottomlands. The willow blooms abundantly in May, covering itself with golden yellow catkins. At the same time the hawthorns are white with fishy-scented flowers, much visited by flies. These are the red haws of autumn, with crimson skin, yellow edible flesh, and several stony "seeds" (carpels). We call them *Crataegus mollis*. But who dares to name a Crataegus?

Peachleaf willow, black willow and sandbar willow are common in suitable places all over the State. So are the acrid smartweeds. The species of *Crataegus* differ from place to place. *Aphanorhegma patens* has been collected in Hardin and Tama Counties, along the Iowa River, and in Polk and Madison Counties. Undoubtedly it is much more widespread.

Relatively high dry river banks, natural levees, are edged with *Betula nigra*. The golden brown, loose papery bark of young trunks and medium sized branches is lovely to look upon. The tree never prospers in competition with elms though it flourishes in upland lawns. It must have a marginal position, often with red haws and green haws and prickly ash (*Xanthoxylum*) on the sunny side.

Frequently found on river banks is the silver maple (*Acer saccharinum*). The trunks attain diameters of 3 or 4 feet, usually with branches low down. Storms break off the branches from time to time, but the trees survive. This maple is the first tree to bloom in the spring. Its buds swell and redden in mid-March. The median date for the blooming of the silver ("soft") maple at Grinnell is March 17, with extremes of February 28 and April 3. In the first week of June the ripe yellow samaras fall spinning to the ground,—tens of thousands of them.

THE ELM ASSOCIATION (ULMETUM)

Elmwoods characterize the broader bottomlands throughout the State. *Ulmus fulva* indicates drier ground, *Ulmus americana* wetter. The former ascends the lower slopes of the hills that bound the level bottoms, mingling there with basswoods. *Gleditsia* is a sparse member of the Ulmetum, ready to take over every opening by means of

its abundance of seeds. The big flat purple curly pods drop throughout the autumn, winter and early spring, and are easily carried for short distances by wind directly through the air, or scurrying along on the surface of snow. The seeds are also distributed by herbivorous animals which eat the pods. The results can be seen wherever cattle are pastured under the trees. The seeds are extremely hard and indigestible.

Populus deltoides and *Platanus occidentalis* send up the most majestic trunks amongst all of our native trees. They occur as scattered specimens over the bottomland as members of the elm association. Cottonwood attains a height of 80 feet and a diameter of 3 feet or more, with blackish, coarsely ridged and furrowed bark. The planetree displays its snow-white trunk and branches only in the eastern part of the State, as far as Hardin County (Eldora). *Fraxinus pennsylvanica subintegerrima* is usual in this community. And this is the home of *Juglans nigra* and *J. cinerea*.

The trees of the elmwood bloom before the leaves come out. At this time also the early spring flowers of the elmwood appear: *Claytonia virginica* common and abundant; *Erythronium albidum* locally abundant, growing in dense stands of 5 to 500 square meters, sometimes flowering freely.

In May *Mertensia virginica* is common. With us it is rarely over 3dm. tall. Blue violets are abundant in the elmwood, and *Arisaema dracontium* is widespread, but always in small numbers. *Phlox divaricata* var. *laphamii* makes sheets and masses of color in late May.

These are followed quickly by *Hydrophyllum virginianum* in great crowds, and *Trillium reflexum* in widely scattered patches of a dozen, more or less.

By mid-June *Laportea* covers the terrain with a meter-high leafy growth that shades the ground. *Tovara virginiana* is interspersed in colonies a meter or more in extent.

We find the moss *Entodon compressus* with abundant capsules (October) only on bases of trees and on rotten logs in the Ulmetum.

In September all of the leaves of the trees of the willow and elm associations turn yellow and yellow-brown, the woodbine (*Parthenocissus quinquefolia*), turns crimson, and the hawthorns bear scarlet fruits. In November (in central Iowa) the leaves fall.

The soil of bottomlands is developed from deposits of fine silt, underlaid at one or two meters by sand and/or gravel. Pore space, involving capacity for air and water, is low. The soil is packed by frequent flooding; dead leaves as a source of humus are largely washed away. Sparse herbage adds but little humus to the soil. Ex-

cess of water is unfavorable for earthworms and ants. The ground is hard and dense.

The seeds of willow, cottonwood and silver maple must find moist earth in which to germinate within a week or perish completely. It is not so with the elms. About half of the seeds of American elm sprout at once. The others lie dormant until the following spring and then come up vigorously. Basswood (*Tilia americana*) germinates in the spring.

Salicetum and Ulmetum as described occur in almost continuous strips along all of the rivers of the eastern half of the State and their tributaries. In very wet places the tree community gives way to stands of slough grass. And where the meandering stream cuts away the old floodplain and burrows into the bordering hills, the community of oak, elm and basswood stands on the brink of a landslide overhanging the stream.

As we go westward the elm association becomes more restricted in area and poorer in species. Green ash becomes more and more abundant until it wholly replaces elm, as at the north end of Spirit Lake. Aikman prefers to call the floodplain forest the elm-green ash community. West of the divide between the Mississippi and Missouri drainage systems the Ulmetum is only found in the most sheltered places, as in the deep ravines between the loess hills bordering the valley of the Missouri and Sioux Rivers. A good example is in the valley of Joy Creek, seven miles north of Sioux City. (Sec. 19, Sioux Twp., Plymouth County).

THE RED OAK ASSOCIATION (QUERCETUM RUBRAE)

Quercus rubra is the most abundant tree of hillsides which are protected by topography from open exposure to summer suns and dry southerly and westerly winds. Usually associated with this is white oak (*Quercus alba*), basswood, and, on lower slopes, american elm. Sugar Maple (*Acer saccharum*) appears singly in this association in its drier phases, but forms pure stands as far west as Madison and Tama Counties. The total coverage of trees is 100%.

A shrub layer with cover rarely over 50% usually occurs. In this layer *Staphylea trifolia* is to be expected, sparsely and far apart. *Ribes missouriense* is common, and on rocky hillsides *R. cynosbati*. *Viburnum affine* is less frequent (Tama, Hardin, Iowa Counties and northeastward). Farther to the northeast (Jones County) *Physocarpus opulifolius* is common. The hairy ovularies of var. *intermedius* are often conspicuous. *Ribes floridum* is usually in this community, flowering in early June. It only rarely produces fruits.

The low herb layer appears in April with *Trillium nivale*. In many

places *Hepatica acutiloba* is abundant. It is host to the rust *Tranzchelia punctata* and the smut *Urocystis anemones*. *Sanguinaria* is present as scattered individuals. *Asarum canadense* forms dense colonies 1 to 3 m. across, the short sepal and long sepal forms showing no geographic or ecologic preference. *Dicentra cucullaria* is nearly always present.

In late May *Trillium flexipes* blossoms, singly, in clusters, or rarely, actually coloring a hillside. *Aquilegia canadensis* is always present. *Orchis spectabilis* occurs frequently, singly or in colonies of 2 to 12. *Anemonella thalictroides* is everywhere in the red oak association, along with *Viola pubescens*.

Flowers are absent in summer, but autumn brings *Aster sagittifolius*, *Solidago flexicaulis* and *S. ulmifolia*. The hickories, elms and basswoods turn yellow in autumn. Red and black oaks turn red, becoming more dazzling into mid October. White oaks take a purplish dull red, which ripens into brown, in which condition the leaves hang on until the snows of winter or the bursting buds of spring push them off. We have included here the communities which Aikman calls red oak-maple and maple-linden (meaning *Acer saccharum* and *A. nigrum*).

White oak acorns germinate in autumn quickly after falling. The other oaks, the hickories and walnuts wait until spring.

The soil in the red oak wood is a soft, loose leafy mull, easily crunched and displaced by a human foot, but so absorbent that the rain never moves it unless concentrated in a depression. This is the soil that makes the oakwood our greatest conservator of rainfall and our best insurance against floods.

Clark (1926) gives the following list of plants of a "Red oak-Linden" woodland on the bluffs of Cedar River above Cedar Falls. The substrate is glacial till covered with 6 to 12 inches of loess of "rather high humus content," and topped with leaf litter.

THE BUR OAK ASSOCIATION (QUERCETUM MACROCARPAE)

The *Quercus macrocarpa* community occupies the higher, drier, gentler slopes and flat uplands, bordered on one side by the red oak community and on the other by a strip of shrubbery and/or the open prairies. Because the topography is favorable for agriculture, the bur oak community has suffered almost universal modification, if not destruction. Other stands are the result of spreading (migration) of bur oak, since settlement of the land, into modified prairie. In western Iowa, where rainfall is normally low, evaporation high, and changes of temperature extreme, bur oaks can exist only in the shelter of the hills. The bur oak association here occupies the slopes above

Woody Species			
Quercus rubra	v.a.[2]	Xanthoxylum americanum	f.
Tilia americana	v.a.	Celtis occidentalis	i.
Hicoria ovata	v.a.	Gleditsia triacanthos	i.
Quercus alba	a.	Populus grandidentata	f.
Acer saccharum	a.	Populus tremuloides	i.
Ostrya virginiana	v.a.	Prunus serotina	r.
Fraxinus lanceolata	f.	Prunus virginiana	r.
Fraxinus americana	f.	Cornus sp	i.
Juglans nigra	f.	Ribes sp	f.
Juglans cinerea	f.	Crataegus sp	f.
Herbaceous Species			
Sanguinaria canadensis	v.a.	Hydrophyllum appendiculatum	f.
Erythronium albidum	a.	Hydrophyllum virginicum	v.a.
Asarum canadense	a.	Viola papilionacea	v.a.
Arisaema triphyllum	a.	Viola pubescens	a.
Podophyllum peltatum	a.	Trillium declinatum	f.
Bicuculla canadensis	f.	Impatiens biflora	v.a.
Bicuculla cucullaria	a.	Phlox maculata	a.
Isopyrum biternatum	v.a.	Polygonatum commutatum	f.
Syndesmon thalictroides	f.	Aquilegia canadensis	f.
Uvularia sessilifolia	a.	Smilax herbacea	f.
Uvularia grandiflora	a.	Anemone quinquefolia	f.
Polemonium reptans	v.a.	Washingtonia claytoni	a.
Caulophyllum thalictroides	f.	Washingtonia longistylis	a.
Claytonia virginica	v.a.	Ranunculus septentrionalis	v.a.
Hepatica acutiloba	v.a.	Vagnera stellata	a.
Geranium carolinianum	v.a.	Vagnera racemosa	a.
Sanicula marylandica	f.	Erigeron philadelphicus	f.

[2] v.a. = very abundant; a = abundant; f = frequent; i = infrequent; r = rare.

Fig. 5. Red oak-linden woodland, after Clark 1926.

a narrow strip of red oak association, or may replace the latter entirely. At the limit of conditions for survival bur oak becomes dwarfed to one or two meters tall, its branches spread along the ground, with upright shoots bearing abundant small acorns. This has been called var. *depressa*. Transplanted to Iowa City it becomes a normal oak tree. Schaffner has pointed out that bur oak comes farther down the slopes as it extends westward into semiarid regions, until it finally becomes the characteristic tree of alluvial bottomlands. A salicetum follows the river banks even to and into the Rocky Mountains. But Ulmetum and Quercetum rubrae dwindle to zero as Quercetum macrocarpae moves down upon the floodplains.

The plants of Boot's (**1914**) woodland station 4 "dense forest on the south side of a deep east-west gulch" in Monona County are given here to represent Quercetum macrocarpae:

Tree Layer, Station 4

M[2] (*Quercus macrocarpa* always present in the area)

M *Carya "glabra"*
M *Carya "glabra" "villosa"*

Shrub Layer

M *Celastrus scandens*
M *Euonymus atropurpureus*
N *Ribes cynosbati*
M *Vitis riparia*

Herb Layer

Th *Ambrosia trifida integrifolia*
H *Campanula americana*
H *Cryptotaenia canadensis*
H *Eupatorium fistulosum*
H *Eupatorium rugosum*
H *Hydrophyllum virginianum*
Th *Impatiens pallida*
G *Laportea canadensis*
Ch *Phlox divaricata*
H *Sanicula marilandica*
G *Arisaema triphyllum*
G *Circaea quadrisulcata*
Desmodium glutinosum
Th *Galium aparine*
H *Geum virginianum*
H *Hystrix patula*
Th *Lactuca floridana*
H *Hackelia virginiana*
H *Phryma leptostachya*

Ground Layer

G *Carex pensylvanica*
H *Fragaria virginiana*
G *Sanguinaria canadensis*
H *Taraxacum officinale*
H *Viola pubescens*
G *Dicentra cucullaria*
H *Ranunculus abortivus*
Sisyrinchium campestre
H *Trifolium repens*
H *Viola pensylvanica*

This list shows certain obvious "strangers" in the association: *Ambrosia*, *Sisyrinchium*, *Trifolium*, and *Taraxacum*.

Sometimes the bur oak makes a complete canopy, 100% cover. With only 75% cover or less bluegrass (*Poa pratensis*), clothes the ground

[2] Life Form. See table at end of Chapter 3.

with a dense, luxuriant sod. Because of the partial shade open bur oak pastures yield much more forage than unshaded areas in hot dry weather. Hence every raiser of livestock likes to have a piece of park-like pasture, and every open grassy oakwood suffers the injuries that pasturing produces.

The available lists of woodland plants do not distinguish the members of the different communities. Shimek has kept the most detailed notes on the flora of Iowa. From his published and unpublished records we copy the lists given at the end of chapter 3.

Clark (**1926**) has described a "Bur oak-Black oak Woodland" on an old floodplain north of Cedar Falls. The soil was a "coarse sandy loam" of "low humus content." His list of plants is photographically reproduced below. This list shows that one species (bur oak) may not determine an association. The oak of dry hills may be at home on extremely porous bottomland. If this community is repeated elsewhere it will have to be recognized as an association, perhaps Quercetum velutinae. Communities near mouth of Cedar River indicate this.

Woody Species

Quercus macrocarpa	v.a.	Tilia americana	r.
Quercus velutina	v.a.	Prunus serotina	r.
Quercus rubra	i.	Juniperus virginiana	a.
Ulmus fulva	f.	Prunus virginiana	r.
Ulmus americana	f.	Populus tremuloides	f.
Hicoria minima	r.	Xanthoxylum americanum	f.
Juglans nigra	f.	Ribes sp.	a.
Gymnocladus dioica	i.	Corylus americana	a.
Acer saccharum	r.		

Herbaceous Species

Mertensia virginica	v.a.	Ranunculus abortivus	i.
Polemonium reptans	a.	Oxalis violacea	a.
Circaea lutetiana	f.	Lithospermum linearifolium	f.
Phlox bifida	f.	Monarda fistulosa	a.
Pedicularis canadensis	f.	Anemone cylindrica	f.
Scrophularia marylandica	f.	Brauneria pallida	f.
Viola pedatifida	a.	Rudbeckia hirta	f.

Fig. 6. Plants of the bur oak-black oak association, after Clark 1926.

THE SHINGLE OAK COMMUNITY (QUERCETUM IMBRICARIAE)

So many plant species are found only in the southern and southeastern part of the State that another woodland community must be recognized. This community may be named for its most abundant, striking and unique member, the shingle oak (*Quercus imbricaria*).

Only by its stiff texture, shiny surface and excurrent midrib does the elliptic, entire leaf of the shingle oak indicate its alliance with the Black Oaks. The small acorns resemble those of the pin oak. The black bark, cracked into cubical bits, is somewhat like the bark of black oak or blackjack. The leaves turn to a rich golden yellow

in autumn, then turn brown and remain on the tree far into the winter. In Iowa the tree is usually small, 25 to 50 feet tall, and up to a foot in diameter.

The shingle oak grows in open park-like woods mixed with hawthorns, wild crab and other oaks (white, black, bur). No considerable pure stand has come to our notice. And because the areas are all pastured, the original native vegetation is not recorded. There is always a shrubbery of *Corylus americana*, *Ribes missouriense* and *Symphoricarpus orbiculatus*. The last named shrub is known in southern Iowa as buckbrush. It and the hazel spread by rhizomes or stolons. Both are destructive to the bluegrass pasture association and to prairie. The gooseberry is also destructive to pasture. The berries are small but well flavored, nearly black when ripe, and were much used for food by the early settlers.

The congeries of woody plants (and two herbs) known in Iowa only in the southeast is shown by the map, **Fig. 7**. In addition to these certain mosses are similarly limited. The big julaceous *Cirriphyllum boscii* grows in yard-square patches on shady banks at the southwest corner of the city of Keokuk, near Sedan in Appanoose County, and in northeastern Davis County. One small depauperate patch about six inches square was found near Red Rock in Marion County. The apparently leafless *Pogonatum pensilvanicum* of moist raw earthy slopes has been collected in Mahaska, Washington, Muscatine, Wapello and Henry counties. These two species extend into New England along the Atlantic coastal plain. *Didymodon tophaceus* is known from Warren and Des Moines Counties, and *Desmatodon plinthobius* from Delaware, Jackson, Poweshiek (introduced), Muscatine and Henry counties. The two last named species grow on dry rocks. The Poweshiek County station is a sandstone retaining wall built to support the bank of a railroad cut west of Grinnell. The plant has not been found in the abandoned quarry from which the stone was taken, though many other mosses are there.

According to the soil, exposure and accompanying species (hazel, gooseberry, coralberry) the shingle oak association must be regarded as a variant of the bur oak association. More humid slopes in the same region have well developed stands of the red oak association. Sugar maple and hornbeam (*Carpinus caroliniana*) occur in Mahaska and Decatur counties, and *Athyrium thelypteroides* and *Dryopteris goldiana* grow on the talus at Raven Rocks in Mahaska County. *Taxus canadensis* dangles over limestone ledges in Van Buren County. Thus in especially favorable stations even in southern Iowa elements of a boreal flora are able to survive. And it must be remembered that

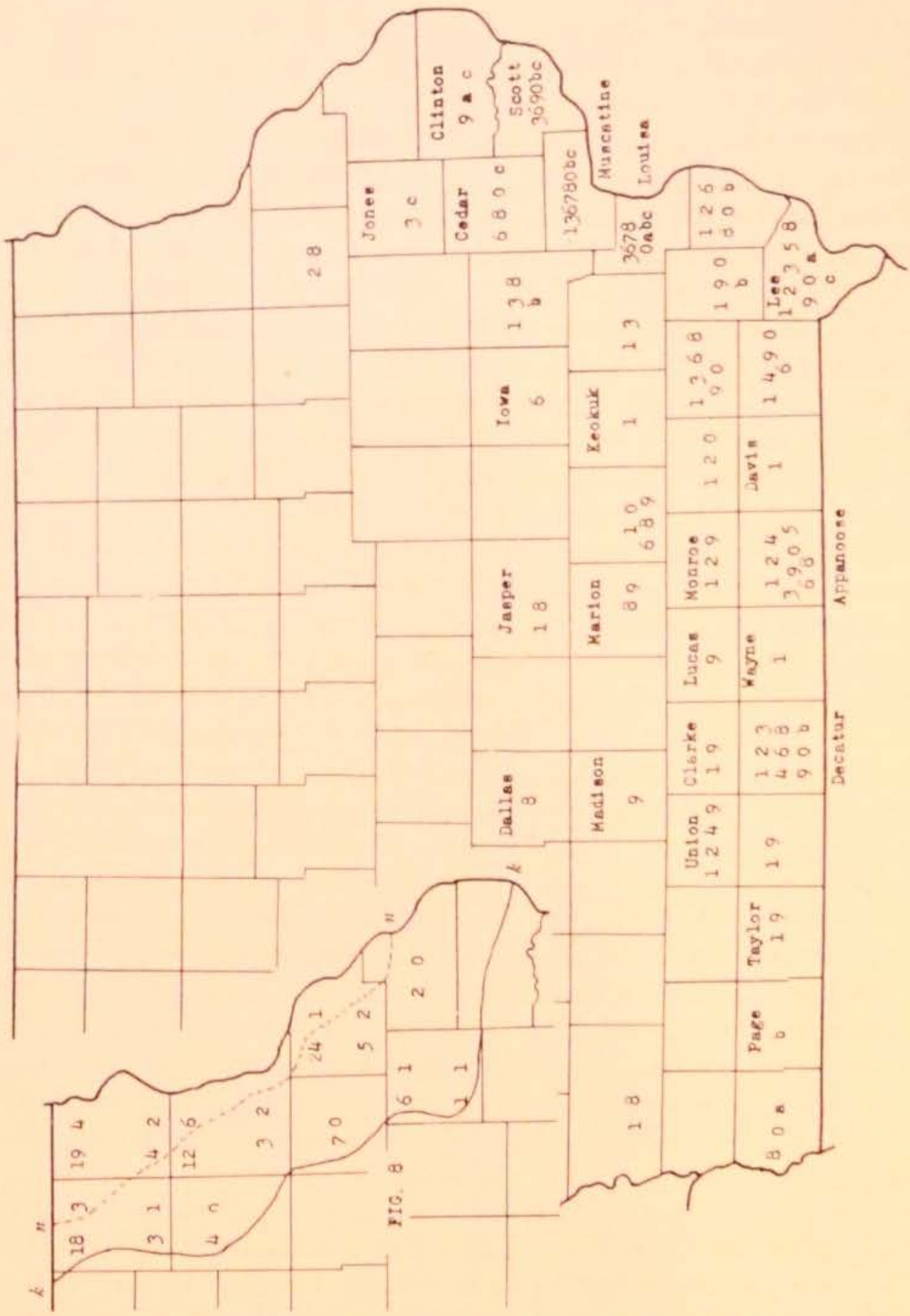


Fig. 7. Plants of Quercetum imbricariae. 1, *Quercus imbricaria*. 2, *Q. marilandica*. 3, *Q. palustris*. 4, *Q. prinoides*. 5, *Q. stellata*. 6, *Carya laciniosa*. 7, *C. illinoensis*. 8, *Morus rubra*. 9, *Aesculus glabra*. 10, *Cercis canadensis*. a, *Asimina triloba*. b, *Seymeria macrophylla*. c, *Froelichia floridana*.

Fig. 8. Mosses and liverworts of the "driftless area." First figure is the number of species of mosses, second of liverworts. Upper row in each county is for species found only in these counties in Iowa. Lower row is for additional species found in boreal communities elsewhere in the State. Drift boundaries smoothed out: k-k, Kansan-Iowan boundary; n-n, Nebraskan-Kansan boundary.

the greater part of all of southeastern Iowa was originally grassland.

Larsen & Dilworth (**1939**) described the forests of southern Iowa from the forester's standpoint, without mentioning the shingle oak. Probably they omitted it because of its lack of commercial value. They classified their stands according to habitat into those of uplands, terraces and bottomlands, finding an average of 12,123 board feet of lumber per acre on uplands, 2,585 on terraces and 3,467 on bottomlands. According to quality of site the trees require from 60 to 130 years to reach a diameter of twelve inches. One can only guess at the associations from these records. Aikman & Gilly (**1949**) give lists that support our interpretation of the associations.

Fuller (**1936**) gives a study of a ten meter quadrat in a woodland, not much disturbed, in Appanoose County, (**Fig. 9**).

TREE LAYER

Carya ovata
Juglans nigra
Prunus virginiana
Quercus alba
Quercus imbricaria
Quercus rubra

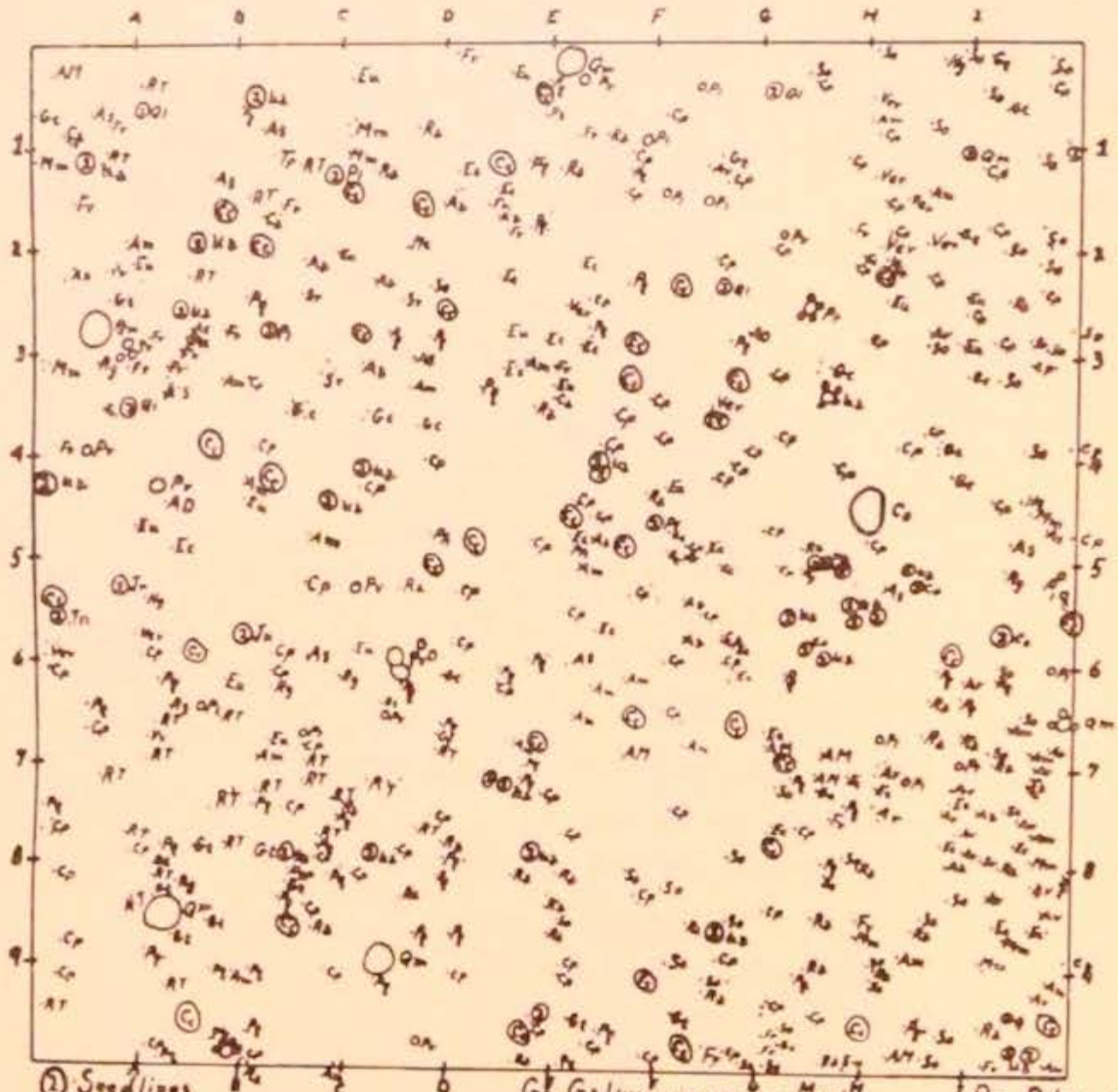
SHRUB LAYER, SCATTERED AND OPEN

Cornus racemosa
Symphoricarpus orbiculatus

OTHERS

Acalypha virginica
Achillea millefolium
Ambrosia artemisiifolia
Amphicarpa bracteata
Aster sagittifolius
Campanula americana
Carex cephalophora
Cirsium altissimum
Erigeron canadensis
Eupatorium rugosum
Fragaria virginiana
Galium circaezans
Galium triflorum
Helianthus grosseserratus
Hystrix patula
Monarda fistulosa
Panicum lanuginosum
Polemonium reptans
Polygonum scandens
Parthenocissus quinquefolia
Rhus radicans
Rubus sp.

Plot VII. Wooded area thirteen and one-half miles northwest of Centerville, Appanoose County, Iowa. Soil rich sand-loam. Ten meters square.



① Seedlings
Stump with sprouts
○ Trees
Av. Acalypha virginica L.
AM. Achillea Millefolium L.
Aa. Ambrosia artemisiifolia L.
Am. Amphicarpa monoica (L.) Ell.
AD. Aster Drummondii Lindl.
As. Aster sagittifolius Wedemeyer
(Cc) Tuft of Carex cephalophora Muhl.
Ca. Campanula americana L.
Co. Carya ovata (Mill.) K. Koch
Ca. Cirsium altissimum (L.) Sprang.
Cp. Cornus paniculata L'Her.
Ec. Erigeron canadensis L.
Eu. Eupatorium urticaefolium Reichard
Fv. Fragaria virginiana Duchesne
Ge. Galium circaezans Michx.
Gt. Galium triflorum Michx.
Hg. Helianthus grosseserratus Martens
Hyp. Hystrix patula Moench
Jn. Juglans nigra L.
Mm. Monarda mollis L.
Ph. Panicum huachucae var. silvicola Hitchc. and Chase
Pr. Polemonium reptans L.
Ps. Polygonum scandens L.
Pv. Prunus virginiana L.
Pq. Psedera quinquefolia (L.) Greene
Pi. Pyrus ioensis (Wood) Bailey
Q. Quercus sp. (seedlings)
Qi. Quercus imbricaria Michx.
Qm. Quercus macrocarpa Michx.
Qr. Quercus rubra L.
RT. Rhus Toxicodendron L.
Rg. Ribes gracile Michx.
Ra. Rubus sp.
Sr. Smilacina racemosa (L.) Desf.
So. Symphoricarpos orbiculatus Moench
Tp. Triosteum perfoliatum L.
Ua. Ulmus americana L.
Ver. Veronica virginica L.
Vv. Vitis vulpina L.

Fig. 9. Quadrat in Quercetum imbricariae, after Fuller 1936.

Smilacina racemosa
Triosteum perfoliatum
Veronicastrum virginicum
Vitis riparia

OUTSIDE THE QUADRAT

Ribes missouriense
Gentiana flavida
Lactuca floridana
Prunella vulgaris

FRAGMENTARY BOREAL COMMUNITIES

In the northeastern 1/8 of the State, including the driftless area, woodlands approach more and more to the composition of the beech-birch-maple-hemlock forest of Shantz and Zon (**1924**). On sheltered hillsides an Aceretum saccahri can be distinguished, characterized by the abundance of *Acer saccharum* and *A. nigrum*, with *Acer spicatum*, *Sambucus racemosa*, *Hamamelis virginiana*, *Dirca palustris*, *Mitella diphylla*, *Polymnia canadensis*. The sunny side of the valley will be covered with the red oak association, or with grasses interspersed with prostrate juniper (*Juniperus horizontalis*). The tops of limestone ledges are lined with red cedars (*Juniperus virginiana*).

A still more boreal association is that of white pine and white birch (*Pinus strobus* and *Betula alba* varr.). This occurs as an outlier in Hardin County (Eldora to Steamboat Rock) and is frequent in Mitchell, Fayette and Clayton Counties and northeastward. Finally on especially cool north-facing taluses with a stony subsoil cooled by dripping spring water and/or air from subterranean galleries, the canada balsam (*Abies balsamea*) grows, accompanied by a number of boreal species characteristic of the Picea-Abies Association of the North Woods.

ACERETUM

The sugar maple (*Acer saccharum* sens. lat.) grows as far west as Pammel Park in Madison County on the steep north slope of the "Backbone," and at Fort Defiance State Park on the western edge of Emmet County. At Red Rock in Monroe County and in Emmet County there are crowds of seedlings under the trees. The tree makes small pure stands (a few acres) near Indianola, in southwestern Tama County, and on the uppermost terrace of the Mississippi River east of Grandview. This last area was once a useful "sugar grove." In all of the places named, and in very many others, sugar maple is associated with the usual members of the red oak association, and is itself a local and subordinate member of that association.

The fragmentary stands of the beech-birch-maple-hemlock forest

present a different picture. The most distant outliers of this forest are between Eldora and Steamboat Rock in Hardin County and at Wildcat Den State Park in Muscatine County. These two localities mark the extreme extensions of the range of white pine (*Pinus strobus*) in Iowa. They are located on a brown Pennsylvanian sandstone, friable and porous, holding and giving out water like a sponge. In both places the pine is feebly reproducing.

The Wildcat Den area (there is a "wildcat cave" near Eldora) has *Gaylussacia baccata*, *Aralia nudicaulis*, *Diervilla lonicera*, *Maianthemum canadense*, and the moss of moist rocks, *Brachythecium flagellare*.

The Eldora area has white birch (*Betula papyrifera*) and its besetting fungus *Polyporus betulinus*, *Diervilla*, *Aralia nudicaulis*, *Carpinus caroliniana*, *Lonicera dioica*, *Hydrophyllum appendiculatum*, *Camptosorus rhizophyllus*, *Pteretis pensylvanica*, *Dryopteris marginalis*, *D. spinulosa*, *Smilacina racemosa*, *Panax quinquefolius*, *Trillium flexipes*, *Climacium americanum*, etc.

Nowhere is the influence of topography more clearly shown than in this area. A mile north of Eldora the flat upland, where untilled, has now a park-like scattering of *Quercus ellipsoidalis*, with a few *Q. alba* and *Q. rubra*. The ground cover of bluegrass, not at all luxuriant, includes *Hypoxis hirsuta*, *Ranunculus fascicularis* and *Carex rosea*. On one knob there is a dense bed of *Polytrichum commune*, and nearby are deep cushions of *Leucobryum glaucum*, infiltrated with *Pohlia nutans*. (I have seen this combination also in eastern Pennsylvania). On the brink of the crumbling sandstone cliff a couple of ancient pines cling precariously by means of roots that run back into the crevices of the rock. The cliff faces northeast. On its ten-foot vertical wall *Polypodium virginianum* occupies the crevices, and the lichen *Amphiloma* covers the surface with greenish gray. The steep rocky talus below (a student once rolled the whole length of it to the river's edge without being able to stop), completely shaded as soon as the trees leaf out, is covered with mosses and ferns. In mid May the fern fronds are unrolling, and tall slim buds of Jack-in-the-pulpit (*Arisaema triphyllum*) are shooting up. Growth has just fairly started. On the meadow across the river spring came a month before. Big bossy hawthorns (*Crataegus spp.*) are white with bloom, and round-headed wild crabs (*Pyrus ioensis*) are gorgeously red and pink and sweet scented. A sunny pasture on the nearby terrace is bordered with prickly ash (*Xanthoxylum americanum*).

A still more boreal community is seen at the foot of a taller cliff a mile farther north, at "Fallen Rock." The brink of this cliff is

edged with white birch and red cedar, over a luxuriant sod of bluegrass. A few remaining trees in the adjacent field are all sugar maples. Deep shade at the foot of the cliff is cast by yellow birch (*Betula lutea*) and butternut (*Juglans cinerea*). The erroneous report of *Betula lenta* from Iowa in Gray's Manual, Ed. 7, is based upon a mis-identification of the yellow birch from this locality (in Pammel **1899**). The big talus blocks lie on a gently sloping terrain, and are covered with *Hypnum curvifolium*, *Heterophyllium haldanianum*, *Anomodon attenuatus* and *Brachythecia*. Tiny bits of *Dicranum montanum*, *Calliergonella schreberi* and *Tetraphis pellucida* have been found here. Amongst the mosses are the ferns *Dryopteris disjuncta*, *D. spinulosa*, *D. goldiana*, and *Maianthemum canadense*, *Asarum canadense acuminatum*, *Solidago flexicaulis*, etc.

Five miles farther up stream a north slope makes a home for *Dicentra canadensis*. And ten miles farther up are the limestone cliffs of Iowa Falls where once was found that extremely rare disjunct, *Primula mistassinica* (last seen in 1921; Cratty **1925**).

White pine and white birch are "frequent" in the "driftless area," along with several characteristic mosses.

An important plant of the understory of our boreal woodlands is the Canada yew (*Taxus canadensis*). In Linn County, and in Van Buren County, and in many other places, *Taxus* clings to the brink of a cliff, hanging over and dangling down a wall of rock. In the fir forests it spreads in dense stands over rough taluses. Such a bed is almost impenetrable. One walks upon the prostrate branches. The twigs are often hung with mosses, or surfaced with the scale-like *Radula complanata* or the tiny *Cololejeunea biddlecomiae*. Always the butternut is a member of the community. In two of these localities in Iowa the rare *Aconitum noveboracense quasiciliatum* ekes out a slender living. The mosses of Pine Hollow in Dubuque County, (Conard **1932**, **1934**) and of Grannis Hollow (Blagg **1928**) in Fayette County have been listed and described.

It is customary to consider that these boreal communities are relics of an early post-glacial vegetation (Gleason **1923**). Communities that were widespread along the margins of the last continental ice sheets have been able to survive in especially favorable habitats Some species have died out. Others have continued to reproduce. That which remains is a fragmentary association, whose members are the lineal descendants of those which lived in these areas 20,000 years ago. This view is favored by the grouping of the boreal species after the fashion that now occurs over wide areas 500 miles to the

north (Dansereau **1943, 1946**). How else could the congeries of species, including two crane-flies, come together at Eldora?

There are equally keen scholars who believe that winds and other agencies of dissemination are constantly strewing the germs of life far and wide. In the course of 10,000 years the seeds of pine and birch (both are winged) and the spores of ferns and mosses have been dropped everywhere in Iowa. Those which fell in suitable places germinated and grew. The plants we now find may have blown in within 200 years or less, and are not at all the lineal descendants of the settlers of 20,000 years ago.

No positive proof can be expected, but papers have been written and will be written presenting evidences for the one view or the other.

THE SPRUCE-FIR COMMUNITY

The balsam fir occurs in six localities in northeastern Iowa, and at one spot a few miles over the line in Minnesota. From the standpoint of the plant sociologist we must add a hillside at Pine Hollow, Dubuque County, although balsam is not there. At these places there are fragmentary stands of an association that is expressed fully in northern Minnesota. Beside *Abies balsamea*, these cool north-facing banks and taluses have *Taxus canadensis*, *Cryptogramma stelleri*, *Acopitum noveboracense quasiciliatum* (Fasset **1929**) and several mosses and liverworts. Thirty species of bryophytes are known in Iowa only from this and a few of the outlying boreal communities such as Fallen Rock in Hardin County. The table below will show the situation at a glance. (Also **Fig. 8**, above).

Boreal Mosses and Liverworts of the Driftless Area

County	Driftless area only		Also in relict colonies	
	Mosses	Hepatics	Mosses	Hepatics
Winneshiek	18	3	3	1
Allamakee	19	3	4	2
Fayette	4	0		
Clayton	12	6	3	2
Delaware	7	0		
Dubuque	24	1	5	2
Jones	6	1	1	1
Jackson	2	0		

Amongst the mosses *Hylocomium splendens* is especially interesting because of its wide distribution in relation to the spruce-fir associations. In the Great Smoky Mountains of North Carolina-Tennessee it is associated with *Picea glauca* and *Abies fraseri*. In the Catskill Mountains of New York and northward, and in northern Minnesota the associates are *Picea glauca* and *Abies balsamea*. An outlying grove of *Abies balsamea* in southern Minnesota, west of Wykoff, also has *Hylocomium*. In Yellowstone Park the associates are *Picea engelmannii* and *Abies lasiocarpa*. In western Washington this moss grows by the square mile associated with *Picea sitchensis* and *Abies amabilis*. In the Swiss Alps, the Carpathians and in northern Europe the associates are *Abies alba* and *Picea abies*. It would be interesting to know its associates in New Zealand. They are certainly not spruce or fir.

Was this moss an associate of the Mesozoic or Tertiary ancestors of our contemporary spruces and firs? Has it remained unchanged while the tree species have been differentiated?

Also interesting is the very tiny moss *Seligeria pusilla*. In Iowa and in southern Minnesota it grows on hard limestone talus at the mouths of small cavities where cold air issues from subterranean chambers, under or adjacent to balsam trees. At Owen Sound, Ontario, it grows with other species of *Seligeria* on the walls of deep narrow crevices in the Niagaran limestone. In southern Austria (Neuberg) I found it covering the face of a meter-cube limestone boulder in a shady ravine at about 4,000 feet above sea level.

WOODLAND FUNGI

Communities of trees furnish many habitats for fungi. Trees, shrubs and herbs have diseases peculiar to each species or genus. The dead leaves and stems and fruits serve as food for many saprobic organisms. Even the forest insects are subject to attack. Cornelia Clarke collected many specimens of *Cordyceps* in the Amana Woods.

We have no lists of fungi assorted according to the associations. Positive inferences can be drawn in some cases from the fidelity of the host species. For example:

SALICETUM

Uncinula salicis on *Salix* spp.
Melampsora bigelowii on *Salix* spp.
Daedalea confragosa on *Salix* spp.

ULMETUM

Gnomonia ulmea on *Ulmus americana*
Gnomonia veneta on *Platanus occidentalis*

Melampsora medusae on *Populus deltoides*
Puccinia peridermiospora on *Fraxinus lanceolata*,
(and on *Spartina pectinata*)
Exidia spp. on fallen branchlets of *Ulmus americana*
Pleurotus ulmarius on *Ulmus* and *Acer negundo*

QUERCETUM

Oak wilt now threatening all of our oaks.
Sclerotinia tuberosa on buried acorns
Sarcoscypha coccinea on dead oak twigs, half buried
Urocystis anemones on *Hepatica acutiloba*
Transchelia punctata on *Hepatica acutiloba*
Aleurodiscus spp. on bark of living bur oaks

SHRUBLANDS

Dibotryon (Plowrightia), *Exoascus* and *Fomes*
ungulatus on *Prunus americana*
Microsphaera alni on *Symphoricarpus orbiculatus*

Shimek enumerated for the forests of the Okoboji Region 29 Myxomycetes, 31 Ascomycetes and 95 Basidiomycetes. Of the last group 76 are mushrooms (Hymenomycetes) and 15 Gasteromycetes. Paige (**1928**) recorded for the woods of Webster County 14 Ascomycetes and 346 Basidiomycetes, of which 230 are gilled mushrooms and 25 Gasteromycetes. In a forest reserve near Cleveland, Ohio, Mr. Maurice Walters has found 800 species of fungi.

Probably many species of vascular plants are kept in their places by the fungi which attack and kill them when they wander into foreign communities or are overtaken by vegetational change. (Cf. *Portulaca*, p. 132).

In clearings, rotting stumps accommodate *Clitocybe illudens* in large clumps, *Armillaria mellea* in wide patches, *Tremella*, *Tremellodendron*, thelephores, polypores, and *Lycoperdon* species. Rotting logs in woods usually beget species of *Stemonitis*, *Comatricha*, *Lycogala*, *Arcyria* and *Trichia* (See Shimek, **1915**). *Hericium caput-ursi* grows on rotten logs in the Ulmetum.

The fungi are not merely interesting accompaniments of the woodlands. They are essential to the equilibrium of the communities. The annual additions of dead leaves and twigs must not be allowed to accumulate indefinitely, nor may the fallen monarchs of the forest be permitted to cumber the ground forever. Where the forest maintains itself in equilibrium the annual increment of detritus is converted *pari passu* into carbon dioxide and water and humus by the ageney of fungi (including bacteria), insects and earthworms. The animal members incorporate the raw humus into the soil. A very precise balance is maintained in terminal communities of long duration.

Another function of fungi is their association with the roots of trees in the form called mycorhiza (or mycorrhiza). Oaks, elms, birches and hickories, etc., have in the upper loose layers of the soil clusters of rootlets covered with a whitish or brownish felt of fungus threads. Maples have fungus threads within the cells of the rootlets (McDougall **1914**). The latest opinion is (Rayner **1927**) that this association of plant and fungus is beneficial to both partners. The idea once prevalent that some trees cannot live without the fungus is no longer held. Such plants as indian pipe and coralroot are obligate mycorhiza plants. Probably all of our orchids require the aid of a fungus to make their living.

The mycorhiza fungi belong to several groups of basidiomycetes, and perhaps to other classes. The fleshy poremushrooms (Boletaceae) are generally makers of mycorhiza. So also are some of the gilled mushrooms (Agaricales) and some smooth mushrooms (Thelephoraceae). Mycorhiza is found in all of the woodlands of Iowa, and in my garden. Lohman (**1926**) found it not only on trees but also on shrubs and herbs. (cf. Kelley **1950**)

GROWTH OF TREES

Bur oak in central Iowa attains a diameter of 3 to 5 feet, and a height of 50 to 60 feet. Of two stands examined, one showed 496 trees per acre. About 48% were 6 inches or more in diameter. Another stand had 211 trees per acre, with 156 that were 6 inches in diameter or larger. From the very great differences in age of the trees it is evident that bur oak was reproducing successfully and that the stand could maintain itself indefinitely.

Counts of annual rings show that our larger trees are from 50 to 150 years old. A few rare very large specimens must be much older, e.g. a walnut section 4 feet in diameter at Grinnell College, hollow at the center; a crooked red cedar 3 feet in diameter in Dickinson County with 369 rings of growth. (Anderson **1938**)

The annual increment is prodigious. Average annual growth in natural timber near Grinnell was found to be:

0.22	inch	in	diameter	for	*Carya ovata*
0.29	"	"	"	"	*Quercus velutina*
0.16	"	"	"	"	*Quercus velutina* after third year
0.30	"	"	"	"	*Quercus macrocarpa*
0.49	"	"	"	"	*Ulmus rubra*
0.63	"	"	"	"	*Acer saccharinum*
0.27	"	"	"	"	*Prunus serotina*
0.34	"	"	"	"	*Juglans nigra*

Maximum growth may occur at any age. One bur oak made its

maximum growth at 124 to 132 years; it was freed from competition at 124 (Conard **1918**). Maximum growths occurred in one tree or another in every year covered by our records. The trees show no evidence of secular variations of climate.

On high prairie soils (Carrington loam) a hundred and fifty species of trees flourish in Grinnell and vicinity. An american elm on Park St., Grinnell, felled in January 1907, was 27.5 inches in diameter and 40 years old. In its last 23 years its diameter increased nearly an inch a year. Green ash reaches 18 inches in diameter in 40 years, cottonwood 3 or 4 feet in 60 years; bur oak 14 inches in 40 years. A list of large trees in Grinnell is appended on page 116.

Tree seeds settle and germinate, or are successfully planted in cultivated grounds. In hedges and perennial flower beds trees are troublesome weeds. In Grinnell, american elm, green ash, bur oak, red oak, silver maple, sugar maple, cottonwood, ailanthus, walnut and boxelder are in this category. In Dickinson County boxelder may vigorously invade heavy bluegrass sod.

Evidently the soil and climate of high prairie in Grinnell are not unfriendly to deciduous trees. Indeed, all over Iowa groves and windbreaks of trees, deciduous and evergreen, have been successfully established on all tillable soils. Any explanation of the original treelessness of the prairie must take account of this.

The rates of growth found by Smith (**1939**) were much less than those reported by Conard (**1918**). She found the rates in Johnson County slightly greater than in Madison County, owing to more mesic conditions in the former. Her figures follow:

	Average annual increase in diameter
Acer saccharinum	1.86 - 2.16 cm.
Quercus macrocarpa	0.47 - 0.64
Ulmus americana	0.32 - 0.58

The oldest oaks were 100 to 150 years old, the elms 155 to 216 years.

A bur oak on the University campus, cut down in 1936, was studied by Briggs (**1937**). The trunk was 175 years old and thirty inches in diameter. At 14 years of age it was four inches in diameter, at 100 years sixteen inches. Especially wide rings were formed after 1840 when neighboring trees were removed for their lumber. Again in 1850 and 1851 wide rings were made, presumably because of very large precipitation in those two years.

If the ages of trees in Iowa range only to 369 years, with medians of 150 to 200 years, we must conclude either that they are relatively

short-lived in this State, or that they have arrived only within the last 300 to 400 years. That they are short lived in this unfavorable climate seems most probable. A large tree reaches a point where it can no longer obtain enough water in these marginal lands, whereas a small tree with relatively few leaves may have no serious difficulty. Evidences for this kind of climatic control are striking in the truly semiarid parts of Nebraska and the Dakotas.

The forester will be interested in the following table representing a stand in Story County. It does not meet the needs of the sociologist.

The maple-linden association as represented on a north slope. Late summer aspect.

TABLE I. *Counts of trees per acre in three upland forest communities based on five one-tenth acre quadrats, tallied in 2-inch diameter classes*

Oak-hickory community species	Diameter classes in inches											Total
	2	4	6	8	10	12	14	16	18	20	22	
Quercus borealis maxima Ashe, red oak		4	6	12	18							40
Quercus alba L., white oak	10	6	6	10	24	20	6	16	4		4	106
Carya ovata (Mill.) K. Koch, shagbark hickory	6	14	16									36
Fraxinus americana L., white ash		10	8	2	6							26
Ostrya virginiana (Mill.) K. Koch, ironwood	6	4	6	2								18
Carya cordiformis (Wang.) K. Koch, bitternut hickory		6	4									10
Acer saccharum nigrum (Michx.) Britt., black maple					2		4					6
Ulmus fulva Michx., red elm			2	2								4
								Grand total				246
Transition community species												
Tilia americana L., linden	4	4	2	6	18	16						50
Ostrya virginiana (Mill.) K. Koch, ironwood	66	48										114
Ulmus fulva Michx., red elm			6	8	18	10	6					48
Ulmus americana L., white elm		4	6	8	8	4						30
Carya ovata (Mill.) K. Koch, shagbark hickory		6		6			4					16
Carya cordiformis (Wang.) K. Koch, bitternut hickory		6		6		2	2					16
Acer saccharum nigrum (Michx.) Britt., black maple						4	2	4				10
Quercus borealis maxima Sarg., red oak					2	4						6
Fraxinus americana L., white ash			2	2								4
								Grand total				294
Maple-linden community species												
Tilia americana L., linden		4	7	14	14	12	2	2				50
Acer saccharum nigrum (Michx.) Britt., black maple	6	14	30	24	20	8	4	4	6	2	4	122
Ulmus fulva Michx., red elm				4	4	2						10
Ostrya virginiana (Mill.) K. Koch, ironwood	4	2										6
								Grand total				188

Fig. 10. Count of trees in "maple-linden association," after Aikman & Smelser 1938.

STATE FORESTS

For purposes of administration the State Conservation Commission divides the State into three districts: 1. the northeastern quarter; 2. the southeastern quarter; 3. the western half. Ten State Forests have been established:

1. Yellow River, 10 m. n. of McGregor, in Allamakee County 4,104 A.
2. B. Shimek Forest, 20 m. w. of Ft. Madison 3,709 A.
3. T. C. Stephens Forest, 10 m. n.e. of Chariton and 10 m. s.w. of Chariton 4,214 A

4.	Holst, 12 m. n.w. of Boone, Boone County	330 A.
5.	Petrus Memorial Forest, 10 m. n. of Council Bluffs	100 A.
6.	White Pine Hollow, 10 m. n.w. of Dubuque	650 A.
7.	Brush Creek Canyon, 10 m. n.e. of Strawberry Point	217 A.
8.	Preparation Canyon, 18 m. s.e. of Onawa, Monona County	186 A.
9.	Wanata, 28 m. s.w. of Spencer, Clay and Buena Vista Co.'s	145 A.
10.	Pilot Mound, 16 m. n.w. of Boone, Boone County	33 A.

(From Report of State Conservation Commission for the biennium ending June 30, 1948).

CHAPTER II

General Considerations: Terms and Concepts

Whenever conditions are such that plants can live and grow, those species that are available and are fitted for the local conditions soon spread a garment over the naked earth. Whether only one species or many occupy an area, a social relation exists. In fact, wherever we look, many individual plants live and work beside one another.

The groupings of species as they are found in Iowa recur with striking similarity in all similar habitats. Equally striking are the differences in the lists of species in unlike habitats. Thus Vegetation as a whole is a tapestry that covers land and water with oft-repeated designs composing a harmonious whole.

Each design, to continue our figure of speech, is a community of living plants. The most conspicuous communities of Iowa are the woodland communities and the grassland communities. As there are many kinds of communities in each of these groups we designate each kind of community as an Association, and each local example of it as a Stand. (cf. Braun-Blanquet, **1932**). We have therefore to consider several kinds of Woodland Associations and several kinds of Grassland Associations, and several other classes as well.

For an understanding of the Association it is necessary to determine what species are present, and the role of each in the life of the community. Obviously a mere list of species is a very inadequate basis for any conclusions. It is necessary to know first of all to what extent each species occurs in the Association. For this purpose one must study several stands of each kind of community, and several sample plots in each stand. For example, my lawn and your lawn are stands of the bluegrass lawn association. One square meter of lawn makes a good sample plot. In oak woods the sample plot should be ten meters square.

The most practical measure of quantity of a species is an estimate of the cover-grade of the species on several sample plots in several stands of the association. The cover-grade expresses the approximate percentage of ground that the plants of that species would cover if projected vertically on the ground. When cover-grade is low, as for example with wild lilies in wet prairie, the frequency of the occurrence of the species in the stand is helpful. This can be expressed as percentage of sample plots in which the species is observed.

When several stands of one kind are compared other generalizations appear. Some species are constantly or practically always found in the stands. Constancy can be expressed in percent of all the stands examined in which a given species occurs. A very different concept is called fidelity. Some species occur in only one kind of association. An example is the cutleaf violet, *Viola pedatifida*, of the prairie. Others occur in two or more associations, as bluegrass in lawns, haylands and pastures. There are various degrees of fidelity. The vitality of a species in an association tells whether the species is really at home there (high vitality) or is a mere interloper. A plant which regularly reproduces in the stand, be it by seeds or by spores, is credited with high vitality. A plum sprout in the lawn, constantly mowed down, ekes out a miserable existence of low vitality.

On occasion the sociability of a species is an important indicator. Sloughgrass often grows in dense stands to the exclusion of everything else. It is highly social. But on the edge of a stand the culms are scattered amongst other plants and are unable to produce flowers and seeds. Vitality and sociability are low. The conclusion is that the species is either working its way into another association ("invading") or is being crowded out by encroachment of the other group. Further study will reveal which conclusion is the better.

All of these terms and concepts are refinements of the older attempts to tell where plants grow and how much. In the older floras we read that a plant is found in "Pine Barrens, common," "in swales, frequent," "dry woods, not rare," or even the double negative "not infrequent." Ecologists listed plants of a community "in order of abundance," the most abundant first, without any measure for abundance.

When the plant associations have been recognized, described and mapped for the State of Iowa, we shall be able to say in what association or associations the plant is found and what is its role in each. As yet we can only give tentative statements, because the associations are not yet defined.

Every plant association is an example of fitness of plant life for the habitat in which it occurs. Every species in the association is fitted for its place in the community. The general appearance of the community (physiognomy) is an expression of fitness, and therefore of the conditions of the habitat. As the conditions change throughout the year, the physiognomy of the community changes. The bare and leafless woodlands of winter take a variety of pastel shades as the spring sunshine woos young leaves from their protective buds. Later on one uniform green prevails until autumn tints the

foliage with crimson and gold. The brown and purple prairie of winter passes through many more seasonal changes as successive waves of different flowers overflow the landscape with kaleidoscopic changes of color. Thus we have seasonal aspects of the vegetation in mid-latitudes. It is not so with the somber monotony of the evergreen forests of the north, on the one hand, or of the broadleaf tropical rain-forest on the other.

In Iowa each community and each species expresses both in structure and behavior its fitness for the habitat. Behavior is responsible for the seasonal aspects. Structure expresses the specific fitness of leaves, stems and roots—yes, and of flowers too. Some of these structures we will now describe.

Submerged aquatics have soft tissues, easily dried out on exposure to air, and a spongy interior due to many large airspaces. This is hydromorphic (water-form) structure. Plants of shady woodlands have firmer tissues, smaller air spaces, and more resistance to evaporation. This is mesomorphic (midway) structure. Leaves exposed fully to sun and wind in Iowa have rigid tissues, very small air spaces, great thickness of epidermis, and hiding of stomata in pits and furrows. They achieve these advantages in so many different ways that a whole book would be needed to describe them all. These adaptations offer a most interesting field of study. Such structure is called xeromorphic (dry form).

In short, our lakes and rivers harbor hydromorphic plants. The lower layers of vegetation in woodlands are mesomorphic. The larger plants of the prairie are uniformly xeromorphic.

CLASSIFICATION OF COMMUNITIES

The Association is defined by the list of plants that compose it. Obviously those species that rank highest in the various respects outlined above make up the Characteristic Combination of Species of the association. This combination of species is peculiar to a certain kind of habitat. So when both association and habitat have been described and correlated, each one may serve as an indicator of the other. Tell me your species and I will tell you where they grow.

It is possible therefore to classify habitats and thence proceed to the naming of the associations. This procedure has been much used. The botanist, however, must classify the associations according to their floristic structure and composition. To him the habitat is "accessory after the fact." We shall follow botanical classification rather than physiographic or climatic. This leaves the way open for a grouping of associations according to physiognomy (appearance).

LAYERING

The simplest possible community is exemplified by the growth of one or a few species of crustose lichens on an exposed rock. This is a one-layered community.

A primeval woodland in eastern Iowa has several layers of vegetation. There is first the layer of tall trees, whose green canopies interlock to form a roof through which only slender shafts of sunshine descend to make pin-hole pictures of the sun upon the ground. Beneath these trees there is a partial layer of shrubs, four to six feet tall. Up to three feet tall there is a more or less dense layer of herbs: nettles, touch-me-nots, grasses and sedges. And on the ground patches of moss and leaves of hepatica form a lowest layer. Ignoring for the moment the layering of roots in the forest soil, this woodland shows four recognizable layers. It will be useful to classify communities by the physiognomy and by the number of layers.

Even in water the plants which root on the bottom occupy definite places, related to depth of water, wave action and currents, silting, and character of substrate. They form definite communities. But there is also a vast floating flora which has no fixed habitation. Even here social relations exist, though in a different manner from that which is found with plants of fixed habitat.

Referring back now to the species of the Woodland Communities we can say that the characteristic species are as already named in Chapter One. They are also those of the highest degree of constancy. Species of high fidelity, that is, found only in one kind of association, are:

Salicetum

Salix amygdaloides
Acer saccharinum
Salix nigra
Betula nigra

Ulmetum

Erythronium albidum
Hydrophyllum virginianum
Platanus occidentalis
Laportea canadensis
Gleditsia triacanthos
Trillium recurvatum

Quercetum rubrae

Hepatica acutiloba
Dicentra cucullaria
Asarum canadense
Staphylea trifolia

The meaning of this is that where one or two of these species of high fidelity are found we can be reasonably certain that the original vegetation was of the community to which those species belong. Along with this conclusion goes an estimation of the type of soil and the microclimate[3] (climate of the exact spot). Several species give much more reliable indications of soil and climate than any one species alone. Species which grow well in two or more associations are much less diagnostic, though they may be much more abundant and conspicuous.

[3] Microclimate is a term used to indicate the climate of one particular spot. The climate of one side of an east-west valley is profoundly different from that of the opposite side. The climate on the south side of a house is very different from that of the north side. And the climate of the north side changes as you go farther and farther from the building. This was clearly brought out in a study of mosses on the Grinnell College campus by Winston Miller (MS unpublished). On the north side of Goodnow Hall about one foot of ground adjacent to the wall was covered exclusively by the broad-leaved moss *Mnium cuspidatum*. Next farther out bluegrass was mingled with the moss, and soon covered the larger portion of the ground. As *Mnium* became weaker a tougher moss, *Brachythecium salebrosum*, appeared with *Mnium* amongst the grasses. Soon *Mnium* disappeared entirely and *Brachythecium* was the only species of moss present. This then became feebler until at fifty feet from the building no moss was to be found. A similar gradation of the same species was observed on the margin of a grove of bur oaks near Heron Lake in southwestern Minnesota. Thus the plant community records and integrates differences in microclimates that would require extensive instrumentation to demonstrate and measure. (cf. Geiger 1950)

CHAPTER III

Shrublands

In many places the woodlands of Iowa end directly on the grasslands. In other places there is an intermediate strip of shrubbery. If this strip is adjacent to the bur-oak-wood the shrubs will be *Rhus glabra* and *Cornus racemosa* over most of the State. In the northeast *Rhus typhina* may substitute for the smooth sumac. Along sheltered slopes and on exposed bottomlands hazel (*Corylus americana*) is a prominent border shrub. These three (or four) are the principal border shrubs. Black raspberry (*Rubus occidentalis*) is usually present. In these borders flourish the blue flowered *Aster laevis*, *A. sagittifolius* and its var. *Drummondii*, some of the white *paniculata* group, the yellow goldenrods (*Solidago canadensis, gigantea*), and the white and the blue bottle Gentians (*Gentiana flavida, andrewsii*). The woodland borders make a splendid foreground for the trees in their autumnal foliage.

On the borders of the elm association, that is, on low moist ground, *Cornus stolonifera* takes the place of *C. racemosa*. Elderberry is common, making 8-inch wide flat white inflorescences in early summer, and equally large heads of little black berries in late summer and fall. The wild plum (*Prunus americana*) often makes dense thickets, bearing the first conspicuous flowers of spring. On the edge of a marsh or pond, button bush (*Cephalanthus occidentalis*) bears white balls of bloom all summer.

In southern Iowa the coralberry (*Symphoricarpus orbiculatus*: coralberry as a garden ornamental, grown for the nurserymen in Holland; buckbrush as a woody weed on bottomland and hillside pastures) is very common in borders and in open woods—so much so as to be a nuisance in pastures. In the west and northwest *S. occidentalis*, wolfberry, with white fruits, makes dense thickets and clumps on the borders of bur oak woods. It is a very vigorous spreader by long shoots just below the surface of the ground. It is much too rampant to be tolerated in a garden.

All of the upland shrubs spread easily and rapidly by means of rhizomes or stolons, i.e., vegetatively. The lowland shrubs more often spread by seeds. In either case the shrubbery is the most mobile of our native plant associations. The borders of the shrubbery are al-

ways moving forward or backward in response to cycles of wet or dry weather. In Iowa they are mostly moving out into the grassland, since the country was settled. What held them in leash before? Time? A long dry cycle? Fire?

The shrublands are in narrow strips wherein vegetational change is easily observed and is often very much in evidence, as will be noted later.

These shrub communities have been extensively studied in Nebraska by Weaver and Thiel (**1917**), Weaver, Hanson and Aikman (**1925**), and Aikman, (**1928**). Curiously enough, they found that along the streams of Nebraska these same shrubs form a strip between woodlands and grasslands, whereas at the head waters of the streams where the flow of water is intermittent, the extreme limit of woody plants is occupied by willow trees (*Salix nigra, amygdaloides*) and cottonwoods (*Populus deltoides*), with no shrubs at all.

In the shrub strip the temperatures of soil and air, the humidity and evaporation, and the light in the lower strata are all intermediate between the values for forest (more humid) and grassland (drier).

COMMUNITIES OF WOODY PLANTS, UNSORTED

The lists of plants made by Professor Bohumil Shimek are of especial value both because he was a very keen observer and because the lists were mostly made before the demands of war and depression and the pursuit of profits had decimated the natural vegetation to its present condition. For our purposes these lists are inadequate because they give no direct clue to the associations represented. Shimek recognized the following categories and made his notes accordingly:

Woodland
Prairie
Swamps, ponds and streams
Sand
Rocks
Weeds

Johnson County. Trip to River Junction, May 9, 1902. On the alluvial bottomlands I noted:

Acer negundo
Acer saccharinum
Arisaema dracontium
Androsace occidentalis
Asarum canadense reflexum
Amorpha fruticosa
Achillea millefolium
Aquilegia canadensis

Betula nigra
Celtis occidentalis
Crataegus mollis
Carya ovata
Carya cordiformis
Capsella bursa-pastoris
Claytonia virginica
Chaerophyllum procumbens
Cardamine douglassii
Clematis pitcheri
Cystopteris fragilis
Ellisia nyctelea
Erythronium albidum
Erigeron philadelphicus
Fragaria virginiana
Geranium maculatum
Gleditsia triacanthos
Galium aparine
Houstonia minima
Isopyrum biternatum
Juglans nigra
Juncus tenuis
Lepidium densiflorum
Menispermum canadense
Populus deltoides
Pyrus ioensis
Onoclea sensibilis
Parthenocissus quinquefolia
Poa pratensis
Phlox divaricata
Podophyllum peltatum
Platanus occidentalis
Prunus americana
Prunus serotina
Prunus virginiana
Potentilla simplex
Polemonium reptans
Quercus bicolor
Quercus imbricaria
Quercus macrocarpa
Quercus palustris
Quercus rubra
Quercus velutina
Rhus radicans
Rhus glabra
Ranunculus septentrionalis
Ranunculus abortivus
Ribes missouriense
Robinia pseudoacacia
Rorippa islandica

Salix amygdaloides
Salix interior
Salix nigra
Smilax herbacea
Sambucus canadensis
Specularia perfoliata
Trillium recurvatum
Tilia americana
Triosteum perfoliatum
Ulmus americana
Veronica peregrina
Viola "cucullata"
Viola pubescens
Vitis riparia
Xanthoxylum americanum

It is obvious that the above list includes characteristic members of the Salicetum, Ulmetum and Quercetum imbricariae, along with strangers from other associations, and some ubiquists.

Jefferson County. On the uplands I noted the following plants:

Achillea millefolium
Aesculus glabra
Antennaria plantaginifolia
Anemonella thalictroides
Adiantum pedatum
Amphicarpa bracteata
Arisaema triphyllum
Aralia racemosa
Asarum "reflexum"
Aquilegia canadensis
Actaea pachypoda
Amelanchier arborea
Corylus americana
Crataegus mollis
Carya ovata
Celastrus scandens
Carex rosea
Cystopteris fragilis
Circaea quadrisulcata
Desmodium glutinosum
Fraxinus americana
Gleditsia triacanthos
Galium triflorum
Galium aparine
Geranium maculatum
Geum canadense
Hydrophyllum virginianum
Juglans cinerea
Juglans nigra

Menispermum canadense
Morus rubra
Ostrya virginiana
Osmorhiza claytoni
Orchis spectabilis
Prunus serotina
Pedicularis canadensis
Potentilla simplex
Potentilla norvegica
Panicum latifolium
Polystichum acrostichoides
Poa compressa
Polygonatum canaliculatum
Polemonium reptans
Parietaria pensylvanica
Podophyllum peltatum
Parthenocissus quinquefolia
Rubus occidentalis
Rubus alleghaniensis
Rhus aromatica
Rhus glabra
Quercus alba
Quercus rubra
Rhus radicans
Rudbeckia serotina
Symphoricarpus orbiculatus
Sambucus canadensis
Smilax tamnoides hispida
Sanguinaria canadensis
Solidago flexicaulis
Solidago ulmifolia
Tilia americana
Ulmus fulva
Uvularia grandiflora
Vitis riparia

This list includes members of Ulmetum, Quercetum rubrae and border associations.

The woodland flora of Dickinson County is extensively listed in The Plant Geography of the Okoboji Region by B. Shimek (**1915**). The floras of nine wooded areas are tabulated. Liehens take 1½ pages, fungi 5½ pages, parasitic fungi and weeds ½ page each, vascular plants 7½ pages. Area 1, Elmerest, consists of Ulmetum and Quercetum macrocarpae. Area 2 is Quercetum macrocarpae along the west shore of West Okoboji Lake. Area 3 at Arnolds Park includes Quercetum macrocarpae and Ulmetum. Area 4, southeast side of East Okoboji Lake, is Q. macrocarpae and Ulmetum, with some elements of Quercetum rubrae. Area 5 between East and West Oko-

boji Lakes, Area 6 at Center Lake and Area 8 along Little Sioux River are forms of Quercetum macrocarpae. Area 9 is the extreme western locality of Quercetum rubrae.

In the following table we have arranged several stands in parallel columns. Column 1 is from Boot's list of woodland plants in Monona County, from his stations 4 and 5, and represents the vegetation of two small areas not definitely bounded, so far as he was able to collect specimens in flower. Number 4 was "dense forest on the south side of a deep east-west gulch"; number 5 was on the north side of the same gulch. Column 2 is Shimek's entire list of woodland plants from Harrison and Monona Counties. Columns 3 and 4 are from Shimek's paper on the Okoboji region, areas 1 and 2 cited above. In column 3 Elmerest, a indicates "deep woods," b "open woods and borders." Column 5 is from Shimek's unpublished notes for Winneshiek County, 1 being near Conover, 2 "toward Moneek."

Although I could indicate the associations to which, in my opinion, each species belongs, I refrain from doing so in the absence of exact data.

The letters preceding the names of plants indicate the life-forms as listed by McDonald (1937).

M, phanerophytes, plants with winter buds 2m. or more above the ground

N, nanophanerophytes, with winter buds 25 to 200cm. above ground

Ch, chamaephytes, with winter buds just above the surface of the earth

H, hemicryptophytes, with winter buds just below or at the surface of the ground, often with a protective covering of dead or living scales, leaves or leaf sheaths

G, geophytes, with winter buds buried in the earth

HH, helophytes (hydrophytes), with winter buds submerged in water, with or without a covering of mud

Th, therophytes, annuals, perennating as seeds; completing the life cycle in one growing season

M	*Acer negundo*	–	–	c	–	–
H	*Actinomeris alternifolia*	–	x	–	–	–
G	*Adiantum pedatum*	–	x	–	–	–
H	*Agastache foeniculum*	–	–	b	–	–
H	*Agastache scrophulariaefolia*	–	–	b	–	–
H	*Agrimonia gryposepala*	–	–	a	–	–
H	*Agrimonia mollis*	5	x	–	–	–
H	*Agrimonia striata*	–	–	a	–	–

H	*Agrostis perennans*	–	x	–	–	–
G	*Allium tricoccum*	–	x	–	–	–
Th	*Ambrosia trifida integrifolia*	4	–	e	–	–
M	*Amelanchier arborea*	–	x	–	x	–
M	*Amelanchier humilis*	–	–	b	x	–
M	*Amorpha fruticosa*	–	–	e	x	–
H	*Amphicarpa bracteata*	–	x	b	–	–
H	*Andropogon gerardi*	5	–	–	–	–
H	*Anemone virginiana*	–	–	a	–	1
G	*Apios americana*	–	x	–	–	1
H	*Aquilegia canadensis*	5	x	b	–	1
H	*Arabis canadensis*	–	x	–	–	–
H	*Arabis perstellata*	–	x	–	–	–
H	*Aralia racemosa*	–	–	a	–	–
G	*Arisaema triphyllum*	5,4	x	–	–	1
H	*Aster cordifolius*	5	x	a	–	–
H	*Aster drummondii*	–	–	–	x	–
H	*Athyrium filix-femina*	–	–	–	–	1
Th	*Bidens vulgata*	–	–	e	–	–
G	*Botrychium virginianum*	–	x	a	–	–
H	*Bromus ciliatus*	–	–	e	–	–
H	*Campanula americana*	4,5	x	a	–	–
G	*Carex davisii*	–	x	–	–	–
G	*Carex gravida*	–	x	–	–	–
G	*Carex gravida laxifolia*	–	–	b	–	–
H	*Carex amphibola*	–	x	–	–	–
H	*Carex blanda*	–	x	–	–	–
G	*Carex pennsylvanica*	4	–	4	–	–
H	*Carex rosea*	–	x	–	–	–
H	*Carex interior*	–	x	–	–	–
G	*Carex sparganioides*	–	x	–	–	–
M	*Carya cordiformis*	–	–	–	–	2
M	*Carya glabra*	5	–	–	–	–
M	*Carya glabra villosa*	5	x	–	–	–
M	*Carya ovata*	–	–	–	x	2
M	*Celastrus scandens*	5	x	b	x	–
M	*Celtis occidentalis crassifolia*	–	x	–	x	–
Th	*Chenopodium boscianum*	–	–	a	–	–
Th	*Chenopodium hybridum*	–	x	a	x	–
G	*Circaea quadrisulcata*	4	x	–	x	–
H	*Cirsium altissimum*	–	x	b	–	–
M	*Clematis virginiana*	–	–	b	–	–

M	*Cornus drummondii*	–	x	–	–	–
M	*Cornus racemosa*	–	x	–	x	2
M	*Cornus stolonifera*	–	x	e	–	–
M	*Corylus americana*	–	x	–	x	2
M	*Crataegus crus-galli*	–	–	–	–	2
M	*Crataegus margaretta*	–	–	–	x	–
M	*Crataegus mollis*	–	x	b	x	–
M	*Crataegus punctata*	–	–	b	x	2
H	*Cryptotaenia canadensis*	4,5	x	a	–	–
H	*Cynoglossum officinale*	–	x	–	–	–
H	*Cystopteris fragilis*	–	x	a	–	–
H	*Delphinium tricorne*	–	x	–	–	–
G	*Dentaria laciniata*	–	x	–	–	–
H	*Desmodium glutinosum*	4,5	x	a	–	–
H	*Desmodium perplexum*	5	x	–	–	–
G	*Dicentra cucullaria*	4	x	–	–	–
Th	*Ellisia nyctelea*	–	x	–	–	–
H	*Elymus villosus*	5	x	a	–	–
H	*Elymus virginicus*	–	–	b	–	–
	Equisetum hyemale robustum	–	x	–	–	–
	Equisetum kansanum	–	x	–	–	–
H	*Erigeron philadelphicus*	–	x	e	–	–
H	*Erigeron pulchellus*	–	x	–	–	–
H	*Erysimum cheiranthoides*	–	–	b	–	–
G	*Erythronium albidum*	5	x	–	–	–
M	*Euonymus atropurpureus*	4	x	–	–	–
H	*Eupatorium fistulosum*	4	x	–	–	–
H	*Eupatorium rugosum*	4,5	x	a	x	–
G	*Euphorbia corollata*	5	–	–	–	–
	Festuca obtusa	–	x	a	–	–
H	*Fragaria vesca americana*	–	x	–	–	–
H	*Fragaria virginiana*	4	x	–	–	–
H	*Fragaria virginiana illinoensis*	–	–	a	–	–
M	*Fraxinus americana*	–	–	–	–	2
M	*Fraxinus pennsylvanica*	–	x	b	x	–
Th	*Galium aparine*	4,5	x	–	–	–
H	*Galium circaezans*	–	x	–	–	–
H	*Galium latifolium*	–	–	a	–	–
H	*Galium triflorum*	–	x	–	–	–
H	*Geranium maculatum*	–	–	–	–	1
H	*Geum canadense*	–	–	b	x	–
H	*Geum virginianum*	4,5	x	a	–	–

	Glyceria nervata	–	x	–	–	–
M	*Gymnocladus dioica*	–	x	–	–	–
H	*Hackelia virginiana*	4	x	a	x	–
G	*Helianthus tuberosus*	–	x	b	–	–
H	*Heliopsis helianthoides*	–	x	–	–	–
G	*Heracleum lanatum*	–	x	c	–	–
H	*Hieracium canadense*	–	–	b	–	–
G	*Humulus lupulus*	–	x	–	–	–
H	*Hydrophyllum virginianum*	4,5	x	a	–	–
H	*Hystrix patula*	4	x	–	–	1
Th	*Impatiens pallida*	4	x	–	–	–
M	*Juglans cinerea*	–	–	–	–	2
M	*Juglans nigra*	–	x	–	–	2
M	*Juniperus virginiana*	–	–	a	–	–
H	*Kuhnia eupatorioides corymbulosa*	5	–	–	–	–
H	*Lactuca canadensis*	–	–	b	–	–
Th	*Lactuca floridana*	4	x	–	–	–
G	*Laportea canadensis*	4,5	x	a	–	–
Th	*Lappula deflexa americana*	–	–	b	–	–
H	*Leersia virginica*	–	–	b	–	–
M	*Lonicera dioica*	–	–	b	–	–
M	*Lonicera dioica glaucescens*	–	x	–	–	–
M	*Lonicera prolifera*	–	x	–	–	–
H	*Lysimachia ciliata*	–	–	c	–	–
M	*Menispermum canadense*	–	x	a	–	–
	Mnium cuspidatum	–	x	–	–	–
H	*Monarda fistulosa*	–	–	b	x	–
G	*Monotropa uniflora*	–	x	a	–	–
M	*Morus rubra*	–	x	–	–	–
H	*Muhlenbergia mexicana*	–	–	c	–	–
H	*Muhlenbergia racemosa*	–	–	c	–	–
H	*Muhlenbergia sobolifera*	–	–	–	x	–
H	*Muhlenbergia sylvatica*	–	–	a	–	–
H	*Nepeta cataria*	–	–	–	–	1
Hs	*Oenothera biennis*	–	–	b	–	–
G	*Orobanche uniflora*	–	–	b	–	–
H	*Osmorhiza longistylis*	–	x	a	–	–
H	*Osmorhiza longistylis villicaulis*	5	x	–	–	–
M	*Ostrya virginiana*	–	x	b	x	2
H	*Oxalis "filipes"*	–	x	b	–	–
H	*Oxalis stricta*	–	x	–	–	–
H	*Panicum lanuginosum*	–	–	b	–	–

Th	*Parietaria pensylvanica*	–	x	a	–	–
M	*Parthenocissus quinquefolia*	–	x	a	x	2
Ch	*Phlox divaricata*	4,5	x	–	–	–
H	*Phryma leptostachya*	4,5	x	a	–	1
Th	*Pilea pumila*	–	x	a	x	–
G	*Poa palustris*	–	–	c	–	–
G	*Poa pratensis*	–	x	–	–	–
G	*Polygonatum commutatum*	–	x	b	x	–
H	*Polygonum cristatum*	–	x	–	–	–
H	*Polygonum punctatum*	–	–	c	–	–
M	*Populus deltoides*	–	–	c	x	–
M	*Populus grandidentata*	–	–	–	–	2
M	*Populus tremuloides*	–	–	–	x	1,2
H	*Potentilla norvegica*	–	–	b	–	–
M	*Prunus americana*	5	x	b	x	–
M	*Prunus serotina*	–	–	–	–	2
M	*Prunus virginiana*	–	x	b	x	–
G	*Pteridium aquilinum*	–	–	–	–	1
M	*Pyrus ioensis*	–	–	–	–	2
M	*Quercus alba*	–	–	a	–	2
M	*Quercus ellipsoidalis*	–	–	–	–	2
M	*Quercus macrocarpa*	5	x	b	x	2
M	*Quercus macrocarpa olivaeformis*	–	x	–	–	–
M	*Quercus rubra*	–	–	–	–	1,2
M	*Quercus velutina*	–	x	–	–	–
H	*Ranunculus abortivus*	4,5	x	–	–	–
M	*Rhamnus lanceolata*	–	x	–	–	–
M	*Rhus glabra*	–	x	b	x	1,2
M	*Rhus radicans*	–	4	b	x	–
N	*Ribes americanum*	–	x	c	x	–
N	*Ribes cynosbati*	4	x	–	–	–
N	*Ribes missouriense*	5	x	b	x	–
N	*Rosa arkansana suffulta*	–	–	–	–	2
N	*Rosa blanda*	–	–	b	–	1,2
N	*Rosa woodsii*	–	x	–	–	–
H	*Rubus alleghaniensis*	–	x	–	–	2
H	*Rubus occidentalis*	–	x	b	x	–
H	*Rudbeckia laciniata*	–	–	c	–	–
H	*Rudbeckia triloba*	–	x	–	–	–
M	*Salix amygdaloides*	–	–	c	x	–
M	*Salix discolor*	–	x	c	x	–
N	*Salix humilis*	–	–	–	–	2

M	*Salix interior*	–	–	–	x	–
Th	*Salsola kali tenuifolia*	5	–	–	–	–
M	*Sambucus canadensis*	–	–	c	–	–
G	*Sanguinaria canadensis*	4	x	–	–	–
H	*Sanicula marilandica*	4,5	x	a	x	1
H	*Scrophularia marilandica*	–	x	b	–	–
H	*Silene stellata*	–	x	b	x	1
H	*Sisyrinchium campestre*	4	–	–	–	–
G	*Smilacina racemosa*	–	–	–	–	1
G	*Smilax ecirrhata*	–	x	a	–	–
H	*Smilax herbacea*	–	x	b	–	1
M	*Smilax tamnoides hispida*	–	x	b	–	–
Th	*Solanum nigrum*	–	x	c	–	–
H	*Solidago canadensis*	–	–	–	x	–
H	*Solidago flexicaulis*	–	–	a	–	–
H	*Solidago gigantea*	–	–	c	–	–
Ch	*Stellaria longifolia*	–	–	c	–	–
N	*Symphoricarpus occidentalis*	–	x	b	x	–
N	*Symphoricarpus orbiculatus*	–	x	–	–	–
H	*Taenidia integerrima*	–	–	4	–	–
H	*Taraxacum officinale*	4.5	x	–	–	–
H	*Thalictrum dasycarpum*	–	–	b	x	–
H	*Thalictrum dioicum*	–	–	a	x	–
H	*Thalictrum revolutum*	–	x	–	–	–
H	*Thaspium aureum*	–	–	b	–	–
M	*Tilia americana*	–	x	a	–	–
H	*Trifolium repens*	4	–	–	–	–
H	*Triosteum perfoliatum*	–	x	–	–	–
M	*Ulmus americana*	–	x	a	–	–
M	*Ulmus rubra*	–	x	b	x	–
M	*Ulmus thomasii*	–	x	–	–	–
H	*Urtica procera*	–	–	c	–	–
M	*Viburnum lentago*	–	–	b	–	–
M	*Viburnum prunifolium*	–	–	b	–	–
H	*Viola cucullata*	–	x	–	–	–
H	*Viola palmata*	–	–	b	–	–
H	*Viola pensylvanica*	4,5	x	–	–	–
H	*Viola pubescens*	4	x	–	–	–
H	*Viola sororia*	–	x	a	–	–
M	*Vitis riparia*	4	x	b	x	1,2
M	*Xanthoxylum americanum*	–	x	b	–	–
H	*Zizia aurea*	–	–	b	x	–

CHAPTER IV

Grasslands

The term prairie as applied to the grasslands of central North America originated with the early French voyageurs. Father Hennepin wrote "Quand on est sur ces côteau [bluffs of the Illinois River valley] on decouvre des belles préries à perte de vue, garnie d'espace en espace de petits bois, qui semblent avoir été plantez exprés" (Whitney **1876**). The word is in common use in France and in Quebec meaning grassland. In Belgium and according to Rübel[4] in Europe generally, a grassy orchard or park with scattered trees may be a "prairie." In the United States the original prairie must be that of Illinois cited above. Whitney, after traveling repeatedly from Chicago to the Rocky Mountains, wrote "Illinois * * * is *par excellence* the prairie State" (italics his). Shimek considered that the grasslands of Iowa were the true prairie. The prairie, he wrote (**1911**), "centers in Iowa." Clements (**1920**) formerly held that "true prairie" was best developed in eastern Nebraska and adjacent portions of Iowa. He called it at its best the *Stipa-Koeleria* Association. Mentzer (**1951**) finds "true prairie" 3 miles north and 1 mile west from Lincoln, Nebraska. Schaffner (**1926**), with more sociological insight, designated the "*Andropogon furcatus* association" as "the true prairie, or *the* prairie." More recently Shively and Weaver (**1939**) tell us that "The true prairie covers * * * northwestern Indiana, most of Illinois, Iowa, northern and eastern Missouri," etc.

Kerner (**1950**) pointed out nearly a century ago that we inevitably run into difficulty when we attempt to use a vernacular word for a scientific concept. He advised that we avoid popular terms and invent, if necessary, new words to express our scientific concepts.

The late Professor Bohumil Shimek of the State University of Iowa was a lifelong student of the prairie. While he never gave a terse dictionary-definition of the word, his usage shows that he included everything in Iowa that is not swamp, lake, river or forest. To him prairie was the product of just one controlling factor: evaporation.

"Exposure to evaporation as determined by temperature, wind and topography is the primary cause of the treelessness of the prairie."

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[4] "Nur diese Wiesen werden von den amerikanischen Botanikern 'Präirie' genannt, während die Gebiete mit armer, offener Strauch und Grasvegetation, die in der allgemeinen und geographischen Literatur Europas meist ebenfalls in den allgemeinen Prarienbegriff gefasst werden, dort nicht dazu gerechnet werden."

(**1911**, p. 230). "* * * the temperature and fineness of the soil, the amount of free soil water, and perhaps other soil qualities, undoubtedly produce some effect, but the determining causes of relative prairie and forest distribution evidently lie in the atmosphere rather than in the soil."[5]

"The prairie was very variable in topography, for it occurred in alluvial valleys, upon flat drift plains, on abrupt slopes,–indeed upon all types of topography in the State, from the flattest to the most broken. Neither was it restricted to particular geologic formations, for it was found, and still exists to a limited extent in its primitive condition, upon every kind of formation which reaches the surface." "—typical prairie is found lying over all the older rocks from the Algonkian to the Cretaceous; on all the drift areas from the Nebraskan to the Wisconsin; on loess of every horizon; on alluvial flats; on sand-dune areas; and on the limited areas in which geest forms the immediate subsoil." "It included territory which varied from the comparatively moist borders of swamps, lakes and streams, to the highest, driest ridges of loess or drift. Indeed, drainage or the absence of water had little to do in determining its distribution." (**1911**, p. 171).

Weaver & Fitzpatrick (**1934**) wrote of the prairie "The absence of trees, the paucity of shrubs and half-shrubs, the dominance of grasses, and a characteristic xeric flora constitute its main features. Neither geological formation, topography nor soil determines the character of the flora which develops under the master hand of climate. In varying the water relations of soil and air they merely bring about changes in the groupings of the dominant grasses and accompanying segregations and rearrangements of the forbs." (A forb is an herbaceous plant that is not a grass, sedge or rush).

Given the near-marginal precipitation of Iowa, with its characteristic seasonal distribution, and the elevation with all that elevation infers, the writers quoted above are right. Defining prairie broadly, it is independent of topography, geology, and even of drainage. It makes its own soil.

The word prairie, then, has no precise scientific meaning. It is a

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[5] "It is our opinion that the steppe zone is a regional phenomenon which represents an intermediate phase between the forest and desert zones. As such it is the result of the regional disposition of climatic factors. The entire combination of climatic features in the steppes is unfavorable to the development of forests. All the remaining factors—the salinization of the soils and subsoils, their mechanical composition and so forth—are of secondary and subordinate importance. The fundamental reasons for the absence of forests in the steppes are: insufficient moisture in summer and dryness of the air with a resulting high rate of evaporation." Berg **1950**.

useful vernacular term for the grasslands of central North America. The map (**Fig. 4**) accurately shows the extent of prairie in Iowa.

No type of vegetation in all the world has been so thoroughly and exhaustively examined as has the prairie. In **1911** Shimek brought together the results of 20 years of mature study in a paper entitled "The Prairies." He gave an extensive review of pertinent literature, along with accumulated data on environmental factors, such as topography, soils, climate, etc., and especially on evaporation. The prairie flora is listed on 8½ pages, with parallel columns for flat, rolling, ridges, prairie openings, alluvial, and sand dunes. Each species is checked in each column for presence, frequency and abundance according to standards then in use. Several areas are included in each column, making sociological evaluation impossible. Shimek's latest ideas are found in the paper of **1948**.

Sampson (**1921**) described the prairie vegetation of Illinois. His "associations" are notably similar to those of Iowa as to species involved, relation to soil and water, and juxtaposition. His diagrams of successions are subject to the criticisms made in our chapter on Vegetational Change.

The most recent and most exhaustive researches are those of J. E. Weaver and his associates in western Iowa and eastern Nebraska. They studied the plants themselves in great detail. The reader is referred to these studies. A few hints of what is covered therein may be helpful.

The beginner may well read Weaver's exact and appreciative "North American Prairie" in The American Scholar (**1944**). The records up to 1934 are admirably summarized in a 180 page illustrated paper on "The Prairie" by Weaver & Fitzpatrick, herein frequently cited as W&F. This paper outlines climate and soils of the prairie, six types of grassland with their major and minor grasses and their principal forbs, the relative importance of each species, height, growth and physiological activity, and the five seasonal aspects. This last topic is treated with an enthusiasm that is all too rare in botanical contributions.

Some of the details are indicated by the following titles. "The environment of the prairie" (**1931**) by Weaver & Himmel gives mechanical and chemical analyses of soils, precipitation, water-content of soil, temperature of air and soil, humidity, wind and evaporation in *Andropogon furcatus* and *Andropogon scoparius* communities at Lincoln, Neb. Clark (**1940**) measured the interception of rainfall by prairie vegetation, and Weaver & Harmon (**1935**) considered run-off and soil erosion. Robertson (**1939**) discussed the ef-

fects of prolonged drought on the prairie, and Weaver & Albertson (**1944**) reported on the recovery of prairie plants after the drought.

"The structure of prairie vegetation" by Steiger (**1930**) is the nearest approach to a sociological account of prairie. The study was made on a 300 acre tract near Lincoln, Nebraska. Two papers, one by Weaver & Fitzpatrick (**1932**) on "Ecology and relative importance of the dominant grasses" and one by Weaver (**1931**) on "Who's who in the prairie," discuss the role of individual species in prairie communities. Blake (**1935**) described the germination and viability of seeds of several prairie plants. Mueller (**1941**) told of the rhizomes of prairie plants, and Weaver (**1920**) published an epoch-making paper on "Root development in the grassland formation." This type of study was extended to include excavations of root systems of mature (50-60 years old) bur oaks on the margin of prairie, to obtain data on the nature and causes of the boundary between grassland and forest (Weaver & Kramer **1932**).

Although only the three western tiers of counties of Iowa are included in the University of Nebraska studies, the general conclusions are quite applicable to our State. Each species that is common to both states plays about the same role in both. Some species considered important by W&F are rare in Iowa. Some important species of eastern Iowa are rare or absent in Nebraska. And it must be remembered that rainfall decreases rapidly from east to west, while evaporation increases, so that the climate of Weaver's studies is perceptibly different from the means for Iowa. Shaffner (**1926**) pointed out that one effect of this increasing drought is to enlarge the domain of the more xeric communities and to move the more mesic down grade into the valleys and bottoms. This phenomenon has already been discussed in relation to the Woodlands.

All of the available lists of prairie plants proceed from a basic classification according to topography and substratum. W&F's most extensive lists are related to "uplands" and "lowlands," and each of these is divided into "high prairie" and "low prairie." The most important grasses are listed first in associations, associes and consociations. The minor grasses and grasslike species are divided into those of "drier grasslands" and those of "wetter grasslands." Apparently the grouping into communities according to their relation to normal vegetational change (succession) does not quite cover the case.

The more refined methods of research and description according to the principles of plant sociology have proved highly instructive and fruitful on the grasslands of Russia, and in the various land-

scapes of central and southern Europe and elsewhere. The next step for the description of vegetation in North America may well be along the lines of plant sociology. In the absence of such studies we can only infer provisionally the major outlines that are appearing. Once the Associations are recognized, their relations to soils and microclimates should become clearer, and each species may be referred to the Associations in which it has a role.

THE ASSOCIATIONS

Hendrickson (**1930**) in his study of insects of Iowa prairies recognized and located eight kinds of grassland communities, distributed as follows:

1. *Stipa spartea-Andropogon scoparius* community. Story, Hamilton, Winnebago, Kossuth and Osceola Counties.
2. *Andropogon scoparius-Bouteloua curtipendula* community. Lyon, Pottawattamie, Fremont and Woodbury Counties.
3. *Andropogon gerardi-Sorghastrum nutans* community. Iowa, Van Buren, Muscatine and Washington Counties.
4. *Andropogon gerardi* community. Story, Hancock, Humboldt, Winnebago, Black Hawk, Kossuth and Plymouth Counties.
5. *Spartina pectinata* community. Story, Iowa, Hancock, Humboldt, Emmet, Winnebago, Black Hawk, Lyon, Plymouth, Kossuth, Harrison, Washington [and Poweshiek] Counties.
6. *Carex* communities. Iowa, Story, Hancock, Winnebago, Black Hawk and Kossuth Counties.
7. *Polygonum amphibium* community. Story, Iowa, Winnebago, Kossuth, Harrison and Mills Counties.
8. *Bouteloua hirsuta-B. curtipendula* community. Story, Hamilton and Osceola Counties.

The grasslands of Iowa will evidently present:

1. a *Stipa spartea-Andropogon scoparius* Association.
2. an *Andropogon scoparius* Association.
3. a *Panicum virgatum-Elymus canadensis* community.
4. an *Andropogon gerardi* Association or Alliance.
5. a *Spartina pectinata* Association.
6. a *Calamagrostis canadensis* Association.
7. a *Phragmites communis* Association, to be compared directly with the Associations of that species on the Atlantic seacoast and in Europe.
8. a *Phalaris arundinacea* Association.

9. a *Scirpus validus* Association.
10. a *Scirpus fluviatilis* Association.

Bordering on these in similar or wetter places are

11. the *Typha latifolia* and *T. angustfolia* Associations.
12. at least two *Carex* Associations (*Carex festucacea, vulpinoidea*).

Perhaps (13) an *Eleocharis palustris* Association. And if this be valid we further postulate a *Leersia* association (14), and (15) a *Sagittaria* Association. The *Sporobolus heterolepis* association of W&F has not been recognized in Iowa.

ANDROPOGON SCOPARIUS COMMUNITIES

Andropogon scoparius is usually the characteristic plant on well drained prairie ridges and slopes. It forms dense round sods from a few inches to a foot or more in diameter, with leaves around 8mm. wide, flat and recurved. The flowering stalks, up to two feet tall, are clustered and bear axillary racemes of clustered spikelets along the upper half. In autumn the silky hairs on the pedicels are conspicuous. And in winter the ruddy umber tints of stems and leaves enable one to recognize a stand at a distance of a quarter of a mile.

In Iowa this grass is accompanied by a large number of other grasses and forbs and a few shrubs. Together they make a dense stand, completely covering the soil. A friend in Nebraska tells me that I will surely find scale-mosses on the ground between the tussocks of prairie grasses. It is not so in Iowa. The stands are too dense.

Characteristic companions of *Andropogon scoparius* in Iowa are *Koeleria cristata,*[6] *Panicum oligosanthes* var. *scribnerianum*, *Sorghastrum nutans*, *Bouteloua curtipendula* and *Stipa spartea* among the grasses, and

Carex pensylvanica
Aster ericoides
Kuhnia eupatorioides corymbulosa
Viola pedatifida
Aster azureus
Aster sericeus

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[6] Rübel (1915) noted in the prairie at Lincoln, Nebraska, "die aus Europa eingeführte *Koeleria cristata* (L.) Pers." On another tour, Dr. Domin of Prague, monographer of *Koeleria* (1907), remarked to the writer during a field trip in Yellowstone Park, "This is *Koeleria* all right but it is certainly not *K. cristata*." Hitchcock (1935) states that *K. cristata* is very variable but "it is not possible to distinguish definite varieties." Clements, Martin and Long report that different environmental conditions can induce the plant to produce only one flower to a spikelet, or two flowers, or three. Certainly no American botanist could say that it is an introduced species.

Hypoxis hirsuta
Viola pedata
Comandra umbellata
Pedicularis canadensis
Baptisia bracteata
B. leucantha
Amorpha canescens
Salix humilis
Liatris scariosa
L. punctata
Solidago missouriensis
S. rigida
S. speciosa angustata
Helianthus laetiflorus rigidus
Psoralea argophylla
P. esculenta
Petalostemum candidum
P. purpureum
Euphorbia corollata
Astragalus crassicarpus
A. canadensis
Agoseris cuspidata
Rosa arkansana suffulta
Sisyrinchium campestre
Ceanothus americanus
Desmodium illinoense
D. canadense
Aster laevis
Lespedeza capitata
Linum sulcatum
Eryngium yuccifolium
Polygala senega
P. sanguinea
Potentilla arguta
Lithospermum canescens
Onosmodium occidentale
Hieracium longipilum
Asclepias tuberosa
A. verticillata
A. viridiflora
Gentiana puberula

Tolstead (1938) found this community occupying well drained ridges in northeastern Iowa. Species he noted accompanying the *Andropogon* were *Bouteloua curtipendula*, *Carex pensylvanica*, *Viola pedata*, *Anemone patens wolfgangiana*, *Oxalis violacea* and *Lithospermum canescens*. Hayden found such communities in northwestern Iowa on rocky hills. She calls the *Andropogon* communities the "true-prairie association of the climax grassland formation."

ANDROPOGON GERARDI COMMUNITIES

The *Andropogon gerardi* communities, "*the* prairie" of Shaffner (1926), occupy places with moister ground. The difference may be due to deeper loessial soils, accumulation of water down slope, or proximity to seepage from beneath. Consequently on relatively steep slopes the two *Andropogon* communities lie at different levels and are easily distinguishable. The intervening strip where the two associations intermingle does not confuse the picture. On very gentle slopes, or on apparently level ground (which never is exactly level) the stands may alternate and merge into one another in a most confusing manner. Furthermore the *A. gerardi* association is as much at home on poorly drained "level" uplands with deep soil as on low moist land. The *A. scoparius* association is mostly on stony ground or on slopes with rapid runoff. On the driest brow of the hill *Stipa spartea* may take the leading role, and on dry mounds of glacial till from Story County northwestward the *Bouteloua* association prevails. In a stand near Ida Grove, Iowa, W&F report 75 to 97% of the basal cover of vegetation was made by *Andropogon gerardi*, 1 to 15% by bluegrass (*Poa pratensis*) and 0 to 4% by *Stipa spartea*. Bluegrass is an introduced species, brought in by the white man.

Some of the companion plants with *A. gerardi* are:

Andropogon scoparius
Panicum virgatum
Koeleria cristata
Sorghastrum nutans
Anemone canadensis
Phlox pilosa
Liatris pycnostachya
Equisetum kansanum
Zizia aurea
Veronicastrum virginicum
Vernonia fasciculata
Hypoxis hirsuta
Heliopsis helianthoides

Thalictrum dasycarpum
Lepachys pinnata
Silphium perfoliatum
Allium canadense
Lathyrus palustris
Monarda fistulosa mollis
Tradescantia ohiensis
Fragaria virginiana

It is these two *Andropogon* communities which, in endless repetition and variation, covered nine-tenths of the grasslands of Iowa.

In the absence of exact association lists these associations can best be described together, as W&F, Tolstead, Shimek, Hayden and others have done, and as the species are listed in Shimek's notes.

MINOR GRASSLAND COMMUNITIES

The *Stipa spartea-Andropogon scoparius* association is a dry land phase of the *Andropogon scoparius* community. Hendrickson locates it in northwestern Iowa. This is in agreement with the findings of W&F. *Stipa spartea* is a frequent component of prairie from Allamakee to Louisa, Harrison and Lyon Counties, but only in the northwest is it abundant enough to give character to an association. In most of the State it is a component of the *Andropogon scoparius* association. Structure of the leaf is almost identical with that figured by Kerner (1894) for the big *Stipa pennata* of the grasslands of central Europe (Hungary).

W&F describe a *Panicum virgatum-Elymus canadensis* community occupying an intermediate zone between the two *Andropogon* associations. The present writer has not seen such a belt in Iowa, nor have I seen these two species in juxtaposition. We find *P. virgatum* in sandy ground with high water table or water content, and *Elymus* in loess soils adjacent to *Andropogon gerardi*. These conditions are not incompatible with the account of W&F, considering differences of climate and soil. The matter needs sociological investigation. But it must always be borne in mind that in different surroundings different combinations of species occur. A plant of dry habitat in a wet climate may be one of wet places in a dry climate. Many examples could be given.

The slough grass association (Spartinetum pectinatae) is the most conspicuous prairie community in contrast with the ubiquitous Andropogoneta. This tall grass usually occupies its terrain to the exclusion of all else. Where the stand is not too dense the dainty little *Galium obtusum* grows more or less abundantly, with tiny white

flowers in clusters in June and July. In autumn *Campanula aparinoides* appears, with small (1 cm.) white bell-shaped flowers striped with pink. Both of these herbs have recurved prickles on the four angles of the stem.

Spartina pectinata is too coarse at maturity for livestock to eat, but may be used for bedding or thatching. The smoothness of the rolled-up leaves makes slough grass hay hard to handle. I have seen a load of it slide off the wagon twice on the way to the barn.

With us the Spartinetum requires a substrate saturated with water most of the time, but with adequate drainage. It occurs on wet river bottoms in acre-wide patches, and on seepage areas ("sloughs") in shallow depressions far up into the uplands. The substrate is densely netted with woody rhizomes, making just the right material for building the sod houses of the early settlers, though *Andropogon gerardi* sods were easier to get and about as good. Thin stands of *Spartina* admit various members of the big bluestem community. Since the land is everywhere drying up, that is, the water table is sinking, this association is usually being invaded by neighboring communities, be they tree, shrub or grass. The wetter margin merges into swamp, with cattail (*Typha latifolia*) and/or reed (*Phragmites communis*). The drier side merges into a *Calamagrostis canadensis* or *Andropogon gerardi* community.

Spartina pectinata is on record from 54 of the 99 counties of Iowa, including all of the four corners. It is undoubtedly in every county, nearly always if not always forming a distinct and well defined Association.

The bluejoint (*Calamagrostis canadensis*) association occurs usually as a pure stand of the grass. The 2 to 3 foot culms are conspicuously naked below the panicle, the leaves are numerous below the uppermost node, producing a dense cover. The community covers a few square rods or yards, on damp but well drained soil. It has not been studied in detail. It occurs all over the State.

The Phragmitetum (*Phragmites communis*) is well developed only in delta land in Muscatine and Louisa counties. But stands of this huge grass are widely scattered over the State. In seepages too wet (?) for *Spartina*, patches of a few square yards or rods of the reed have been seen in Poweshiek, Jasper and Tama counties. Here we must count them in with the prairie. In Louisa and Dickinson counties they are better treated along with hygrophilous and hydromorphic communities.

Canary grass (*Phalaris arundinacea*) occurs in small clumps or

large patches in wet land. A beautiful meadow of this grass may be seen south of Rush Lake in Osceola County.

SOCIOLOGY OF THE PRAIRIE

Tentatively we may consider that the vast Andropogonetalia (alliance of prairie grasses) including all of the communities so far described, covering seven-eighths of Iowa, is characterized by the presence of

Andropogon gerardi, recorded from	72 counties
Andropogon scoparius	59
Panicum virgatum	46
Spartina pectinata	54
Stipa spartea	66
Aster sericeus	50
Viola pedatifida	70

The first four of these are widely distributed from the Atlantic Coast to the Great Plains or beyond, and from Maine to the southern states. On Long Island, Blizzard (**1931**) described an Andropogonetum scoparii as a temporary association on abandoned agricultural land, and Cain et al. (**1937**) described the permanently stabilized natural Andropogonetum Hempsteadi of the Hempstead Plains.

Stipa spartea seems to extend somewhat beyond the limits of the grasslands both east (Pennsylvania) and west (New Mexico). It may well be that in these places it indicates reliets of former extensions of prairie associations.

The *Aster* and *Viola* seem to have a range exactly coextensive with that of the tall grass prairie. They are the species of greatest Fidelity, exclusive species, of the Andropogonetalia, perhaps of an Andropogonion of the prairie region. They are therefore the best indicators of the Andropogoneta of the Prairie Province. It happens often that the plants which give character to the physiognomy of a community are not the most characteristic, i.e. diagnostic, of the community.

There can be no doubt that sociological studies of grassland will reveal a number of subdivisions of the *Andropogon* communities. Some of these will be Associations, some sub-associations and variants. Each will correspond to some combination of soil and water supply, combinations which often recur, forming an extremely variegated pattern of environments matching the gorgeous ever-changing tapestry of colors from May to October in the vegetation. If not that, then chance plays a predominant role—incredibly predominant—in the arrangement of the flower beds that decorate the prairie landscape. We can only suggest some of the conditions, remembering

all the time that so many species are seeking places in the sun that the slightest difference may determine which one succeeds.

Along railroads and roadsides we still can see remnants of prairie. In Iowa County a strip between highway and railroad is brilliant in late May and early June with red-purple cymes of *Phlox pilosa*. As these are fading away there is occasionally a number of 3-foot tall panicles of white flowers of *Melanthium virginicum*. On slightly disturbed banks masses of the deep blue-purple blooms of *Tradescantia ohiensis* stand 2 or 3 feet above the ground. In Tama County it is *Tradescantia bracteata* in broad beds that colors the railroad banks with red, white and blue. In low places *Anemone canadensis* makes beds 20 to 100 feet across, white with inch-wide flowers. In the northern tiers of counties *Galium boreale* vies with *Anemone* for the attention of the traveler, and *Zigadenus* substitutes for *Melanthium*.

In midsummer *Heliopsis helianthoides*, *Echinacea pallida* (or *E. angustifolia* in the northwest), are conspicuous in all prairies, above the grasses.

A prairie with a gentle slope has on the upper levels *Anemone patens*, *Astragalus caryocarpus*, *Psoralea esculenta* and *Viola pedatifida* in the spring; *Liatris punctata* and *aspera*, *Astragalus canadensis*, *Solidago missouriensis* and *Helianthus laetiflorus rigidus* in midsummer; *Aster azureus*, *A. sericeus*, *A. ericoides*, *Solidago rigida* and *S. speciosa angustata* in autumn. The season ends with the enchanting deep blue flowers of *Gentiana puberula*, which open their ciliated eyelids only in bright sunshine.

In slightly lower ground, where excess water drains away (when there is any) *Habenaria leucophaea* (*H. blephariglottis* of Shimek **1911**) stands among the summer grasses. Later *Liatris pycnostachya* decks the field, while in the scarcely perceptible valley *Spartina pectinata* comes into bloom.

In the dense sod of the prairie each plant survives because it can best meet the situation year in and year out. For nearly all are perennials. The variables of the situation are mostly a matter of the amount and kind of water.

The ground water is saturated with salts of lime. When this water seeps out slowly, as where loess meets gumbotil, it may evaporate and concentrate without any runoff. The result is a wet alkaline spot or fen, to be considered later. If the seepage is sufficient to maintain a flow, concentration does not occur, the water is relatively neutral, and a spring exists, with *Caltha palustris* and *Lobelia siphilitica* and *Spartina* and *Phragmites*.

When the water rises by capillarity to the surface of the ground and evaporates, concentration of salts occurs. A gentle rain will wash these salts down again, and then bathe the upper roots with distilled water. The osmotic adjustment of the plant must be considerable. A heavier rain will wash the surface salts to a lower level on the surface. This may be a depression of only an inch or two. Here the salts accumulate from all around with increased speed throughout the season of summer showers. Thus great variations in "the situation" may exist in very short distances. The significance of such conditions has been well described by Adriani (**1945**) for the salt-marshes of Holland. Similar studies might shed much light on the "spotty" arrangement of plants of the prairie. It is a matter of daily analyses of soil and soil water under each type of vegetation.

These conditions are clearly indicated by the findings of W&F. They noted an abundance of *Andropogon gerardi* on level upland where there is slow drainage and little or no runoff. On the margin where flat land turns to sloping, *Stipa spartea* is abundant; drainage and runoff are at a maximum and there is no accumulation of water; this is the driest strip. The upper slope is the realm of *Andropogon scoparius* and its associates; runoff is rapid and there is very little accumulation of water from above. Base of slope and flat land below have accumulation of water by runoff from above as well as from subsurface moisture, that is, a shallow water table. In these places *A. gerardi* again is abundant.

Clearly it confuses the picture to speak of upland and lowland plants. The vegetation is actually dispersed in associations, each one related to certain climatic factors rather than to altitude of the land. Braun (**1936**) has described similar conditions, on a larger scale, in southern Ohio, where the moisture-loving *Lobelia cardinalis* occurs on flat (i.e. undrained) uplands in oakwoods.

BIOLOGY OF THE PRAIRIE

From this point onward we are obliged to consider the Grasslands as a unit, for we want to examine the relation of grasslands to animals, and of the grasses and forbs to one another. The latter topic includes root relations, relation of tops as shown by layering and seasonal aspects, the accumulation and disposal of humus, and the maintenance of nitrogenous and mineral foods.

The Tallgrass Prairie seems to be peculiarly independent of the animal world except for the destructive hand of man. It is not likely that bison or antelope were ever numerous enough in Iowa to make perceptible inroads upon the vegetation. They may have helped to transport seeds. Badgers and various rodents were once numerous.

The spermophiles and pocket gophers still are. But there is little evidence that they are or were important for the vegetation. Gophers will gnaw off the roots of small oak trees close to the trunk. The advance of oaks into grasslands may have been hampered in that way. On the other hand it is likely that squirrels have planted many an acorn and hazel nut in the margins of prairie. There are no precise data.

The brilliant display of showy flowers in the prairie from May to October is evidence that anthophilous insects always had an important place in the pollination of prairie plants. The functioning insects were of various classes: butterflies and moths, flies, bees. The honey bee was imported from Europe, but, running wild, it moved into the prairie country ahead of the white man (Irving 1835). Hunting bee trees was a common pursuit when the northern boundary of Iowa was being surveyed. Washington Irving (1835) tells of such an exploit in "Indian Territory" in 1832. The insect visitors of prairie flowers in Illinois were listed in a long series of papers by Charles Robertson of Carlinville. Pammel's little book entitled Ecology deals only with the pollination of flowers by insects. The Yucca moth performs its miracles on the bluffs of western Iowa, and, *mirabile dictu*, in gardens all over the State.

The flowers that depend upon insects for pollination indicate to the botanist the extent and importance of this phenomenon, even though it is not possible, in many cases, to prove that self pollination does not occur. We have in the State many Ranunculaceae, Geraniaceae, Rosaceae, Hypericaceae, Umbelliferae and Liliaceae whose flowers are open to all comers. We have also the red columbine and trumpet creeper for the humming birds. Larkspurs and the very rare aconite admit only certain visitors. The mints and snapdragons (scus. lat.) are often highly specialized insect-flowers. Composites are free for all, and the most abundant flowers of the State. Leguminosae are on every prairie, but not all are truly papilionaceous: e.g. *Amorpha*, *Petalostemum*, *Cassia*. We have a big blue iris (*I. virginica*) in wet land pollinated by bumble bees. And the Iowa orchids run the gamut from the relatively simple *Liparis*, *Aplectrum*, and *Spiranthes* to the gorgeous big yellow, the big pink and white, and the little white *Cypripediums*, the *Orchis spectabilis* with half inch spurs, and the big white *Habenaria leucophaea* with spurs up to an inch and a half long. This last flower exhales a delectable fragrance at twilight, and must be pollinated by crepuscular sphinx moths.

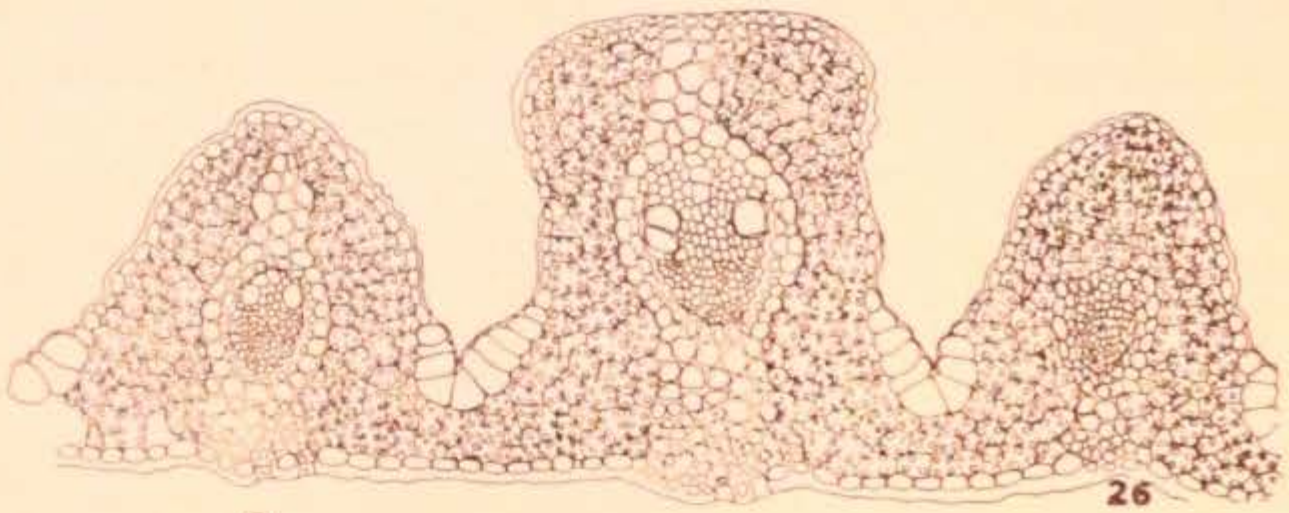
The movements of flowers or their parts in relation to pollination

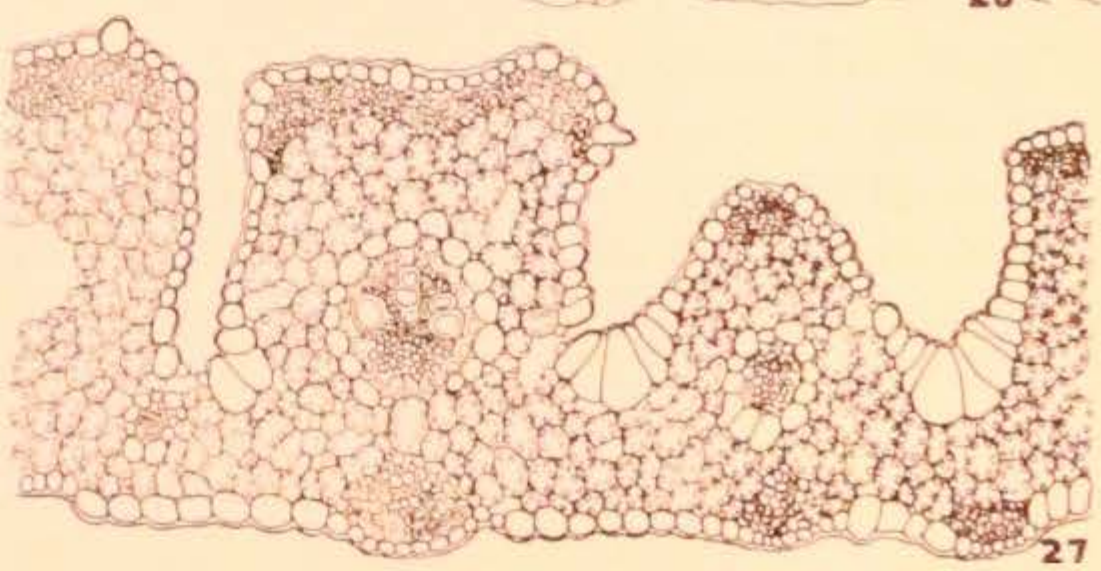
are especially shown by the first and last flowers of the seasonal pageant, the pasque flower and the prairie gentian. The lovely pasque flower spreads its two-inch lavender perianths only in warm sunshine, that is, at such times as insects may be on the wing. At night or on dull days the sepals bend up and in, completely covering the green carpels and golden anthers and exposing only their silvery furry backs to the weather. How many times one flower can do this is not known, nor do I know whether the movements are due to unequal growth at the base of the floral leaves as in the tulip, or to changes in turgidity of the cells as with the leaflets of clover and oxalis. The behavior of the pasque flower seems especially appropriate because it blooms in early spring, April, when nights are cold and rains frequent. Cold nights in autumn make the behavior of the gentian similarly appropriate.

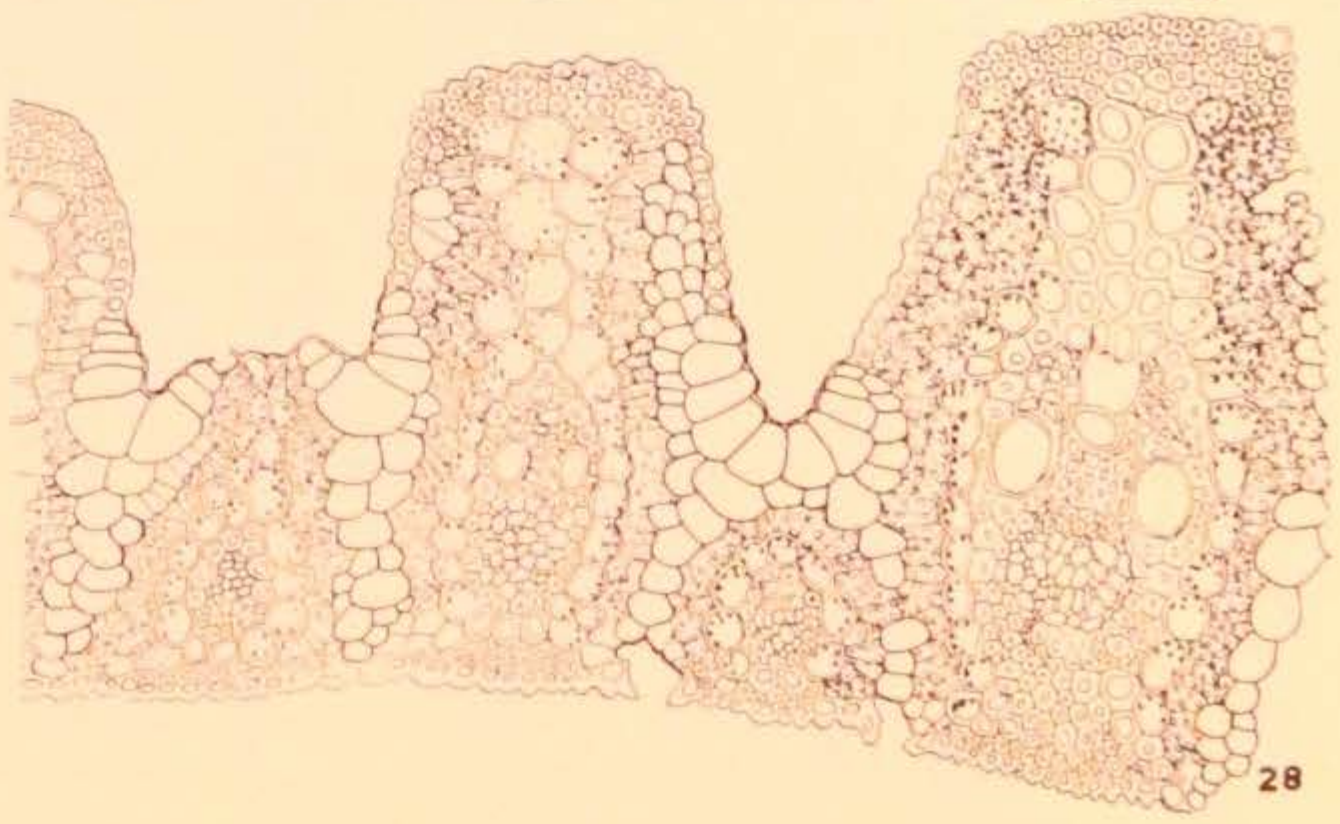
The xeromorphic structures of 67 species of "prairie plants" were studied and tabulated by E. Shimek (**1915**). She gave drawings of leaf sections of seven forbs and one grass. Of these *Dalea alopecuroides*, *Oxytropis Lambertii* and *Panicum oligosanthes scribnerianum* are the most suggestive. All of the figures show very small internal air spaces, or none at all. *Andropogon scoparius* and *Sorghastrum nutans* were well figured by C. B. Weaver (**1897**), *Echinochloa crus-galli* and *Sporobolus* spp. by Serrine and Pammel (**1896**), and *Zea mays* by Combs (**1898**).

W&F (**1932**) gave very characteristic sections of *Andropogon gerardi*, *A. scoparius*, *Boutelona curtipendula*, *Elymus canadensis*, *Koeleria cristata*, *Panicum virgatum*, *Sorghastrum nutans*, *Spartina pectinata* and *Stipa spartea*. They recognized three types of structure. *Elymus*, *Andropogon* and *Sorghastrum* have leaves of nearly uniform thickness, with groups of large hinge-line cells in the upper epidermis. *Stipa*, *Koeleria* and *Spartina* (**Fig. 11**) have deep longitudinal furrows in the upper surface of the leaf, with hinge-cells at the bottom of the furrows. In both of these types the hinge cells lose water readily, contract, and cause the leaf to roll up into a long tube, with the air pores inside. The exposed lower surface of the leaf is very impervious to water. In the third type, shown by *Panicum* and *Boutelona*, the leaf has slight depressions between the parallel veins, and each vein is surrounded by a "wreath" of photosynthetic cells.

Lommasson (**1948**) gives photographs of cross sections of leaves of eight species of grasses. His *Agropyron repens*, *Phalaris arundinacea picta* and *Phragmites communis* are of the *Elymus* type. *Aristida basiramea*, *Sphenopholis obtusata* and *Stipa columbiana* ap-







FIGS. 26–28.—Fig. 26, cross-section of leaf of *Stipa spartea;* fig. 27, cross-section of leaf of *Koeleria cristata;* fig. 28, cross-section of leaf of *Spartina michauxiana;* ×150.

Fig. 11. Xeromorphic structures of grass leaves, after W&F 1932, Figs. 26-28

proach the *Stipa* type of W&F. *Panicum virgatum* is alike in both papers. *Poa pratensis* is of a mesic type unlike any of the others.

Amongst forbs *Eryngium yuccifolium* and *Yucca glauca* show very pronounced xeromorphic structures. The latter species belongs to the Great Plains flora, reaching its eastern limit on the sun-baked wind-swept loessial hills bordering the Missouri River Valley. Both species have a stout cord of lignified fiber cells along the margins of the leaves (**Fig. 12**). This makes it almost impossible to tear the leaf crossways, and almost impossible for a caterpillar or grasshopper to attack the leaf along the margin. The jaws of an insect work right and left, not dorso-ventrally as in vertebrates. A caterpillar stands astride of the margin of the leaf to gnaw away the tissues. Strong lignified bands along the margin make this procedure difficult.

Both species have strong cords of lignified tissue accompanying the veins. In *Yucca* the cord is on one side of the vein. In *Eryngium* a cord fills the space between epidermis and vein on both sides, forming the familiar I-beam structure emphasized by Haberlandt, and making for rigidity in the dorsiventral plane.

The stomata of *Eryngium* are slightly depressed on the upper surface of the leaf, not at all on the lower. The stomata of *Yucca* are sunken into a pit within a pit. The guard cells are reinforced by special neighbor cells. The epidermal cells have the outer walls greatly thickened and cutinized. (**Fig. 12**)

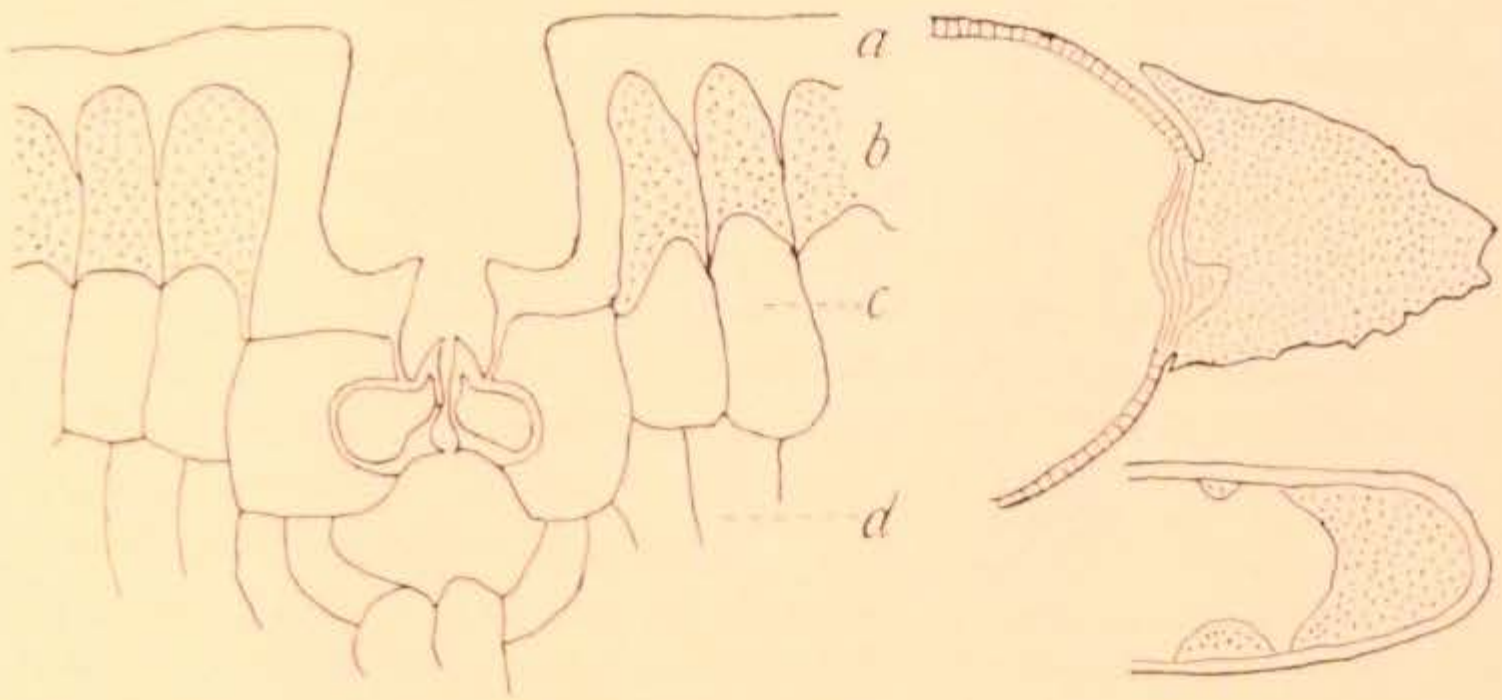


Fig. 12. Stoma of *Yucca glauca*; a, cuticle; b, cutinized layer; c, lumen of epidermal cell; d, palisade. On right, upper, margin of leaf of *Yucca*; lower, margin of leaf of *Eryngium yuccifolium*. Fiber tissue stippled. Original.

In considering the relation of prairie plants to one another we may begin with the root systems. There is a greater weight—more pounds—of plant material in the ground than in the air on an Iowa

grassland. And Weaver's (Weaver and Kramer 1932) oak trees had about the same weight of wood in the ground as in the air.

Roots of different species in the prairie penetrate and spread out at different depths, thus utilizing all of the resources of the soil down to about five feet below the surface. The result is a kind of layering, like the layering of trees, shrubs and herbs in woodland. Weaver (1920) states that of 43 species of typical prairie plants in Nebraska 14% absorb almost entirely in the upper two feet of soil. Among these are *Elymus canadensis*, *Koeleria cristata* (1.5 ft.), *Sporobolus asper* and *Stipa spartea*. 21% are rooted mostly from two to five feet down; e.g. *Andropogon scoparius*, *Sorghastrum nutans*, *Petalostemum candidum*, *Solidago rigida*, *Verbena stricta*. 65% have roots that reach depths below five feet, a penetration of 8 to 12 feet being common and a maximum of over 20 feet sometimes being attained.

Some of these are

Agropyron repens
Amorpha canescens
Andropogon gerardi
Aster ericoides
Astragalus crassicarpus
Baptisia bracteata
Boutelova curtipendula
Ceanothus ovatus
Echinacea pallida
Glycyrrhiza lepidota
Kuhnia eupatorioides
Lespedeza capitata
Liatris punctata
Lygodesmia juncea (in western Iowa only)
Meliilotus alba (introduced)
Panicum virgatum
Poa pratensis (introduced)
Psoralea argophylla
Rosa arkansana
Silphium laciniatum
Solidago canadensis and *missouriensis*
Spartina pectinata
Vernonia baldwinii

The lateral spread of roots is usually very small, six inches more or less.

Weaver's (1920) records show a much greater mass of plant material in prairie soils of Iowa than in Nebraska, owing to the greater rainfall and more luxuriant growth in Iowa. He notes also that depth and spread of roots of a given species differ with the climate.

His figures cannot be assumed to apply exactly to plants growing in central or eastern Iowa.

This vast amount of sub-surface vegetation is the chief source of the humus in the rich black prairyerth soils. The dead tops of plants add a copious annual increment of humus, much of which is oxidized where it falls, adding only its mineral constituents to the soil. Some surface humus is mixed with the soil through the activities of earthworms, ants and small rodents.

Apparently the processes that remove the dead tops of plants on virgin prairie were able to keep pace with the annual accumulation, so that a layer of peat did not develop as would be the case in a cooler, wetter climate, and as did occur in water-logged spots in northern Iowa. The age-long stability of prairie vegetation is proof of an equally age-long equilibrium in soil conditions.

If we wish to preserve some remaining bits of prairie it is necessary to know whether the disposal of dead vegetation takes place in an enclosure as it did on the primeval prairie. It seems very likely that occasional burning of the dry grasses and forbs during the resting season was necessary to prevent excessive accumulation of such material. If fires contributed to the natural equilibrium of plants and soil, we will be obliged to burn our prairie relicts at intervals of three to five years, or to mow them in the resting season and haul off the dry and useless crop. Mowing during the growing season will certainly prevent some species from producing seed. As commonly practised mowing for hay does encourage the invasion of bluegrass and the sweet clovers, to the great detriment of the prairie. Pasturing is much more destructive than mowing. Many a so-called "virgin" prairie, that is, a pasture that has never been plowed, proves to be only a poor bluegrass sod with some native goldenrods, *Verbena stricta* (*Grindelia squarrosa* in western Iowa) and a few introduced weeds. Enclosure of such a remnant is likely to result in complete mastery of bluegrass, knee-high when erect, ankle deep when down, to the exclusion of every other herb (Dickinson and Jasper Counties). It was Shimek's belief that prairie vegetation will return when cultivated prairie land in Iowa is abandoned. Apparently sometimes it does. Other observers find that regeneration of prairie takes place extremely slowly (Anderson **1936, 1946**) or not at all.

Mineral nutrients were brought up from considerable depths by the deeper-rooting plants, and were left on or near the surface. The

nitrogen balance was maintained by the numerous leguminous plants, with root tubercles, which are always important constituents of prairie. This contribution to the fertility of the soil and the stability of the prairie is absolutely essential. Some of the species are *Baptisia bracteata* and *leucantha*, *Psoralea esculenta* and *Amorpha canescens*, which occur as scattered individuals; *Petalostemum* species at closer intervals; and *Lespedeza capitata*, *Desmodium canadense* and *illinoense*, *Psoralea argophylla* and *floribunda* which usually occur in large social groups. The silvery leaves of the last two are conspicuous in the landscape. The others are noticeable chiefly for their showy flowers. Freshly turned prairie sod yields a soil so rich in nitrogen as to be unfavorable to plants accustomed to more sterile conditions.

SEASONAL ASPECTS

No botanist can describe the prairie without reference to the different heights of the plants, the layering of the vegetation, and the seasonal aspects of it. As in the woodlands, but more so, the earliest flowers of spring must complete the life cycle before their supplies of light and water are taken over by the dense growth of taller plants. So we have *Anemone patens*, *Agoseris cuspidata*, *Antennaria neglecta*, *Viola pedata*, *Oxalis violacea*, *Viola pedatifida*, *Androsace occidentalis*, *Draba caroliniana*, *Houstonia minima* and *Hypoxis hirsuta*, none of them over six inches tall, blooming before the middle of May. In late May and early June *Phlox pilosa* and the *Tradescantias* are the chief show pieces, with *Anemone canadensis* in low places. After that dozens of species crowd one upon another until frost. This pageant has inspired the encomiums of lovers of beauty, and drawn forth the eloquence even of botanists.

The earliest prevernal bloomers of the prairie, according to W&F are *Carex pensylvanica*, *Antennaria neglecta*, *Anemone patens*, *Erythronium mesochoreum*, *Anemone caroliniana* and "fennel-leaved parsley."

The vernal aspect, beginning late in April, brings rapid growth of later-flowering tall grasses and forbs, and the flowering of the following, which I have arranged in groups according to color:

Blue to purple

Tradescantia bracteata
Tradescantia occidentalis
Tradescantia ohiensis
Viola pedata
Viola pedatifida

Yellow to orange

Hypoxis hirsuta
Lithospermum canescens
Lithospermum incisum
Zizia aurea

Pink to red and purple

Astragalus caryocarpus
Oxalis violacea
Phlox pilosa
Tradescantia bracteata
Vicia americana

White

Allium mutabile
Anemone canadensis
Baptisia leucophaea
Ceanothus americanus
Fragaria virginiana
Sisyrinchium campestre
Tradescantia bracteata

Grass

Poa pratensis

There is some predominance of purple colors.

Summer, beginning the last week of May, brings:

Blue to purple

Amorpha canescens
Delphinium tricorne
Penstemon grandiflorus
Psoralea argophylla
Psoralea floribunda

Yellow to orange

Asclepias tuberosa
Lilium michiganense
Linum sulcatum
Oenothera spp.
Rudbeckia hirta
Silphium integrifolium
Silphium laciniatum
Silphium perfoliatum
Solidago missouriensis
Heliopsis helianthoides

Pink to red and purple

Desmodium canadense
Desmodium illinoense
Echinacea angustifolia
Echinacea pallida
Lilium philadelphicum
Petalostemum purpureum
Rosa arkansana suffulta
Rosa woodsii

White

Achillea lanulosa
Delphinium virescens
Erigeron ramosus
Galium boreale
Glycyrrhiza lepidota
Penstemon albidum
Petalostemum candidum
Zygadenus glaucus

Grass

Stipa spartea

In late summer come:

Blue to purple

Gentiana puberula

Yellow to orange

Helianthus grosseserratus
Helianthus laetiflorus rigidus
Helianthus maximiliani
Helianthus tuberosus
Kuhnia eupatorioides
Rudbeckia subtomentosa
Silphium spp.
Solidago canadensis
Solidago gigantea
Solidago nemoralis
Solidago rigida
Solidago speciosa

FUNGI OF THE PRAIRIE

Parasitic and saprophytic fungi are abundant but usually not conspicuous on the Iowa prairie. One may usually see in autumn rusts on sunflower and goldenrod and sloughgrass, but the hosts

seem to be unhurt by the disease. The coarse weed, *Iva xanthifolia*, in northwestern Iowa always harbors *Basidiophora* in white sheets on some of the lower leaves, again apparently unhurt. I have seen a prairie knob in Tama County with thousands of the tiny plants of *Draba caroliniana* white with bloom, and the leaves mostly white with a mildew, *Peronospora parasitica*. Next year only one *Draba* was found, and afterward none at all. Apparently the fungus completely wiped out that outpost of the little crucifer. Other than this we have no record of damage to prairie plants by the numbers of parasitic fungi—at least one species of parasite on nearly every species of flowering plants. An exhaustive host index of all known parasitic fungi in Iowa has been published by Gilman and Archer (1929).

The importance of saprophytic fungi in destroying the vast quantity of dead leaves and stems added annually to the ground cover by prairie vegetation cannot be overestimated. A stabilized grassland can exist only when soil and surface conditions are stable, that is where the annual increment of dead material is somehow removed as fast as it tends to accumulate. Otherwise the ground cover would consist of an ever deeper and deeper layer of such material. Inevitably some plants would be suppressed, others would enter the community, and a new community would replace the old. In an enclosure of bluegrass this increase of dead material makes an ankle-deep layer where no seed can take root and even the bluegrass itself is reduced to purely vegetative growth (Jasper and Dickinson Counties).

That the equilibrium of the prairie was greatly if not wholly mediated by saprophytic fungi is beyond doubt. Any handful of surface debris will yield in cultures a whole flock of fungi, among which certainly species of *Alternaria*, *Chaetomium*, *Cladosporium*, *Sordaria* and *Trichoderma* are common and important. The myxomycetes *Physarum cinereum* and *Didymium squamosum* are also common.

Whether these fungi and perhaps various bacteria, insects, earthworms and snails accounted for the entire equilibrium is a serious question. It is highly likely that prairie fires at intervals of one to five years were necessary in order to maintain the balance. Certain it is that the prairie as we knew it flourished with a regimen of occasional burning, and we know of no prairie that was not occasionally burned.

Nature herself experimented with areas where abundance of water prevented the destruction of vegetable matter. Depressions on the recent glacial drifts have developed a genuine sedge-peat with a

unique flora. And calcareous seepages have built up raised bogs, fens, with accumulation of peat and tufa to as much as 14 feet in depth.

The maintenance of the State-owned prairie preserves requires a solution to the problem of the equilibrium of growth and decay, as well as that of the invasion of the normal bordering shrubs and trees, and introduced plants.

Most botanists will inquire about the large saprophytic fungi of the prairie. Did, or do, mushrooms and puffballs grow on the prairie? This question cannot be satisfactorily answered. We find many species in pastures, to be considered later. But if and how they existed before the advent of agriculture in these lands will never be known. A friend tells me that puffballs grew on the prairie in Hamilton County, Nebraska, in 1878, in the era of the sod house. Schaffner (**1913**) reported for the "typical prairie" of Kansas giant puffballs and various other species of puffballs, toadstools and stinkhorns. Macbride (**1896**) had several species from meadows and pastures, but none from tallgrass prairie in Iowa. Paige (**1928**), in Webster County, Iowa, remarked that "prairie is generally poor for the collecting of fleshy fungi." I have never seen fleshy fungi in a tallgrass community.

Parasitism among the flowering plants exists in small amount on the prairie. *Comandra umbellata* is abundant in the *Andropogon scoparius* association and is said to attach its roots to the roots of neighboring asters and goldenrods. Several species of dodder (*Cuscuta*) are native in Iowa, but they occur in thickets or wet lands rather than on prairie proper. *Orobanche ludoviciana* is rarely found, associated with species of *Artemisia* (Lyon County, Shimek **1899**).

SAND FLORA

We have surveyed briefly the major components of natural vegetation in Iowa: Woodlands and Grasslands. These take on peculiar expressions in sandy lands, as on the old dunes near Missouri Valley (Shimek **1910**) and on the east side of glacial lake Calvin (Schoewe **1920**; Kay and Graham **1943**), and on the flat delta lands near the mouth of the Iowa-Cedar River. These areas were minutely studied by Shimek (**1917**). More recently the Browns (**1939**) have described Great Sand Mound in Louisa and Muscatine Counties and R. Brown (**1949**) has collected from sandy areas along the Wapsipinicon and Maquoketa Rivers in Jones County.

The sands of Jones and Muscatine Counties have many species in common and can be considered together. The tree communities have already been mentioned. Treeless areas present a unique congeries of plants, mostly in very open stands. Nearly everywhere the 2 to 3 foot woolly stalks and flower clusters of *Froelichia floridana* (*F. campestris* Small) are to be seen. Beneath and among these are the serrate leaves and glandular inflorescences of *Croton glandulosus septentrionalis*, and the spiny burs of *Cenchrus longispinus*. About as tall as *Froelichia* are the smooth, branching stems of *Euphorbia hexagona*. This group of species, occurring on the delta and dune sands of Muscatine and Louisa and Jones Counties may well be called an Association of *Froelichia* and *Euphorbia hexagona*. At certain spots in all three counties *Tephrosia virginiana* (var. *holosericea*) is a member of this association, and again *Opuntia rafinesquii* or *Euphorbia dentata*. The principal grass, often coloring the landscape, is *Tridens flavus*. *Cyperus filiculmis* and *C. schweinitzii* are additional members of the community and often *Hypericum gentianoides*, *Monarda punctata*, *Strophostyles leiosperma* and *Polanisia trachysperma*.

Shimek (**1917**) listed 397 species of "sand plants," most of which are by no means characteristic of sand. Many are the merest accidentals, or plants that happen to be close enough to sandy areas to be counted. In the report of the State Geological Survey, Vol. 10, 1910, Shimek described the dune vegetation of Harrison County.

Sandy beaches of Iowa lakes present very few unique features. *Potentilla paradoxa* is one of these, seen only in such places. *Polanisia graveolens*, usually on such sandy areas, occurs in many dry places all over the State.

In the following pages I have assembled lists of prairie plants from limited, though not bounded, areas. These give some idea of possible association lists. They relate primarily to the two *Andropogon* associations.

Column 1. Allamakee County. High hill west of New Albin. Prairie. 1, on lower slopes; 2, in middle section added; 3, near the top; 4, on very top of hill. Shimek's notes.

Column 2. Clinton County. "Large prairie openings on top of Eagle Point above ledges. *Andropogon scoparius* very common." Prairie. Shimek's notes.

Column 3. Fremont County. Prairie-steppe, top of loess ridge, Hamburg, Aug. 28, 1917. Shimek's notes.

Column 4. Johnson County. Rock Island right-of-way two to four miles east of Iowa City, according to Lotz (1935) and Shimek's 1925 paper and unpublished notes. "Upland prairie," "true prairie." Several associations and mixtures are included and cannot be unscrambled.

Column 5. Lyon County. "Upland prairie near Larchwood." Aug. 16, 1910. Shimek's notes.

Column 6. Muscatine County. "Upland prairie west of Bayfield on Illinois Drift." Aug. 29, 1923. Shimek's notes.

Column 7. Poweshiek County. From observations of H. S. Conard.

Column 8. Weaver & Fitzpatrick. Chief forbs and grasses of Upland Prairie; 2, chief forbs and grasses of Lowland Prairie. Of this list *Coreopsis palmata, Ceanothus americanus, Liatris squarrosa, Salix humilis, Oxytropis lamberti* and *Potentilla arguta* are found only on uplands. *Cicuta maculata, Asclepias incarnata* and *Polygonum coccineum* are found only in lowlands. The others range from uplands to lowlands or vice versa.

Some of the differences between Shimek's lists and those of W&F are due to chance, but some are due to different ideas as to what is prairie. With a careful working out of the Associations discrepancies will disappear or be adequately explained and agreement on the facts of distribution will be complete. We can hardly expect agreement on classification and nomenclature before the millenium.

The letters preceding the names of plants indicate life-forms, as given by McDonald 1937.

HH	helo- and hydrophytes
M	microphanerophytes
MM	mega- and mesophanerophytes
N	nanophanerophytes
Ch	chamaephytes
Gb	bulb geophytes
Grh	rhizome geophytes
Grt	root-tuber geophytes
Gst	stem-tuber geophytes
Hp	proto-hemicryptophytes without runners
Hpr	proto-hemicryptophytes with runners

Hrr rosette plants with runners
Hs semi-rosette plants without runners
Hsr semi-rosette plants with runners
Th therophytes (annuals)

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Muscatine County	Poweshiek County	W & F
Hsr	*Achillea millefolium*	1	–	–	x	–	x	x	x
Grh	*Agropyron smithii*	–	–	–	x	x	x	–	–
Hs	*Agropyron trachycaulon*	–	–	–	–	x	–	–	–
Hsr	*Agrostis alba*	–	x	–	–	–	–	–	–
Hs	*Agrostis scabra*	–	–	–	x	x	–	–	–
Gb	*Allium canadense*	–	–	–	–	–	–	x	2
Gb	*Allium stellatum*	–	–	–	–	–	–	–	x
Th	*Amaranthus albus*	–	–	–	–	x	–	–	–
Th	*Ambrosia artemisiifolia*	2	x	–	x	x	x	–	–
Hpr	*Ambrosia psilostachya*	2	–	x	–	x	–	–	–
Th	*Ambrosia trifida*	–	–	–	–	–	x	–	–
M	*Amorpha canescens*	1,4	x	x	x	x	–	x	x
Hpr	*Amphicarpa bracteata comosa*	–	–	–	x	–	–	x	2
Hs	*Andropogon gerardi*	1	x	x	x	x	x	x	2
Hs	*Andropogon scoparius*	2,4	x	x	x	x	x	x	x
Hs	*Anemone canadensis*	–	–	–	–	–	–	x	2
Hs	*Anemone cylindrica*	2	x	–	x	x	–	x	x
Ch	*Antennaria campestris*	–	–	–	–	–	–	–	x
Ch	*Antennaria neglecta*	2	–	–	x	–	–	x	–
Ch	*Antennaria plantaginifolia*	1	x	–	–	–	–	x	2
Hp	*Apocynum cannabinum*	2	–	x	–	–	x	x	2
Hp	*Apocynum sibiricum*	–	–	–	x	–	–	–	–
Hs	*Artemisia caudata*	2,4	–	–	–	–	–	–	–
Hs	*Artemisia glauca*	2	–	–	–	–	–	–	–
Hs	*Artemisia ludoviciana*	–	–	–	x	x	–	x	2
Hp	*Asclepias incarnata*	–	–	–	–	–	–	x	2
Hp	*Asclepias longifolia*	–	–	–	–	–	x	–	x
Hp	*Asclepias stenophylla*	–	–	–	–	–	–	–	x
Hs	*Asclepias sullivantii*	–	–	–	–	–	–	–	2
Grh	*Asclepias syriaca*	4	x	–	x	x	x	x	–
Hp	*Asclepias tuberosa*	–	–	–	x	–	–	x	x
Hp	*Asclepias verticillata*	–	x	x	x	x	x	x	2
Hp	*Asclepias viridiflora*	2	–	–	–	–	–	x	x
Hp	*Asclepias viridiflora linearis*	–	–	–	–	x	–	–	–

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Muscatine County	Poweshiek County	W&F
Grh	*Asparagus officinalis*	–	–	–	–	–	x	–	–
Hs	*Aster azureus*	–	x	–	x	–	–	x	x
Hs	*Aster laevis*	2	–	–	x	x	–	x	x
Hsr	*Aster ericoides*	1,4	x	x	x	x	x	x	x
Hpr	*Aster novae-angliae*	–	x	–	x	–	–	–	–
Hsr	*Aster praealtus*	–	–	–	–	–	–	x	2
Hsr	*Aster oblongifolius*	2,4	–	–	–	–	–	–	–
Hs	*Aster sagittifolius*	–	–	–	–	–	–	x	x
Hs	*Aster sericeus*	1,4	–	–	x	x	–	x	x
Hp	*Astragalus canadensis*	–	–	–	–	x	–	x	2
Hs	*Astragalus caryocarpus*	–	–	–	–	x	–	x	x
Hs	*Astragalus lotiflorus*	–	–	x	–	–	–	–	–
Hp	*Baptisia leucophaea*	–	x	–	x	–	–	x	x
Hp	*Baptisia leucantha*	–	–	–	x	–	x	x	x
Hsr	*Boutelova curtipendula*	1,4	–	x	x	x	–	x	x
	Boutelova hirsuta	1	–	x	–	–	–	–	–
	Boutelova oligostachya	–	–	x	–	–	–	–	–
Gst	*Cacalia tuberosa*	–	–	–	x	–	–	x	2
Grh	*Calamovilfa longifolia*	–	–	x	–	–	–	–	–
Hpr	*Campanula rotundifolia*	2	–	–	–	–	–	–	–
Th	*Cassia fasciculata*	–	–	x	x	–	–	x	2
Hs	*Castilleia sessiliflora*	–	–	x	–	–	–	–	–
	Carex cephalophora	2	–	–	–	–	–	–	–
Hs	*Carex cristatella*	–	–	–	x	–	–	–	–
Hs	*Carex festucacea*	–	–	–	x	x	–	–	–
Grh	*Carex pensylvanica*	–	–	–	x	–	–	–	–
	Carex sartwellii	–	–	–	x	–	–	–	–
N	*Ceanothus americanus*	4	x	–	x	–	x	x	x
N	*Ceanothus ovatus*	2,4	–	–	–	–	–	–	–
N	*Ceanothus ovatus pubescens*	–	–	x	–	–	–	–	x
Th	*Cenchrus longispinus*	1	–	–	–	–	–	–	–
Th	*Chenopodium leptophyllum*	4	–	–	–	–	x	–	–
Hs	*Cicuta maculata*	–	–	–	–	–	–	x	2
Gr	*Cirsium arvense*	–	–	–	–	x	–	–	–
Hs	*Cirsium canescens*	–	–	–	–	x	–	–	–
Hs	*Cirsium discolor*	4	x	–	x	–	x	–	–
Hs	*Cirsium hillii*	2	–	–	x	–	–	x	–
Hs	*Cirsium iowense*	–	–	–	x	x	–	x	–
Hs	*Cirsium undulatum*	–	–	–	–	–	–	–	2

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Muscatine County	Poweshiek County	W&F
Grh	*Comandra umbellata*	2,4	–	–	x	–	–	x	x
Hp	*Convolvulus sepium*	–	–	–	x	–	x	x	–
Hs	*Coreopsis palmata*	1,4	x	–	x	x	–	x	x
Hs	*Coreopsis tripteris*	–	–	–	x	–	x	x	–
N	*Cornus racemosa*	4	–	–	–	–	–	x	–
M	*Corylus americana*	2,4	–	–	–	–	x	x	–
Th	*Dalea enneandra*	–	–	x	–	–	–	–	–
Hs	*Delphinium virescens*	–	–	–	–	–	–	x	x
Hp	*Desmodium canadense*	–	–	–	x	x	x	x	x
Hp	*Desmodium illinoense*	1	x	–	x	–	–	x	x2
Hs	*Echinacea angustifolia*	–	–	–	–	x	–	–	–
Hs	*Echinacea pallida*	–	–	–	x	–	–	x	x
Th	*Ellisia nyctelea*	–	–	–	x	–	–	–	–
Hs	*Elymus canadensis*	3	x	x	x	x	x	x	2
Hs	*Elymus virginicus*	–	–	–	x	–	–	–	–
Grh	*Equisetum arvense*	–	–	–	x	–	–	x	2
Grh	*Equisetum hyemale intermedium*	–	–	–	x	–	–	–	–
Grh	*Equisetum kansanum*	–	–	–	x	–	–	x	2
Hs	*Eragrostis spectabilis*	–	–	–	–	–	x	–	–
Th	*Erigeron annuus*	–	–	–	–	–	–	–	2
Th	*Erigeron canadensis*	4	–	x	x	x	x	x	–
Hsr	*Erigeron philadelphicus*	–	–	–	–	–	–	–	2
Th	*Erigeron ramosus*	2	–	–	x	x	–	x	x
Grh	*Eryngium yuccifolium*	–	–	–	x	–	–	x	x
Hp	*Eupatorium altissimum*	–	–	–	–	–	x	–	–
Grt	*Euphorbia corollata*	1,4	x	–	x	–	x	x	x
Hp	*Euphorbia heterophylla*	–	–	x	–	–	–	–	–
Th	*Euphorbia supina*	4	–	–	–	–	–	–	–
Th	*Euphorbia maculata*	–	x	x	x	–	x	–	–
Th	*Euphorbia marginata*	–	–	x	–	–	–	–	–
Th	*Euphorbia serpyllifolia*	–	–	x	–	x	–	–	.
Hsr	*Fragaria virginiana*	2,4	–	–	x	x	–	x	2
Th	*Gaura* spp.	–	–	–	–	–	–	–	2
Hp	*Galium obtusum*	–	–	–	–	–	–	x	2
Hp	*Gentiana puberula*	–	–	–	x	x	–	x	x
Th	*Gerardia aspera*	–	–	x	–	–	–	x	–
Grh	*Glycyrrhiza lepidota*	–	–	–	–	–	–	x	2
Th	*Gnaphalium obtusifolium*	2	–	–	–	–	–	x	–
Th	*Hedeoma hispida*	–	–	x	–	x	–	x	x

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Muscatine County	Poweshiek County	W & F
Hs	*Helenium autumnale*	–	–	–	–	–	–	x	2
Ch	*Helianthemum bicknellii*	2	–	–	–	–	–	x	–
Hp	*Helianthus grosseserratus*	4	–	–	x	–	x	x	2
Grt	*Helianthus laetiflorus rigidus*	1	–	x	x	x	x	x	x
Hp	*Helianthus maximiliani*	–	–	–	–	x	–	–	2
Hsr	*Helianthus occidentalis*	2	–	–	x	–	–	–	–
Gst	*Helianthus tuberosus*	–	–	–	–	–	–	x	2
Hs	*Heliopsis helianthoides*	4	–	–	x	x	–	x	2
	Heuchera richardsonii	–	–	–	x	–	–	–	–
Hp	*Hieracium canadense*	–	x	–	–	–	–	–	–
Hs	*Hieracium longipilum*	–	–	–	–	–	–	x	x
Th	*Hordeum jubatum*	–	–	–	x	–	–	–	–
Hs	*Houstonia angustifolia*	–	–	x	–	–	–	–	–
N	*Hypericum spathulatum*	–	–	–	–	x	–	–	–
Hp	*Hypericum sphaerocarpum*	–	–	–	x	–	x	–	–
Gst	*Hypoxis hirsuta*	–	–	–	x	–	–	x	2
Th	*Iva xanthifolia*	–	–	–	–	x	–	–	–
N	*Juniperus communis*	1	–	–	–	–	–	–	–
Hs	*Koeleria cristata*	3	–	–	x	x	–	x	x
Hs	*Krigia biflora*	–	–	–	x	–	–	–	–
Hp	*Kuhnia eupatorioides corymbulosa*	1,4	x	x	x	x	x	x	x
Hs	*Lactuca canadensis*	–	x	–	x	–	x	–	–
Hs	*Lactuca ludoviciana*	2	–	–	x	x	–	x	–
Hs	*Lactuca scariola integrata*	–	–	–	–	x	–	–	–
Hp	*Lathyrus palustris*	–	–	–	–	–	–	–	2
Hs	*Lepachys pinnata*	1,4	–	–	x	x	x	x	x2
Th	*Lepidium densiflorum*	–	–	–	x	x	–	–	–
Hp	*Lespedeza capitata*	–	x	–	x	–	x	x	x
Gb	*Lilium michiganense*	–	–	–	–	–	–	x	2
Gb	*Lilium philadelphicum*	–	–	–	–	–	–	x	–
Gst	*Liatris cylindracea*	1	–	–	–	–	–	–	–
Gst	*Liatris punctata*	–	–	x	–	–	–	x	x
Gst	*Liatris pycnostachya*	–	–	–	x	–	x	x	x
Gst	*Liatris aspera*	1,4	x	–	x	x	x	x	x
Gst	*Liatris squarrosa*	–	–	–	x	–	–	–	x
Th	*Linum sulcatum*	2,4	–	–	x	x	–	x	x
Hs	*Lithospermum arvense*	–	–	–	–	–	–	–	2
Hp	*Lithospermum canescens*	3	–	–	x	x	–	x	x

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Mountaine County	Poweshiek County	WAP
Hp	*Lithospermum croceum*	–	–	–	–	–	–	–	x
Hp	*Lithospermum incisum*	1	–	–	–	x	–	–	x
Hs	*Lobelia spicata*	–	–	–	x	–	–	x	2
Hpr	*Lycopus americanus*	–	–	–	–	–	–	–	2
	Lygodesmia juncea	–	–	x	–	x	–	–	x
Hpr	*Lysimachia ciliata*	–	–	–	–	–	–	x	2
Hpr	*Lythrum alatum*	–	–	–	–	–	–	x	2
Hs	*Melilotus alba*	–	–	x	–	–	x	–	–
Grt	*Mirabilis linearis*	–	–	–	–	–	–	–	x
Grt	*Mirabilis nyctagineus*	–	–	–	x	–	x	x	2
	Monarda fistulosa mollis	1,4	x	x	x	–	x	x	2
Hs	*Muhlenbergia cuspidata*	–	–	–	x	–	–	–	–
Hsr	*Muhlenbergia racemosa*	–	–	x	x	x	–	–	–
Hs	*Oenothera biennis*	3,4	–	–	x	–	x	x	2
Hs	*Oenothera parviflora*	–	–	–	x	–	–	–	–
Hs	*Oenothera rhombipetala*	–	–	–	–	–	x	–	–
Hs	*Oenothera serrulata*	–	–	x	–	x	–	–	–
Hs	*Onosmodium occidentale*	1	x	x	–	–	–	x	x
	Oxalis "corniculata"	–	–	–	x	–	–	–	–
Hp	*Oxalis stricta*	–	–	x	–	–	–	–	2
Gb	*Oxalis violacea*	–	–	–	x	–	–	x	2
Hs	*Oxytropis lambertii*	–	–	x	–	x	–	–	–
Th	*Panicum capillare*	–	–	x	–	x	–	–	–
Hs	*Panicum lanuginosum fasciculatum*	–	–	–	–	–	–	x	–
Hs	*Panicum leibergii*	–	–	–	x	–	–	–	–
Hs	*Panicum oligosanthes scribnerianum*	1	x	–	x	–	x	x	–
Grh	*Panicum virgatum*	3	–	–	x	–	x	x	2
Hpr	*Parthenium integrifolium*	–	–	–	x	–	x	–	–
Hs	*Pastinaca sativa*	–	–	–	–	x	x	–	–
Hs	*Pedicularis canadensis*	–	–	–	x	–	–	x	x
Hs	*Pedicularis lanceolata*	–	–	–	–	–	–	x	x
Hs	*Penstemon grandiflorus*	–	–	–	–	x	–	–	–
Hs	*Penstemon "hirsutus"*	–	–	–	x	–	–	–	–
Hp	*Petalostemum candidum*	1,4	x	x	x	x	–	x	x
Hp	*Petalostemum purpureum*	1,4	x	–	x	x	x	x	x
Hp	*Phlox pilosa*	–	–	–	x	x	–	x	2
Grh	*Physalis heterophylla*	2	x	–	x	–	–	x	2

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Muscatine County	Poweshiek County	W&F
Grh	*Physalis lanceolata*	–	–	–	–	–	–	–	x
Grh	*Physalis virginiana*	2	–	–	x	x	–	x	2
N	*Physocarpus opulifolius*	3,4	–	–	–	–	–	–	–
Th	*Plantago purshii*	–	–	–	x	x	–	–	x
Hr	*Plantago rugelii*	–	x	–	–	–	–	–	–
Hsr	*Poa compressa*	4	x	–	x	–	–	–	–
Grh	*Poa pratensis*	4	–	–	x	–	x	–	–
Th	*Polygala incarnata*	–	–	–	–	–	–	–	x
Th	*Polygala sanguinea*	–	–	–	x	–	–	x	–
Hp	*Polygala senega*	–	–	–	–	–	–	x	x
HH	*Polygonum coccineum*	–	–	–	–	–	–	x	2
Th	*Polygonum convolvulus*	–	–	–	–	x	–	–	–
Th	*Polygonum ramosissimum*	–	–	–	–	x	–	–	–
Hs	*Potentilla arguta*	1,4	–	–	x	x	–	x	x
Hs	*Potentilla norvegica*	–	–	–	x	–	–	x	2
Hsr	*Potentilla simplex*	2	–	–	x	–	–	x	–
Hs	*Prenanthes racemosa*	–	–	–	x	–	–	x	–
Hsr	*Prunella vulgaris*	2	–	–	–	–	–	–	–
Hp	*Psoralea argophylla*	–	–	–	–	x	–	x	x
Grt	*Psoralea esculenta*	–	–	–	–	–	–	–	x
Hp	*Psoralea floribunda*	–	–	–	–	–	–	–	x
Hpr	*Pycnanthemum tenuifolium*	–	x	–	x	–	x	x	2
Hpr	*Pycnanthemum virginianum*	–	–	–	–	–	–	–	2
M	*Rhus glabra*	1,4	x	x	x	–	x	x	–
N	*Rhus radicans*	2	–	–	x	–	–	x	2
N	*Rosa arkansana*	–	–	–	–	–	–	–	x
N	*Rosa arkansana suffulta*	–	x	–	x	x	x	x	–
Hs	*Rudbeckia serotina*	–	–	–	x	–	x	–	2
Hs	*Rudbeckia subtomentosa*	–	–	–	x	–	x	x	–
Grh	*Ruellia humilis*	–	–	x	x	–	–	–	x
Hs	*Rumex altissimus*	–	–	–	x	–	–	–	–
Hs	*Rumex crispus*	–	–	–	–	–	x	–	–
N	*Salix humilis*	–	–	–	x	–	–	x	x
Th	*Salsola kali tenuifolia*	–	–	x	–	–	–	–	–
Hp	*Scrophularia lanceolata*	3	–	–	x	–	–	–	–
Gst	*Scutellaria parvula*	2	–	–	x	–	–	x	–
Hs	*Senecio aureus*	–	–	–	–	–	–	x	2
Hsr	*Senecio plattensis*	–	–	–	x	–	–	–	x
Th	*Setaria glauca*	–	–	–	–	x	–	–	–

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Muscatine County	Poweshiek County	W & F
Th	*Setaria viridis*	–	–	x	–	–	x	–	–
Th	*Silene antirrhina*	2	–	–	–	–	–	–	–
Hs	*Silene stellata*	–	–	–	x	–	–	–	–
Hpr	*Silphium integrifolium*	–	–	–	x	–	x	x	2
Hs	*Silphium laciniatum*	3	–	–	x	–	x	x	2
Hs	*Silphium perfoliatum*	–	–	–	–	–	x	x	2
Hsr	*Sisyrichium angustifolium*	–	–	–	–	–	–	–	x
Hsr	*Sisyrinchium campestre*	–	–	–	x	–	–	x	x
Grh	*Smilacina stellata*	–	–	–	x	–	–	–	x
Hsr	*Solidago altissima*	–	–	–	–	–	–	–	2
Hpr	*Solidago canadensis*	–	x	x	x	x	x	x	2
Hpr	*Solidago gigantea*	–	–	–	x	–	–	x	–
Hpr	*Solidago graminifolia*	–	–	–	x	–	x	x	x
Grh	*Solidago missouriensis*	1	–	x	x	x	x	x	x
Hs	*Solidago mollis*	–	–	–	–	–	–	–	x
Hs	*Solidago nemoralis*	1,4	x	x	x	x	x	x	–
Hs	*Solidago rigida*	1,4	x	x	x	x	x	x	x
Hs	*Solidago speciosa angustata*	2,4	–	x	x	–	–	x	x
Hsr	*Sorghastrum nutans*	–	x	–	x	x	–	x	2x
Hsr	*Spartina pectinata*	–	–	–	–	–	–	x	2
Th	*Specularia perfoliata*	–	–	–	x	–	–	x	x
Hs	*Sphenopholis obtusata*	–	–	–	x	–	–	–	–
Hs	*Sporobolus cryptandrus*	–	–	–	x	–	–	–	–
Hs	*Sporobolus heterolepis*	–	–	–	x	x	–	x	x
Gst	*Stachys palustris*	–	–	–	–	–	–	x	–
Hs	*Stipa spartea*	3	–	–	x	x	–	x	x
N	*Symphoricarpus occidentalis*	–	–	x	–	–	–	–	–
Hpr	*Teucrium canadense*	–	–	x	x	–	–	x	2
Hs	*Thalictrum dasycarpum*	–	–	–	x	–	–	–	2
Hp	*Tradescantia bracteata*	–	–	–	–	–	–	–	2
Hp	*Tradescantia ohiensis*	–	–	–	x	–	–	–	–
Hs	*Verbascum thapsus*	4	–	–	–	–	–	–	–
Hp	*Verbena hastata*	–	–	–	–	–	–	x	–
Hp	*Verbena stricta*	1,4	–	x	x	x	x	x	–
Hp	*Vernonia baldwini*	–	–	–	–	–	–	x	2
Hp	*Vernonia fasciculata*	–	–	–	–	–	–	x	2
Grh	*Veronicastrum virginicum*	–	x	–	x	–	–	x	–
Hp	*Vicia americana*	–	–	–	–	–	–	–	2
Hr	*Viola "fimbriatula"*	–	–	–	x	–	–	x	2

		Allamakee County	Clinton County	Fremont County	Johnson County	Lyon County	Muscatine County	Poweshiek County	W & F
Hr	*Viola papilionacea*	–	–	–	x	–	–	x	2
Hr	*Viola pedata*	–	–	–	–	–	–	x	–
Hr	*Viola pedatifida*	2	–	–	x	x	–	x	x
MM	*Vitis riparia*	2	–	–	–	–	x	x	–
Ch	*Yucca glauca*	–	–	x	–	–	–	–	–
Hs	*Zizia aurea*	–	–	–	x	–	–	x	2

Following is a record of a 10 m. quadrat in the "Floete Prairie" a half mile south of Iowa Lakeside Laboratory in Dickinson County (plowed and planted with corn in 1949). For these notes I am indebted to Mr. Harry Blomstrand of Denison, Iowa, a student at the laboratory. The date was June 26, 1947.

	Species	C	V
G	*Poa pratensis*	2	4
H	*Andropogon scoparius*	3	4
H	*Stipa spartea*	x	4
H	*Koeleria cristata*	x	4
H	*Panicum oligosanthes scribnerianum*	x	4
H	*Phlox pilosa*	x	4
M	*Amorpha canescens*	1	4
H	*Lithospermum canescens*	x	4
H	*Solidago rigida*	1	4
H	*Anemone cylindrica*	x	4
G	*Solidago missouriensis*	x	4
H	*Aster laevis*	x	4
H	*Aster ericoides*	x	4
G	*Helianthus laetiflorus rigidus*	x	4
H	*Coreopsis palmata*	x	4
G	*Eryngium yuccifolium*	x	4
H	*Melilotus officinalis*	x	3
G	*Comandra umbellata*	x	4
N	*Rosa arkansana* ?	x	4
H	*Astragalus caryocarpus*	x	4
H	*Sisyrinchium campestre*	x	4
H	*Silphium laciniatum*	x	sdl.
Ch	*Antennaria neglecta*	x	4
	Psoralea esculenta	x	4
H	*Kuhnia eupatorioides*	x	4
H	*Viola pedatifida*	x	4

Outside of the quadrat but evidently in the same association:

H *Zizia aurea*
H *Cirsium iowense*
G *Physalis heterophylla*
H *Astragalus canadensis*
M *Rhus glabra*
H *Tragopogon pratensis*
G *Liatris* sp.
H *Trifolium pratense*
H *Petalostemum* sp.
H *Aster sericeus*
Equisetum kansanum
N *Ceanothus americanus*
Psoralea argophylla
H *Heliopsis helianthoides*

Plants present but foreign to the association: *Poa pratensis, Melilotus officinalis, Rhus glabra, Trifolium pratense.* All of these are destructive of the association except *Trifolium.* It seems to be neutral.

C is covergrade: x, present; 1, 20% or less; 2, 20% to 40%; 3, 40% to 60%.

V is vitality: 4, completing the life cycle regularly; 3, occasionally completing the life cycle, but growing well.

The letter preceding the name of the plant indicates the life-form.

PRAIRIE AREAS

In 1944 Dr. Ada Hayden (**1946**) prepared a list of areas of unbroken prairie that might well be preserved by the State under the care of the Conservation Commission. The list follows:

Cherokee County

Pilot Rock Township, Sec. 15 and 22. 160 acres
Cedar Township, Sec. 16, north ½. 320 acres

Crawford County

East Boyer Township, Sec. 7, n. ½. 25 acres

Dickinson County

Lakeville Township, Sec. 23W. 20 acres (mostly plowed in 1949)
Lakeville Township, Sec. 17, w. ½. 320 acres
Lakeville Township, Sec. 29, n.e. ¼ and s.e. ¼. 200 acres
Lakeville Township, Sec. 28, s.w.¼. 200 acres
Lakeville Township, Sec. 33, s.w. ¼.
Okoboji Township, Sec. 4
} 320 acres

Lakeville Township, Sec. 17, 20, 21, 28, 33. 2½ sections
Diamond Lake Township, Sec. 28, n.w. ¼. 160 acres

Emmet County

Emmet Township, Sec. 28, w. ½. 314 acres
Estherville Township, Sec. 18. 10 acres

Guthrie County

Seeley Township, Sec. 22, n.w. ¼. 20 acres

Howard County

"Hayden Prairie," acquired by State 1948
Chester Township, Sec. 23, n.e. ¼
Chester Township, Sec. 33, n.e. ¼, and n.e. ¼ of s.w. ¼ } 199 acres

Ida County

Battle Creek Township, Sec. 33, s. ½ of s.w. ¼. 60 acres (one-half was plowed in 1949)

O'Brien County

Waterman Township, Sec. 33, w. ½. 400 acres
Waterman Township, Sec. 34, s. ¼. 320 acres

Pocahontas County

Belleville Township, Sec. 36, n.e. ¼. 160 acres. Kalso Prairie, acquired by the State.
Roosevelt Township, Sec. 13, s. ½ of s.e. ¼.

Pottawattamie County

Washington Township, Sec. 21, n. ½ of s.e. ¼. 20 acres

In general old cemeteries and strips of land along the railways are the most promising places to look for prairie remnants. E.g.

Black Hawk County

Cemetery near Waterloo.

Butler County

Butler Center cemetery near Allison.

Cedar County

Rochester cemetery near Tipton.

Hamilton County

Between Highway U. S. 20 and railroad, east of Duncombe.

Iowa County

Between Highway U. S. 6 and railroad east of Ladora.
At crossing of Highway U. S. 6 and railroad west of Homestead.

Johnson County

East of airport, Iowa City.

Monroe County

Cemetery near Albia.

Palo Alto County

Highland cemetery 4 miles n.e. of Ruthven.

Poweshiek County

Grant Township, Sec. 19, s.e. ¼ of n.w. ¼ of n.w. ¼, 2 miles southwest of Grinnell, along railroad. About 10 acres.

CHAPTER V

Aquatic Communities

The waters of Iowa make homes for a number of unique plant communities. Fresh deposits of sand and silt on the inner sides of sharp curves of streams and on lake shores are quickly overgrown with vegetation. Different plant forms follow one another on these "new lands" in such rapid succession that we defer their description to a later page where Vegetational Change must be considered. Confining ourselves now to plant associations of greater permanence, we find in deep blowouts where ponds exist, in oxbow ponds along the streams, whether permanently watery or drying up in summer, and in the countless ponds and lakes of the three later Wisconsin drifts, many submerged, emersed and littoral types of communities of greater or lesser extent and duration. Akin to these on the landward side are the communities of poorly drained swales which characterize the Iowan drift, the similar communities of seepage places in the prairie, and the peculiar alkaline (calcareous) seeps in northern Iowa properly called fens, locally known as "Hanging bogs."

EMERSED AQUATIC COMMUNITIES

The most conspicuous and ubiquitous of these aquatic communities are those of the bulrush (*Scirpus validus*) and cattail (*Typha latifolia* and *angustifolia*). A band of *Scirpus* runs along the shores of Clear Lake for miles, in water from one to three feet deep. Rush Lake in Osceola County is surrounded and dotted all over with stands of *Scirpus*. Along the south shore of Rush Lake the cattails (both species) occupy the ten foot belt nearest shore, in dense stands, 6 to 7 feet tall above the water. With the cattails we expect to find *Utricularia vulgaris*, *Spirodela polyrhiza*, *Lemna minor*, *L. trisulca* (frequent) and *Wolffia punctata*, the smallest flowering plant, smaller than an ordinary pin head.

Scirpus and *Typha* appear in lesser quantity almost everywhere that water is permanently on the surface of the ground. In smaller or larger clusters they await the course of events, spreading rapidly if the wet place grows larger, dwindling and dying out if the land dries up.

Of similar growth and habit is that most tolerant yet not common giant grass, *Phragmites communis*. In small clusters in fresh prairie

seeps, and on peaty calcareous fens, this grass forms large exclusive stands in the Iowa-Cedar delta region. In Europe it is a common weed, even in potato fields. With us it never invades arable land.

Wild rice (*Zizania*) is one of the most stately and useful of our aquatic grasses. It must have 3 to 12 inches of water continuously. The long slender seeds, wild rice of the Indians and the grocery stores, attract countless birds: migrating bob-o-links, slaughtered by thousands as "reed birds"; blackbirds and starlings. Wild rice has been so much planted for the attraction of birds that one cannot be sure which stands are native. A five acre stand of the tall form (8 to 10 ft.) in southeastern Jasper County (recently destroyed) and a small patch of the short form on the east side of Spirit Lake seemed to be native. The species was reported by Pammel et al. (1905) for Lyon, Emmet, Story and Decatur Counties, and eastward.

A plant distinctly of the shores of ponds and lakes where there is no wave action is the water smartweed, *Polygonum amphibium*, and var. *harturightii*.

Arrowleaf (*Sagittaria*) makes exclusive communities up to an acre in size in shallow water or on mud around the margins of ponds and lakes, with leaves as much as 18 inches tall. The muddy bottom contains a dense mat of roots and rhizomes, with tubers the size of a walnut. These solid starchy tubers are eaten by some kinds of ducks. They were much used for food by Indians of the northern plains, and these aborigines taught the Lewis & Clark party to dig and use them. Three species occur in Iowa: *S. latifolia*, *S. rigida* and *S. cuneata*. *S. cuneata* (Tama County) is here reported for the first time. Any of these will produce broad leaves in absence of standing water, narrow leaves in shallow water, and almost filiform blades and lobes when "up to their necks" in water. Like *Scirpus* and *Typha*, *Sagittaria* occurs in small groups along streams and seeps, awaiting the course of events.

The rarest and strangest of our big emersed aquatics is the American lotus, *Nelumbo lutea*. Where it grows at all it covers acres in pure stands—perhaps with duckweeds floating between.

Because of its edible portions it was customary for Indians to plant seeds in suitable places. The lotus pond at Onawa is believed to have been planted by Indians (Taylor 1927). The pond at Hamburg may have been. The pond at Amana was planted by the colonists. Of the ponds at Muscatine Slough, Farmington, McGregor and Lansing there is no known history. They may be "natural." Were the Indians natural?

We are now well out in the water where we must look for the

spatterdocks (*Nuphar advena*), the waterlilies (*Nymphaea tuberosa*) and the riverweeds (*Potamogeton*).

Our waterlilies have pure white flowers, slightly sweet-scented, and must, I think, all be referred to *Nymphaea tuberosa*. When little prairie oxbow pools held water all the year waterlilies grew in many places—in Poweshiek and Jasper Counties—and northern pike as much as a foot long ran up into the sloughgrass seeps nearly to the top of the prairie. Now we find waterlilies in sluggish waters in Muscatine County, in pools of the braided streams of the Mississippi at McGregor, near the west end of Clear Lake, and in Dead Man's Lake on a shelf half way up the side of the great glacial dump known as Pilot Knob. Our waterlily does not always have brown stripes on the petioles as does typical *N. tuberosa*, nor are the rhizomes always beset with the easily detached tubers which gave the species its name. Its flowering time and size of seed are typical. And sometimes the stripes and tubers do occur. Are they introgressive hybrids with *N. odorata*?

One of the rarest and oddest plants of Iowa is the watershield, *Brasenia schreberi*. It was found in a shallow pond in Muscatine County (now drained and dried up), in Little Wall Lake, and in Dead Man's Lake. Though *Brasenia* is now known in only two spots in Iowa (the Muscatine County pond was restored in 1951, and *Brasenia* reappeared), it is distributed all over the world: North America, Europe, Asia, Africa, and Australia.

A wealth of riverweeds (*Potamogeton* spp.) inhabit the streams and ponds of Iowa. Almost everywhere they are of the narrow-leafed, wholly submerged *pectinata* types. The determination of the exact species is a matter for a specialist. In West Okoboji Lake the shallows near shore, 1 to 3 feet deep, are occupied by the submerged, broad- and crinkly-leaved *P. richardsonii*. Next further out the similar-looking *P. praelongus* pushes its spikes of flowers to the surface of the water on a leafless internode 1 to 2 feet long. Still farther out, in relatively sheltered places, the floating-leaved *P. nodosus* and *P. natans* spread their elliptic leaves on the surface of the Lake. A half dozen other species occupy special niches in the economy of the Lake. Some of these are valued as food for ducks.

SUBMERSED AQUATIC COMMUNITIES

But apparently more pleasing to ducks is the eelgrass, *Vallisneria*, whose long narrow translucent leaves grow well in an aquarium and are famous for showing under the microscope the circulation of protoplasm in the cells—the life process in action, at its lowest terms. It is found in many of the lakes of Iowa.

In other sheltered places, and once on a rock in the midst of Skunk River, *Elodea* prospers. It too is used for showing circulation of protoplasm, and also for the evolution of oxygen in photosynthesis. The type locality for *Elodea iowensis* is at the extreme northern end of Spirit Lake.

Jones (dissertation S.U.I., **1925a, b**) found in West Okoboji Lake four zone-associations along most of the shores. The first, or *Potamogeton richardsonii* Association, includes *P. pectinatus* and *Najas flexilis*, and extends from the land out to a depth of one meter. The plants are far apart.

In the second zone *Chara contraria* is dominant, in dense stands, having its upper limit from 0.7m. to 3 or 3.5m., and extending to a depth of six meters. Sawyer (dissertation S.U.I., 1926) estimated the area of the Characeae zone in West Okoboji Lake at 200 acres. In this zone Sawyer found *Vallisneria spiralis, Heteranthera dubia, Najas flexilis* and *Potamogeton* species "very common," *Ceratophyllum demersum* "very rare." Wylie (**1918**) has described the cleistogamic pollination of *Heteranthera*. Amongst the *Charas* the filamentous algae *Rhizoclonium, Oedogonium* and *Bulbochaete* are "very abundant" and *Spirogyra* is "common." The association of *Bulbochaete* epiphytic on *Chara* has been noticed also in Wyoming. Many Cyanophyceae, Chlorophyceae, diatoms and small animals live attached to the *Charas*.

In the third zone *Ceratophyllum demersum* is dominant. The inner margin is from 2.6 to 3m. deep, the outer 4.5 to 5m. Extreme limits were found at one meter to 8m. for the inner margin and 2.5 to 8.5 for the outer margin. This zone extends along nearly all of the shores of West Okoboji Lake and covers, according to Jones, 434 acres of the 3788 acres of the entire lake. Clear water and a mud bottom are required. *Ceratophyllum* was found in seven other lakes and ponds in the Okoboji region. It is in many bodies of water, both natural and artificial, all over the State. Seeds have never been found in Lake Okoboji. They were produced freely in a shallow pond near Gull Point, now drained and dry. The reason seems to be that the water of the lake is too cold. The pond water reaches the 91°F necessary for fruiting.

Jones recognized a fourth zone composed of *Nitella* and *Tolypella*, at depths of 4 to 7m., located on Sawyer's map along the southeastern shore of West Okoboji south of Pillsbury's Point. Sawyer found *Nitella* on fine black silt, *Chara* on a sandy substratum mixed with silt.

Sawyer collected Characeae in many small ponds and creeks in the Okoboji region. She points out that "*Chara* is a pioneer plant in

new fresh-water areas and helps materially in developing conditions suitable for the growth of aquatic seed plants." When the latter take hold they completely crowd out the *Chara*. *Chara* communities are not common outside of the lake region in Iowa. There are records for Linn (?) and Jasper Counties. Cain & Slater (1948), found in Sodon Lake, Oakland County, Michigan, extensive beds of *Chara contraria* from near shore to a depth of 14 or 15 feet. In the deeper parts, 11 to 14 feet, *Nitella* mingles with the *Chara*, and at a depth of 7 to 9 feet species of *Potamogeton* take root and grow up to the surface. Amongst species not present in West Okoboji Lake, Sodon Lake has a marginal zone of *Eleocharis palustris*, a scattering of *Drepanocladus fluitans* at 15 to 20 feet depth, and occasional colonies of *Nymphaea odorata* and *Nuphar advena* near shore.

There is a group of plants in our northern lakes which undoubtedly begin life attached to and rooted in the mud in water from one to ten feet deep, but which ultimately break loose and make large floating mats in protected bays and ponds. These are principally *Ranunculus trichophyllus* and *Myriophyllum exalbescens*. Amongst these will be *Ceratophyllum* and some slender *Potamogetons*, and uprooted plants of *Vallisneria*, *Najas*, and *Heteranthera*.

In late summer another finely cleft leaf appears, this time in the zone of *Potamogeton richardsonii*, viz. *Megalodonta beckii*. Sometimes its flowers rise above the surface of the water, each stalk bearing one terminal yellow-rayed composite head two inches across. But if the water is too deep this flower will open just as beautifully, and produce seed, wholly submerged.

THE ALGAE OF IOWA

Prescott enumerated nearly 1000 species of algae exclusive of diatoms, "the grass of many waters," in Iowa. They are functionally the grass, the basic food from which all other aquatic life directly or indirectly derives its nourishment. They are, of course, most numerous in the lake region, where they swarm in ditches, canals, ponds, lakes and innumerable glacial kettleholes. Gilbert Smith (1926), working on plankton (floating) algae at Lakeside Laboratory, is quoted as being of the opinion that nowhere else on earth could so many species be found in so small a compass. Tiffany (1926), also at Lakeside Laboratory, brought in throughout the summer dozens of species of *Spirogyra*, *Mougeotia*, *Zygnema*, *Oedogonium* and *Bulbochaete*, and bushels of *Hydrodictyon*.

In early spring the boulders on the shore of West Okoboji acquire a green velvet of *Ulothrix*. In mid-June this quickly vanishes, and

thereafter only six-inch-long bushy tufts of dark green *Cladophora* dangle in the ripples.

A few times during the summer the water suddenly becomes soupy with millions of tiny globules of a *Gloeotrichia*. All of the shallower lakes develop a variety of waterblooms: the little green splinters of *Aphanizomenon* or the roundish but not exactly spherical particles of *Microcystis* or *Anabaena*. When the water is rich in sewage or sewage-like washings from the land these waterblooms multiply prodigiously. They are washed up on the beaches in long windrows of lurid bluish green, where they die and rot and smell. They cause the death of countless fishes. One of the *Anabaenas* is responsible for the fatal poisoning of horses, cattle and hogs in southern Minnesota. The waterblooms are common and troublesome at least as far down the State as Poweshiek County.

Also in Poweshiek County, as in Dickinson, and in eastern Pennsylvania, *Rhizoclonium* makes huge felt-like mats on the ponds, mixed, in the south, with *Pithophora*.

A curious plant and animal relation is shown in the northern lakes by two species of the slender unbranched threads of *Basicladia*, which are known only as growing on the backs of turtles!

The little streams that run among the hills in the region of the Kansan Drift have a small but characteristic quota of algae. Where the water first seeps out of the ground, amongst marsh marigolds and various culms, it may lie in shallow pools filled with silky green strands of a slender *Spirogyra* with one or two spiral bands. If there is mud continually wet, dark green felts of *Vaucheria*, up to an inch thick, develop. In this condition the alga never produces spores. Only when it spreads in thin films over drier earth (in my garden or on a greenhouse bench) or when the branching threads grow very loosely totally submerged, does sexual reproduction occur.

On every dead grass stem in the little brook, and on the muddy bottom, swarms of diatoms flourish: yellow-brown cylindrical *Melosiras*, end to end in long filaments; clusters of the stalked *Gomphonema*; zigzag ribbons of the rectangular *Diatoma*, and plain flat ribbons of *Synedra* like rows of needles laid side by side. Boat-shaped *Pinnularias* and *Nitschias* creep over all.

In early spring *Draparnaldia* dangles in little bushy clusters from pebbles in the brook. Somewhat later, and in streams a foot wide, *Tetraspora* lies in pale green gelatinous tubes and sheets, up to two feet long. But after the "harmless" effluent from the sewage disposal tanks enters the stream, no green thing exists in the next mile. Only pale watermolds adhere to stones and sticks. And below the

drain from the city gas works the phenol-scented water is entirely devoid of life for a mile and a half.

On wet banks and stones and sticks the common mosses, *Hygroamblystegium irriguum* and *Leptodictyum riparium* are everywhere. Only very clean permanent springs accommodate *Brachythecium rivulare* (rarely fruiting) and *Drepanocladus aduncus* (very rarely fruiting in Iowa).

CHAPTER VI

Communities of Rocks and Cliffs

Communities of rocks and cliffs are of particular interest to us in Iowa because they are so few and far between. Such communities and the plants that compose them are always for us "rare" or "local," even though some of them are found wherever there are rocks.

There is a fern community which may be named for its most widespread member, the *Pellaea glabella* Association. From crevices of limestone cliffs, and boulders of disintegration, the black stipes and tough little leaflets of *Pellaea* jut out in small clusters, up to 8 inches tall. Nearby the fragile fern, *Cystopteris fragilis*, should be found, in other crevices and pockets. Dangling over these are the red-and-yellow five-fold trumpets of *Aquilegia canadensis*, and often the half-inch blue bells of *Campanula rotundifolia*. *Arabis canadensis* may stand stiffly erect against the rock wall.

If the rock is a dolomite (magnesian limestone) *Cheilanthes feei* will occupy some of the pockets. Ellison Orr, who knew every square foot of Allamakee County topographically, geologically and biologically, said that Fee's fern is a sure sign of the Oneota Dolomite. And so it seems to be. In Dubuque and Jones Counties it grows on other dolomites. It seems to be an obligate magnesium plant.

An entirely different community is that of the walking fern (*Camptosorus rhizophyllus*). It is found in many places (Hardin and Marion Counties and eastward) on moist shaded rock faces and talus blocks, both on limestone and sandstone. For our sandstones are cemented with lime salts and are calcareous unless subjected to very long leaching at the surface of the ground. This plant wanders over the face of the rock, forming a dense exclusive sheet of foliage. It is able to revive after being dried to a crisp in its native place. But that place is always shaded and is mostly moist.

On fine sand or earth in similar moist shady places *Cystopteris bulbifera* is abundant and luxuriant. Well grown leaves will be 18 inches long and 4 inches wide at the base.

Certain very dry knobs of St. Peter Sandstone in northeastern Winneshiek County have been so long exposed on the top of the world that their lime is completely leached out, and the surface presents a purely silicious substratum. On two of these *Selaginella rupestris* and *Potentilla tridentata* flourish, and on one are found *Pyrus*

melanocarpa, *Arctostaphylos uva-ursi*, *Prunus pumila*, *Polygonum tenue* and *Polygonella articulata* (reported by Shimek (1906) as *Polygonum Douglasii*).

Moss communities independent of all other living things (?) occur on rocks. *Grimmia apocarpa* is very widespread over the State wherever hard limestone rocks occur. The half- or quarter-inch-long black, densely leafy shoots are in clusters or cushions or extensive layers, mostly on the nearly flat tops of rocks, either in full sun or in shade. The capsules nestled among the leaves open in mid-April, disclosing a single row of wedge-shaped crimson teeth, very beautiful under a lens. On the same ledge with these, in the northeast we find greener tufts with narrow leaves which seem to be the variety *alpicola*. And alternating with these in Jones County are little round pads of *Tortella tortuosa*, collected only once.

A little earth on the rock is required to accommodate the small scale-moss *Mannia fragrans*.

On thoroughly leached knobs of St. Peter Sandstone in Allamakee County is a very short, broad-leaved form of *G. apocarpa* which Holzinger called var. *brunnescens*. It is accompanied by *Bryum caespiticium* and *Ceratodon purpureus*.

These *Grimmia* tufts readily fall apart as separate shoots; one can hardly keep a tuft together. Not so with *Grimmia laevigata*, which makes firm grey silky pads or pancakes on the Sioux Quartzite (Lyon County), exposed to full sunshine. It shares these blistering red rocks with *Selaginella rupestris* and *Opuntia fragilis* and *Talinum parviflorum*. Exactly the same community occurs in southwestern Minnesota. *Grimmia laevigata* never produces spores in Iowa. But we found small tufts of it on tombstones in Ida County.

Orthotrichum strangulatum lives abundantly and quite alone on fully exposed limestone blocks in northeastern Iowa, and on a rock from a quarry, beside *Grimmia apocarpa*, in Jasper county. On hard damp limestone ledges we expect 1/8 inch thick sheets of *Gymnostomum calcareum*, and on dripping ledges inch-deep balls and cushions of *G. recurvirostrum*.

Homomallium adnatum belongs to the deciduous forest where it covers boulders that are mostly sunk in the ground.

Calcareous sandstone of whatsoever geological horizon has its vertical faces covered with *Desmatodon obtusifolius*, if it is somewhat exposed and not too wet. In Mahaska County this species shares the shaded ledges with *D. Porteri* and *Sematophyllum carolinianum*.

The same Pennsylvanian sandstone in Marion County presents a magnificent wall of rock, clothed with mosses, liverworts and ferns.

At the base *Conocephalum* plasters a solid sheet of dappled green over the rock. Above this, according to moisture and exposure, are walking fern and *Reboulia* (rather dry), *Jamesoniella autumnalis* (not so dry), and *Philonotis longiseta, Scapania nemorosa* and *Plectocolea hyalina* (wet but not dripping). 15 to 25 feet up the wall, where very dry, *Dicranum fulvum* is abundant. Near a cleft with rounded rim *Hypnum curvifolium* covers the bulging rocks, and above the cliff on the steep wooded slope *Polytrichum commune* grows by the square rod. One projecting knob is dry enough and exposed enough to accommodate *Mannia fragrans*. The sides and base of a little intermittent waterfall are wet enough often enough to make a place for several square feet of the dark green *Fissidens minutulus* and the somewhat glaucous *F. obtusifolius*.

A low ledge (6 ft.) of similar sandstone in Wapello County has square yards of *Jamesoniella*, square feet of *Scapania nemorosa* and *Desmatodon obtusifolius*, square inches of *Anthoceros laevis*, and two or three little circles of *Nowellia curvifolia*, big and stout but the only bits in the State. In a nearby little canyon, at the foot of an intermittent waterfall, a three-foot-high block of sandstone standing in the bed of the stream has one side covered inch-deep with *Tetraphis pellucida*, and an adjacent smaller boulder is covered with *Brachythecium flagellare*. The lower walls of another narrow canyon are covered with *Plectocolea hyalina*.

Many rocks in woods in the eastern quarter of the State have colonies of *Porella platyphylloidea* on top or sides, and *Frullania riparia* on the side under an overhang. In general, however, every shaded limestone ledge or talus is covered on the top with *Anomodon attenuatus* in thick luxuriant sheets, and on sides or overhangs with *A. rostratus*. The big true typical *Anomodon minor* grows on a rock in Winneshiek County. In the southeastern states (Tenn., N. C.) I find *A. attenuatus* as a slender moss on trees; not so in Iowa. Our *A. minor* is nearly always on trees, a small or medium sized form of the species. *A. rostratus* is rarely on the base of a tree, and then is likely to be thin and straggling.

Two special localities of great interest remain to be considered. One is a beautiful dripping ledge of mosses, liverworts and flowers and ferns at Quandahl. The other is the amazing congeries of species at Giard School (the schoolhouse has been removed, and the railroad station was abandoned long ago).

At Quandahl, where there were once two commercial banks, there are now two dwellings, one abandoned store building, and the walls of a former creamery and cheese factory. Bear Creek runs straight

along the foot of an eight foot wall of Cambrian sandstone. The steep slope above this is always dripping with water. On the rock wall, the slope and around the old ruins is a continuous carpet of plants. There are sheets of *Conocephalum* on the vertical faces. *Marchantia* flourishes in the drip, and on the brink the very rare *Mannia rupestris* produces its little round heads in early June. An old wall has a square yard of *Cratoneuron filicinum*, always dripping wet. Species of *Bryum*, *Brachythecium* and *Mnium* abound. Occasionally on a dry ledge a big cushion of *Plagiopus oederi* appears. And various places are adorned with the round, toothed leaves and little airy white flowers of *Sullivantia renifolia*.

At Giard School a vertical wall of St. Peter Sandstone, facing north, bounds the old school yard. The wall is about 25 feet high. Most of it is covered inch deep with *Tetraphis pellucida*, every stalk with a sporophyte. In places *Jamesoniella* covers the rock. *Blepharostoma trichophyllum*, *Lepidozia reptans* and *Preissia* also occur. There are a few half-inch long tufts of *Bazzania trilobata*, the only locality in Iowa, and a few thin pale patches of *Harpanthus scutatus* (only locality in Iowa), easily mistaken for the ubiquitous *Lophocolea heterophylla* (and vice versa). The steep slope above the rock face, heavily shaded by oak trees, is bare of dead leaves but densely sodded with mosses. The chief component is *Dicranella heteromalla*. With it are *Pohlia nutans*, *P. elongata* and the two twin *Tritomarias*, *exsecta* and *exsectiformis*, easily seen by the clusters of orange red gemmae at the ends of the shoots. There are pockets of *Sphagnum tenerum*. Strangest of all, on the face of the rock is a goodly amount of *Brothera leana*. This odd moss was collected years ago by Professor Shimek in Johnson County on rotten wood, its usual habitat in Ohio and elsewhere. It is known from Pennsylvania, Ohio, Tennessee, Minnesota, Siberia, the Himalaya region and Japan.

The occurrence on porous sandstone in Iowa of so many species that inhabit rotten wood elsewhere deserves comment. The common denominator of these two substrates is the water supply. A spongy old rotten log holds water like a sponge, and pays it out to whomsoever can draw upon it. The porous sandstones are just as well supplied with water, and pay it out at least as easily.

The Cambrian Sandstone which crops out at Quandahl is one of the best aquifers underlying the eastern half of Iowa. It dips down to 2200 feet below ground level at Grinnell, and is the source of the city water supply.

The St. Peter Sandstone which crops out at Giard School is the

next best aquifer. It is 1700 feet under ground at Grinnell and was formerly the source of the city water.

The Pennsylvanian Sandstone of Wapello and Marion Counties seems to function just as well for the mosses. It is a fairly adequate aquifer. Many farm homes get their water supply from wells bored into this rock. The mosses discovered these three best aquifers of Iowa long before the white man did.

ROCK LICHEN COMMUNITIES

Ecologists like to say that the first plant settlers on bare rocks are the lichens; that these prepare the way for mosses, and the mosses for ferns and flowering plants. Sometimes that is the sequence of events—and sometimes it is not. Many mosses settle on rocks without any intermediary lichens.

There are lichens, certainly, which live on rocks as first settlers. Fink says: "The rocks are in some instances so completely over-run with them that the rock itself can scarcely be seen, and here they display even greater beauty of form and color than on trees."

The rock lichens belong to all three of the physiognomic groups: crustose, foliose and fruticose. Fortunately for us the lichens of Iowa were carefully collected and studied by the North American authority on lichens, Bruce Fink. Whatever we can say about these plants—or pseudo-plants—will be largely drawn from Fink.

Bruce Fink (**1904**) studied a lichen society of a sandstone ledge in Ledges State Park in Boone County. Along with the lichens, or nearby, were walking fern, *Woodsia obtusa*, *Conocephalum* and an unidentified liverwort, probably *Reboulia*. On this moist, shaded rock wer gray-green filamentous *Usneas* and flat, branching *Ramalinas*, the round sea-green scale-like *Parmelias* several inches in diameter, the similar but ashy *Physcias*, the brown or black gelatinous *Collema* and *Leptogium*, and the greenish white powdery films of *Amphiloma*. On the harder surfaces the crustose lichens were abundant, mere speckled patches of color, whitish, ashy, sea-green, brownish or blackish. They are scarcely more than round stains, impossible to remove except by chipping off a piece of the rock. But they are alive, and carry on their hereditary specific distinctions as well as any other plants. In all Fink found 33 species of lichens at the Ledges. It was, however, a very different list from the 31 species on an exposed sandstone riprap on a north-facing bank of the Rock Island Railroad 7 miles west of Grinnell. These were nearly all crustose. On a south-facing bank with similar riprap only 12 species were found, these being the best able to survive in such a xeric site. Sets of Fink's

Iowa lichens were deposited in the herbaria of Grinnell College and the State University of Iowa.

A definite lichen association on a continuous uniform habitat is that of the exposures of Sioux Quartzite in Lyon County. The lichens are especially conspicuous against the background of hard reddish silicious rock. They prosper in full sunlight, on smooth surfaces with enough slope to allow no water or dust to lie. Most abundant are the big (to 6 inches) circles of the greenish papery *Parmelia conspersa*, which can be peeled off in pieces with a penknife. Mature plants bear upraised shallow cup-like fruiting dises, "apotheeia," with chestnut-brown inner surface. Much less abundant are the smaller light sea-green papery circles of *Physcia caesia*, with brownish black dises. Eight species of crustose lichens make up the association, all of them appearing as films inseparably attached to the rock, removable only as crumbled scrapings. Most abundant of these is the greenish to yellowish *Rinodina oreina*, with black convex dises. In less abundance are the greenish *Lecanora rubina* and *L. muralis*, with convex dises of yellow to brown coloration, and three *Placodermas* making orange to gray circles or patches with orange to brown dises.

The above names of species and genera are from Shimek (1897), from whom we quote: "The lichen flora of the exposure, very conspicuous by its abundance and variety, is an exceedingly interesting one. The rock in many places is fairly covered with these persistent forms, and the species are, for the most part, identical with those which occur on surface granite boulders in the northern or northeastern part of the State."

Many lichens are confined to calcareous rocks, others to granitic, others to living trees, others to dead wood, and others manage to live on a variety of substrates. We have no record of any definite grouping of species on calcareous rocks, but Fink stated that "one large rock doubtless has as many" as 20 species (in northeastern Iowa). In Allamakee County many calcareous ledges, boulders and even small hand specimens are covered with orange colored scaly sheets of *Solorina crocea*.

Societies of crustose lichens on rocks are the very simplest of subaerial associations. They consist of but a single paper-thin layer of plants, often of several species crowded together. But if we recall that a lichen is a partnership of fungus and alga, attaining specific characteristics that neither member could attain alone, we have a biological problem of extreme complexity. This incredible and unexplainable compound organism may be very simple in structure, and it certainly forms the most elementary community.

CHAPTER VII

Communities of Epiphytes

The only epiphytic plants in Iowa are the mosses, liverworts, lichens and fungi (if fungi are plants). The only epiphytic habitat is the bark of trees. These deserve special mention here, though we shall have to return to them in considering plant migration and vegetational change.

I do not know of any moss in Iowa which *never* occurs anywhere except on trees. On occasion every one may grow on earth or rocks. The occasions are sufficiently infrequent, however, to permit us to speak of bark-inhabiting (corticolous) species, and certainly of corticolous communities. Such communities have been studied in Virginia by Patterson (**1940**), in North Carolina by Billings & Drew (**1938**), in Tennessee by Cain & Sharp (**1938**) and Quarterman (**1949**), in Indiana by Potzger (**1939**), in Ireland by Richards (**1938**), in Switzerland by Oehsner and in Austria by Gams (**1932**). The bibliographies by Gams, Cain & Sharp, and Quarterman are very complete.

In northwestern Iowa soft-barked trees (willow, elm, bur oak) are covered at base with continuous exclusive dull green sheets of *Leskea gracilescens*. Often there will be abundant sporophytes near the ground, becoming fewer and fewer upward, to cease at three feet up, though the gametophyte flourishes for another foot or two. This distribution is evidently due to supply of water. Water running down the tree drains away above and accumulates below (Penfound & Pennebaker **1940**). Where *Leskea* is only in crevices (on oaks and elms), at 3 to 8 feet up, shreds of *Lindbergia* are to be expected. Tufts of *Orthotrichum pumilum* are found at about the same levels as *Lindbergia*, in flourishing condition, with abundant capsules and furry calyptras.

On the hard bark of red oak in Webster County *Platygyrium repens*, takes the place of *Leskea*. In the eastern half of Iowa *Anomodon minor* often takes the place of *Leskea*. If it fruits at all it will be near the base of the tree. *Platygyrium* is common all over the State. Occasionally on the same tree but higher up, out of reach, the shiny pads of *Pylaisia selwynii* spread over trunk and branches. And also high up in moist woods in the two eastern tiers of counties the south-

ern *Leucodon julaceus* makes loose coarse tufts and sheets, the curved stems being one or two inches long.

The most widespread of our epiphytic mosses is the very variable *Chamberlainia acuminata*, growing in dense sheets on the bases of trees and in little patches higher up. The shoots tend to hang down in parallel, sometimes very slender, sometimes as stout as the lead of a pencil.

Two other Iowa mosses are so strictly epiphytic as to deserve mention. *Entodon compressus* spreads sheets of flat glossy shoots around the lowest ten inches of a tree, or appears as little patches higher up. *Thelia asprella* makes half-inch thick layers of glaucous-green at the base of a white oak—rarely of some other tree.

All of these mosses have sporophytes that stand at right angles to the substratum in defiance of gravitation. On a fallen log they bristle out on top and sides at every angle from vertical to horizontal. Many ground mosses are strongly directed by light or gravity, and turn accordingly. The capsules and setae of tree mosses are straight, whereas their nearest relatives on the ground have curved capsules and/or setae. And strangest of all, the tree mosses usually lack cilia in the inner peristome, whereas their earthly relatives have 1, 2 or 3 good cilia between the segments.

If the tree mosses were all closely related, this group of peculiarities might be due to a common inheritance. But they are not nearly enough related for that. Each genus or species must have acquired these characteristics independently. One would suppose that there must be some selective value in such mutations—which is hard to imagine—or that the environment induces such changes—which is worse! Here are facts which I see no way to explain and for which I see no way to seek an explanation.

The epiphytic lichens of trees, like all other lichens, are found only at a distance from human habitations. Whether it is our dust or our coal smoke that discourages them is still unknown. Anyway they are always wildlings.

Seventy-one of the 196 species of lichens of Iowa enumerated by Fink (1895, 1897) grow on trees. On one tree near Fayette, Fink found 20 species of lichens. Bur oaks at Miller's Bay in Dickinson County have big green papery circles of *Parmelia;* a pale grey and a dark grey *Physcia;* small patches of bright yellow or orange *Theloschistes* (2 species). The graphic lichens occur on smooth, often hard, bark: hickory, etc. Both *Graphis* and *Opegrapha* are common. One fungus is so common on oak bark that it must be mentioned: *Aleurodiscus*. There are three species.

Several species of slime-molds (Myxomycetes) are known only on the bark of trees. They are minute and ephemeral, and are best studied from bark cultures in the laboratory. Some of these are so closely associated with the one-celled alga *Protococcus* (*Pleurococcus*) as to suggest an obligate symbiotic relation.

CHAPTER VIII

Communities of Springs and Seeps. Fens

The big springs of the Driftless Area (there are 25 of them in Allamakee County) pour out continually vigorous streams from subterranean limestone caverns. When this water comes from nearby sinkholes, carrying mud after every rain, or when it is a branch of a nearby river briefly running under ground, there may be no vegetation at all, or mats of green, or even bluegreen algae: *Rhizoclonium*, *Vaucheria*, *Phormidium*. But when there are adequate settling basins under ground and the water gushes out crystal clear and perennially near 40°F, a unique biota is native. Too often this community has been overshadowed and destroyed by the introduced watercress (*Nasturtium officinale*).

The members of the primeval biota are a black-shelled snail, a big colorless amphipod ("shrimp," *Gammarus*) and a large coarse blackish-green moss, *Hygroamblystegium noterophilum*. All of these are confined to a short distance from the point of issue of the spring. They continue down stream for a foot, a few feet, or as much as a quarter of a mile, according to the quantity of the flow and, perhaps, exposure to the sun. In every big clear spring in northeastern Iowa one or all of these organisms occur, and nowhere else. How is it possible for all of them to find these stations? The moss never produces spores in Iowa. Again 500 miles south in the really big springs of Missouri the same moss and snail and crustacean live together, near to the place of issue of the spring.

And what is the change in the waters that limits the range of this biota? Seven of the big springs of Missouri are locally known as "Blue Spring" (Beckman and Hinchey **1944**). When the spring originates in a big deep basin the water has a faint cloudy bluish tint. This suggests the presence of ferrous salts. It is well known that such salts oxidize and precipitate with great rapidity on exposure to air. Perhaps the oxidation of iron salts sets the limits for the *noterophilum* moss and its companion animals.

The big springs of Iowa also have, on exposed rocks, large glossy beds of *Brachythecium rivulare*, and dark green patches of *Hygroamblystegium irriguum*, the latter fruiting abundantly.

The spring basin is sometimes fringed with the yellow-flowered

Mimulus jamesii, and the brook, if exposed to sunshine, should have the blue-flowered racemose *Veronica anagallis-aquatica*.

SEDGE COMMUNITIES OF WET LAND

The Iowan Drift east of the Mankato Lobe is characterized by numerous large rounded granitic glacial boulders standing as much as three feet tall, and also by communities of sedges on poorly drained swales. Unfortunately we have no list of the characteristic carices. Shimek's notes for Buchanan County include *Hypericum pyramidatum, Lythrum alatum, Lysimachia quadriflora, L. lanceolata, Stachys palustris, Cicuta maculata, Calamagrostis canadensis, Lilium michiganense, Asclepias incarnata, Salix petiolaris* and 3 *Carex* spp. unidentified. *Eleocharis palustris* is also to be expected.

Such communities may cover several acres and are frequently repeated. They are generally pastured. Cattle working over them make paths which distinctly accentuate the tussocks of sedge, sometimes 18 inches high. It is on these tussocks south of Coggon that the acidophilous mosses *Aulacomnium palustre* and *Atrichum crispum* grow, neither ever fruiting. And between the tussocks in Linn and Muscatine Counties the calciphobe *Sphagnum palustre* is found (extinct in Muscatine). Drexler finds *Aulacomnium* and other species of *Sphagnum* at several stations in Linn County.

In the Iowa-Cedar delta region sedge tussocks of large size and great age make a genuine "Szombek Formation" like that described by Kerner (**1950**) in the plains of Hungary. The area needs further study.

PEAT BOGS

In the northern tiers of counties, Emmet to Cerro Gordo, there are, or were, several peat bogs of greater or lesser extent. The peat, as much as three feet thick, is a sedge peat, entirely without *Sphagnum*. The only common moss is *Drepanocladus aduncus*, whose contribution to the total mass is negligible. In recent years most of these bogs have been drained, and in some cases the whole layer of peat has been burned by accidental fires. The plant communities of these bogs were characteristically boreal, even suggesting the Arctic tundra.

The flora of Iowa peat bogs was described by Pammel in 1908. This report does not clearly distinguish between bog flora and the floras of neighboring areas, the innocent bystanders. The list of plants includes *Ulmus americana, Populus tremuloides, Nymphaea tuberosa*, etc. The species peculiar to these boreal bogs are *Carex lasiocarpa*, "a prevailing and predominant species," *Parnassia glauca, Lobelia kalmii, Cicuta bulbifera, Rumex orbiculatus, Solidago riddellii, Meny-*

anthes trifoliata, Potentilla palustris, Eriophorum sp., *Calamagrostis inexpansa, Hypericum virginicum, Galium trifidum, Salix lucida, S. pedicillaris* and *S. candida.*

In addition to these strictly northern species the peat bogs have many species which are found in boggy places as far south as central or southern Iowa, such as:

Equisetum fluviatile
Dryopteris thelypteris
Onoclea sensibilis
Typha latifolia
Alisma trivialis
Zizania aquatica
Leersia oryzoides
Phalaris arundinacea
Calamagrostis canadensis
Spartina pectinata
Phragmites communis
Glyceria grandis
Scirpus fluviatilis
S. validus
Iris virginica
Salix cordata
S. petiolaris
Polygonum amphibium
Caltha palustris
Penthorum sedoides
Apios tuberosa
Lythrum alatum
Ludwigia polycarpa
Cicuta maculata
Sium suave
Lysimachia thyrsiflora
Gentiana crinita
Asclepias incarnata
Cuscuta gronovii
Scutellaria lateriflora
Stachys palustris
S. tenuifolius
Chelone glabra
Pedicularis lanceolata
Campanula aparinoides
Lobelia siphilitica
Eupatorium perfoliatum
E. maculatum
Boltonia latisquama
Solidago canadensis
S. gigantea
Aster novae-angliae

A. prenanthoides
A. umbellatus
Helenium autumnale
etc.

It is obvious from this list that several distinct associations are involved, which it is impossible to unravel at present. We read "This beach is followed [pondward] by abundant growth of *Phragmites communis, Scirpus validus, Typha latifolia, Menyanthes trifoliata* and *Zizania aquatica.*" If these plants were intermingled, as might be inferred, the community was indeed unique. Almost certainly the large monocots grew in separate stands, as they do everywhere else. And where the *Menyanthes* was one can only guess. And where were *Salix candida* and *Hypericum virginicum* and *Calamagrostis inexpansa* and the abundant *Carex lasiocarpa*? Perhaps enough remnants of this vegetation remain to provide an answer. The one bog I have visited had been completely burned out during a dry season.

The list given above for boggy places in general applies to certain places well known to the writer in Muscatine, Poweshiek and Tama Counties, as well as in eastern Pennsylvania. In all of these the physiognomy is the same—a ground cover of sedges with the forbs rising in isolated clumps.

FENS

The associations just described occur over most of the State on gentle slopes where water seeps out continuously. A very different condition ensues in northern Iowa where strongly calcareous water seeps out and an accumulation of peat and tufa builds up an alkaline raised bog or fen. A small and diagrammatic fen on the south shore of Silver Lake in Dickinson County has been briefly described by Anderson (**1943**).

The principal part of the Silver Lake fen starts from a rounded knoll jutting out northward from the end of a ridge of glacial drift. (**Fig. 13**). The knoll consists of sedge-peat and calcareous tufa to a depth of 15 feet. Water wells up in a spring near the northern edge of the knoll and seeps away over the surface amongst dense vegetation. The temperature of the spring is very constant at 8.5 to 9.5°C. The water is strongly alkaline and carries 1183.5 parts per million of solutes, mostly $CaSO_4$, $CaCO_3$ and $MgSO_4$ (Carter **1939**). The surrounding tufa is 87% $CaCo_3$.

The top of the knoll bears a community of sedges, *Calamagrostis inexpansa, Eupatorium fistulosum, E. maculatum, Helenium autumnale, Solidago riddellii* and *Viola nephrophylla.* The mat of roots

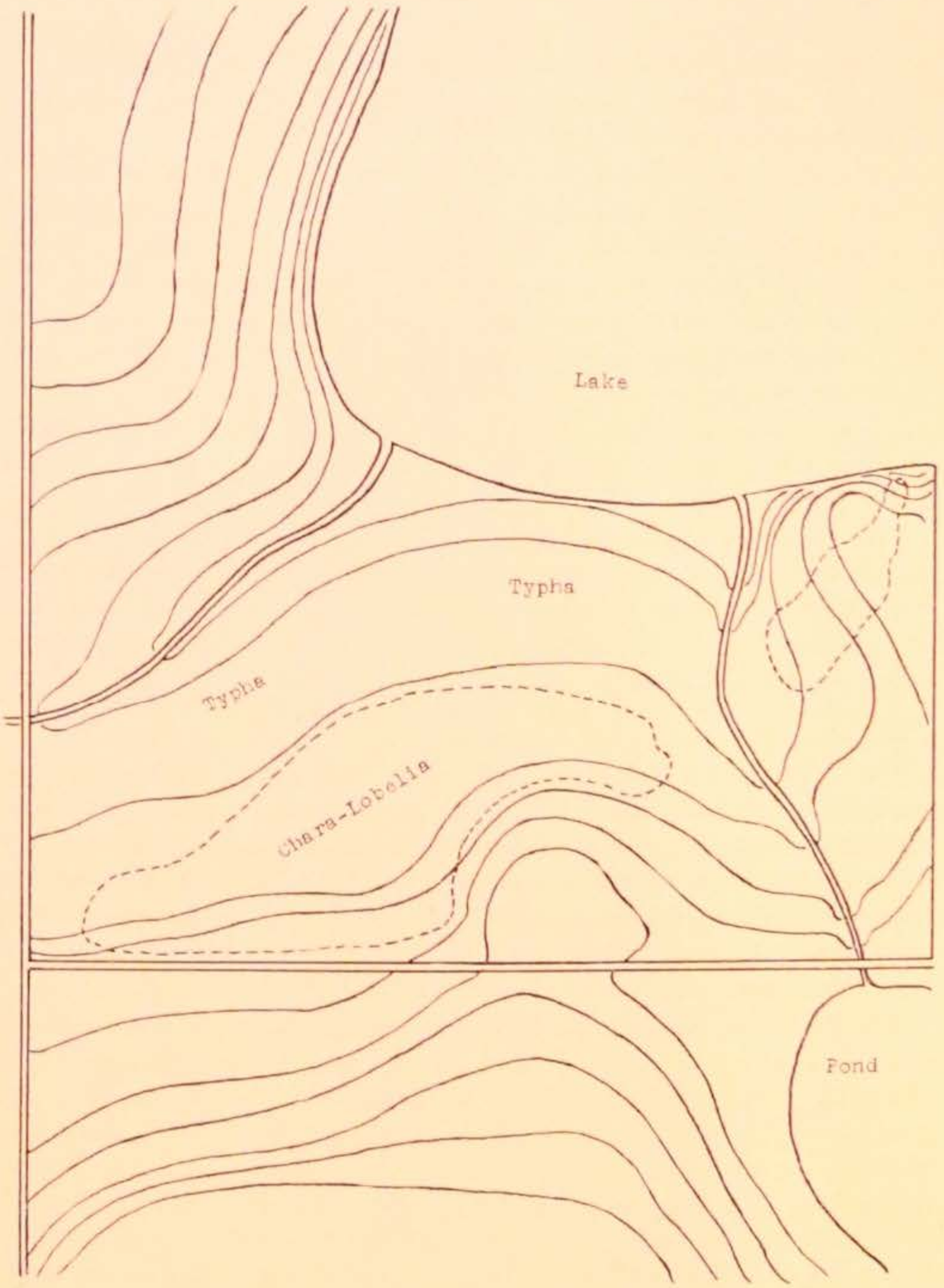


Fig. 13. Diagram of Silver Lake fen, with approximate contours. Original.

supports one's weight but trembles when you jump on it. Toward the west pools of water interrupt the sod, surrounded with the moss *Campylium stellatum*. At the brow of the slope this knee-high vegetation suddenly stops and the pools of shallow water occupy more space than the 2-inch high sward that separates them. The sward seems to be chiefly the foliage of *Rhynchospora capillacea*. In the pools *Chara vulgaris* abounds and fruits copiously. It is an annual 2 to 4 inches long lying flat in dense green bunches. The spores germinate by thousands in early June, showing all the stages pictured in the textbooks.

Much of the bottoms of the pools is white with films of sulfur bacteria, feeding on H_2S from the decaying vegetation beneath. Another effect of the H_2S is to blacken the mud by converting the abundant iron salts to sulfide. The water of the pools may reach a temperature of 31.5°C on a summer day, and a pH of 8.05.

In the sods between the pools *Triglochin maritima* blooms in June and July, *Spiranthes cernua* comes in July. In August *Utricularia vulgaris* sometimes blooms in the pools. And the sods are decorated in August and September with the dainty blue *Lobelia kalmii* of which Wolden wrote: "Perhaps the most welcome stranger of all is the lovely brook lobelia (*Lobelia kalmii*). Stranger it is, for, like the others, it is a northern plant barely coming within our territory. It is a very lithe and graceful little plant with small delicate flowers of a light blue color, borne on threadlike pedicels." The 2-inch snow-white flowers of *Parnassia glauca* dot the foreground. Here and there the smaller fringed gentian (*Gentiana procera*) adds another tint of blue. This showy society covers the entire west and north sides of the knoll below the tall-herb sod, and on down 50 to 100 yards along the flat below, the sods becoming gradually the disperse phase and the watery areas fusing to become the dispersion medium.

The margin of the densely sodded area is a hard crust of tufa tightly packed with leaves of innumerable *Parnassias*—which bloom en masse—and bordered for a few inches with luxuriant sods of *Calliergonella cuspidata*, *Drepanocladus aduncus* and *Campylium stellatum*, with a few small strips of *Drepanocladus revolvens* and *intermedius*.

Across a little valley on the east, filled with shoulder-high *Spartina*, *Solidago* and *Helianthus*—an ordinary wet-land community—the fen takes up again, with *Chara* pools and sods of *Rhynchospora*, *Triglochin*, *Lobelia*, *Parnassia* and gentian, and rims of *Drepanocladus*, *Calliergonella* and *Campylium*.

The knoll has on its northwest top a 10 ft. wide stand of *Phrag-*

mites, bordered to landward with a clump of *Typha latifolia* and a stand of *Scirpus validus*. Sloping down northward to the border of the tall herbs there is a scattering of *Scirpus americanus*. The gentle eastern slope is the home of *Cypripedium candidum*, which blooms in early June before the other plants are a foot high. Later it is hidden in a waist-high common wet-land community of sedges, scirpi, goldenrods, sunflowers, *Eupatoria* and *Pedicularis lanceolata*.

A large fen northwest of Estherville (Emmet County) has been described by Wolden (1926). Here an eighth of a mile of *Scirpus validus* covers the horizontal brow of a hill, making a very strange skyline as seen from the river bank below. Two species of *Triglochin* grow there. *Drepanocladus revolvens* is bigger and redder. And in the margin of one pool there is an 18 inch strip of *Catascopium nigritum*, not only living in this climate, but bearing its characteristic crooked little black capsules. I first collected *Catascopium* in nearly pure sand among dunes on the east side of Lake Huron; it is abundant near snow-line in Jasper Park, Canada.

Triglochin maritima grows in so-called "tide pools" on the salt marshes of Long Island, along with sulfur bacteria. It grows in many mineralized waters both cold and hot in Yellowstone Park. It was seen flourishing, rising through ten inches of water so hot that one could hardly bear his hand in it long enough to uproot the specimen. *Scirpus americanus* dominates an association on the borders of the tidal flats of the Atlantic shores.

The peculiar fen plants are of boreal distribution (Gray 1950: MFNA):

Parnassia glauca, New Brunswick to Minnesota, Virginia, Illinois, Iowa.

Rhynchospora capillacea, New Brunswick to Minnesota, New Jersey, Pennsylvania, Indiana, Missouri.

Lobelia kalmii, Nova Scotia to New Jersey, Manitoba, Ohio, Iowa.

Triglochin maritima, Labrador to New Jersey; Alaska to California, Mexico, Europe, Asia.

Triglochin palustris, Greenland to Alaska; New York, Indiana, Colorado, Europe, Asia.

Gentiana procera, New York to Ontario, Minnesota, South Dakota, Manitoba.

Campylium stellatum, northern U. S. and Canada south to Pennsylvania and Ohio; Colorado, British Columbia, Alaska, Europe.

Calliergonella cuspidata, northern U. S. and Canada across the continent; south to New Jersey, Pennsylvania and Iowa.

Drepanocladus revolvens, Colorado to Alaska; Vancouver Island.

Drepanocladus intermedius, northern U. S. and Canada across the continent. Rare.

Drepanocladus aduncus, across northern U. S. and Canada and northward; south to North Carolina and California.

Catascopium nigritum, Great Lakes region and Rocky Mountains; Alaska, British Columbia, Montana.

Such ranges have to be accompanied by the warning that a state must be mentioned even though the species is known from only one spot unique for its microclimate. *Catascopium* occurs in Iowa, but in only one small sod about 2½ miles from the Minnesota line.

Similar calcareous alkaline fens are reported for Ohio, New York and Missouri. Gordon's (**1933**) fen at Urbana, Ohio, is the most like those of Iowa, a "raised bog" on recent glacial drift. He says "the constancy of water supply from artesian sources has maintained alkaline bog vegetation in a region where the prevailing natural vegetation is oak-hickory forest and tallgrass prairie." "The water is distinctly alkaline." The coldest waters issuing from the bog were 55° F on July 24, 1932. "In the swampy fields below and surrounding the raised bog a number of interesting marsh species may be found, such as the following:

Valeriana edulis
Lathyrus palustris
Triglochin maritima
Parnassia glauca
Solidago riddellii
Lobelia kalmii

Zenkert (**1934**) described "The Unusual Plant Association of a Marly-Sphagnous Bog" in Bergen Swamp, Genesee County, New York. Here "knolls and hummocks and islands of *Sphagnum* abound on the marl substratum, calciphilous and sphagnophilous plants growing in close proximity." The real question is "How close?" And what differences in calcium content and pH of the waters occur in close proximity? Zenkert's list includes *Salix candida*, *Zigadenus glaucus*, *Triglochin maritima*, *Triglochin palustris*, *Cypripedium candidum*, *Spiranthes romanzoffiana*, *Lobelia kalmii*, *Aster junceus*, *Phragmites communis* and *Rhynchospora capillacea* as does Anderson's list for our Silver Lake fen. But with us the *Cypripedium*, *Lobelia* and *Phragmites* do not grow intermingled. It may be the same in Bergen Swamp. For Zenkert also lists *Sphagnum*, *Ledum groenlandicum*, *Gaultheria procumbens*, *Vaccinium oxycoccus* and others which can hardly exist in calcareous alkaline waters. There must be several associations in the marly-sphagnous bog of Bergen Swamp, as there are at Silver Lake.

Muenscher (**1946**) describes the same marly area in similar terms, and with a similar list of plants. He adds that E. T. Wherry found

in Junius bog in Seneca County, N. Y., that the marl soil was alkaline in reaction and the soil from raised sphagnum hummocks was acid in reaction. This explains the spotty distribution of plants in the Bergen fen. The *Triglochin*, *Rhynchospora* and *Lobelia* are true caleiphiles. There is some evidence that *Triglochin* is benefitted by H_2S. Zenkert's list is perfectly consistent with the known facts. He did not assort his plants into sociological units, but lumped together all of the species from a certain landscape. That kind of record is no longer adequate. It leaves too many basic questions unanswered.

By way of calling attention to the need of accepted definitions we note that in one sentence Gordon uses swamp, bog and marsh as though interchangeable. Can we not agree that a swamp is an area with surface water most of the time, with more than 50% cover of trees; a bog is similar land without trees, with a ground cover of *Sphagnum*; a fen is like a bog but is alkaline and without *Sphagnum*; a marsh is similar land with a cover of culm plants. Examples: Dismal Swamp; a sphagnum bog; the Silver Lake fen; a salt marsh on the Atlantic coast.

In letters from Mr. Charles Boardman of Pittsburgh, Pa., I have accounts of a calcareous alkaline hillside fen in northwestern Pennsylvania which has the same *Parnassia*, *Campylium* and *Drepanocladus aduncus* as our Iowa fens, with *Gentiana crinita*, *Pedicularis lanceolata* and *Chara* sp.

These paragraphs do not by any means account for all of the plants of Iowa's waters and waterways. We have only touched upon the principal communities that are relatively permanent.

CHAPTER IX

Communities of Cultivated Plants

A. communities of woody plants

1. Trees of lawns and streets. When timberlands were settled in Iowa it was customary to retain as many as possible of the native trees for shade. As the settlements were mostly on uplands—bottomlands are too easily flooded—the trees are those of the Quercetа. Such trees are likely to be slow growers. But the making of lawns and raking off of fallen leaves in autumn soon changes the soil for the worse. The surface immediately loses its protective covering of duff. The packed ground encourages runoff of rain rather than absorption. The trees no longer flourish, though they may live through their normal span of life.

Grading operations remove top soil around the trees, or pile it up over their roots. Trees of the Quercetа are not accustomed to either process, least of all to surface deposits of soil. Oaks will endure a little covering; pines none at all. Native trees in towns and villages have a hard life.

Settlers in treeless areas were eager to have shade trees as quickly as possible. So they avoided the slow growing oaks, whose big seeds are so easily handled, and adopted especially the elms, so characteristic of the New England homelands. Silver maple was also highly esteemed. Walnut, hackberry and green ash were occasionally planted, and cottonwood frequently. Seeds and seedlings were collected along the nearest river, or purchased from local nurserymen who did the collecting. In this case the bottomland trees proved very much easier to transplant than the oaks.

Bottomland trees are accustomed to both silting over of the land and erosion. Cottonwoods go merrily on under the most extreme conditions of covering and uncovering, as Kerner and Cowles have described. Elms along our city streets seem unharmed by being left standing on a little mound of earth. On the other hand one of our largest specimens has been so graded up around that no widening of the trunk downward appears above the ground. The spreading roots are deeply covered up. It is fortunate that we selected bottomland trees for our streets and lawns!

At the location of Grinnell no tree could be seen when the first

settlers came. Now the airman looks down in summer upon a mile-square grove, surrounding a few bare business blocks. An early landholder told me that he first planted Lombardy poplars around his property for immediate effect. When these were well grown he set out silver maples. One of these now measures fifteen feet in circumference, a cripple but very much alive. When the streets were definitely located american elms were planted. They still stand, along Highway 6, in the prime of life. One of them is 11 feet in circumference. This landholder owned the property from 1860 to 1871. The elms were probably planted about 1867 or 1870.

The sugar maple (*Acer saccharum* and *A. nigrum*) and Norway maple are popular and successful trees for lawns and residential streets in the eastern half of the State. Their dense foliage and broad, low crowns make it difficult to maintain a ground cover under them. Bluegrass survives only when the branches are trimmed off so high as to mar the beauty of the tree. But their splendid coloring in autumn makes up for any shortcomings.

Over most of Iowa the american elm is certainly the very best shade tree. Its growth in the soil of the treeless prairie is prodigious. A street tree felled in 1907 at about 40 years of age has wood 25 inches in diameter above the bulging base. Some of the rings are a half inch wide, indicating a growth in diameter of one inch in one year. Near the center of the slab is a scar marking the date of the tornado that ripped through Grinnell in June 1882.

Other elms in Grinnell have circumferences of 12 to 13½ feet. Silver maples measure 12 to 15 feet. A recently cut stump is 3 ft. 4 in. in diameter, including bark. Cottonwoods in Grinnell are 10 ft. to 15 ft. 4 in. in circumference, and a hackberry measures 7 ft. 6 in. Most surprising is an english oak (*Quercus robur*) with a girth of 7 ft. 10½ in. This tree was planted about 1903. Shall we say it is just 50 years old from the seed? My bur oak just 40 years from the seed has a girth of 4 ft. 11 in. breast high. Among the most annoying weeds in my garden are seedlings of elm, ash and boxelder, which come up in the midst of my peonies and currant bushes.

Why, then, was the prairie treeless?

A list of trees that grow in Grinnell and vicinity is given below. By a little padding there are 142 of them.

In Lyon County and northwestward the boxelder is the most reliable tree—not very good, but better than none. A grove of european larches at Larchwood grew to a height of 50 feet and then began to fail and die.

In cities and elsewhere at the arid limit of growth for trees it is

often noted that trees will do well for a few years, but perish before reaching fully mature size. The roots may be able to gather enough water for a small crown, but there just is not enough available for a large one. And though the tree may seem to fall a prey to insects and disease, the predisposing cause may be inadequate supply of water. It is well known that the birch bark borer is only destructive in a dry cycle; even then injury can be averted by abundant watering. The death of groves and windbreaks does not necessarily indicate a change of climate. There never was enough water in semiarid climates to support the crowns of fully grown trees.

TREES THAT GROW IN GRINNELL

Those marked (—) are short lived or tender.)

Pinus strobus
Pinus cembra
Pinus flexilis
Pinus sylvestris
Pinus banksiana
Pinus nigra austriaca
Pinus resinosa (—)
Pinus ponderosa
Pinus densiflora
Picea abies
Picea glauca
Picea glauca albertiana
Picea pungens
Abies balsamea
Abies concolor
Tsuga canadensis
Pseudotsuga taxifolia
Thuja occidentalis
Thuja orientalis
Juniperus virginiana
Taxodium distichum
Ginkgo biloba
Larix decidua
Larix laricina
Acer ginnala
Acer negundo
Acer platanoides
Acer platanoides Schwedleri
Acer nigrum
Acer rubrum
Acer saccharinum
Acer saccharinum Wieri
Acer saccharum
Aesculus arguta
Aesculus glabra
Aesculus hippocastanum
Aesculus octandra
Ailanthus altissima
Alnus glutinosa
Amelanchier arborea
Aralia spinosa
Aralia chinensis
Betula lenta (—)
Betula lutea
Betula nigra
Betula papyrifera
Betula pendula
Betula pendula laciniata
Betula populifolia
Carpinus caroliniana
Carya illinoensis (—)
Carya laciniosa
Carya ovata
Castanea dentata
Castanea mollissima
Catalpa bignonioides
Catalpa bungei
Catalpa speciosa
Celtis occidentalis
Crataegus mollis
Diospyros virginiana
Elaeagnus argentea
Euonymus atropurpurea
Fagus grandifolia
Fraxinus americana
Fraxinus nigra
Fraxinus pennsylvanica subintegerrima
Gleditsia triacanthos
Gleditsia triacanthos inermis
Gymnocladus dioica
Juglans cinerea
Juglans mandshurica
Juglans nigra
Liquidambar styraciflua (—)
Liriodendron tulipifera
Maclura pomifera
Magnolia acuminata
Morus alba tatarica
Ostrya virginiana
Phellodendron amurense
Platanus occidentalis
Populus alba
Populus alba bolleana
Populus balsamifera
Populus deltoides
Populus x eugenei
Populus x generosa
Populus nigra italica
Populus tremuloides
Prunus americana
Prunus avium (—)
Prunus armeniaca
Prunus domestica (—)
Prunus x hanska
Prunus hortulana
Prunus insititia
Prunus padus
Prunus pennsylvanica
Prunus persica
Prunus serotina
Prunus sargenti
Prunus virginiana
Pyrus aucuparia
Pyrus communis
Pyrus x keiffer
Pyrus baccata
Pyrus prunifolia
Pyrus atrosanguinea Hopa
Pyrus hybrida (Sorbus)
Pyrus ioensis
Pyrus ioensis plena
Pyrus x Rivers
Pyrus malus
Quercus alba
Quercus imbricaria
Quercus macrocarpa
Quercus montana
Quercus palustris
Quercus robur
Quercus rubra
Quercus velutina
Robinia pseudoacacia
Salix alba
Salix alba vitellina
Salix x blanda
Salix amygdaloides
Salix babylonica
Salix babylonica pendula
Salix fragilis

Salix nigra
Sassafras albidum molle (—
Syringa amurensis
Syringa amurensis japonica
Syringa pekinensis
Tilia americana
Tilia cordata
Tilia petiolaris
Ulmus americana
Ulmus procera
Ulmus rubra
Ulmus thomasii
Viburnum lentago

Undoubtedly the following native trees would grow in Grinnell: *Carya cordiformis*, *Quercus bicolor*, *Quercus ellipsoidalis*, *Quercus Shumardi*, *Quercus Shumardi Schneckl*.

2. Windbreaks. Every well-cared-for farmstead in Iowa has a windbreak of trees on the west and north. The sheltering effect of such a planting is distinctly felt for 300 ft. to leeward. Usually this protection is sought only for dwellings and stables,—for people and livestock. Judge Whiting of Monona County (1874, 1881) urged the planting of a windbreak around every quarter section, to turn aside the cold winds of winter and catch as much snow as possible, and quite as much to break the power of hot, dry south and southwest winds in summer. He was successful in starting miles of walnut trees on the bottomlands south of Sioux City. It is now believed that the land used by such plantings is more valuable for crops than for windbreaks.

In no part of the State is the climate too inclement for the growth of a properly selected windbreak. For greatest service it should consist partly or wholly of evergreen conifers. The best growth all over the State is made by Norway spruce. Next best is blue spruce, and next the white spruce, either canadian or Black Hills. The hardy native red cedar cannot be used because it is intermediate host of the rust of apple trees. The Wealthy apple is especially susceptible to rust and may be killed by the disease. The infection can spread as much as two miles.

In the earlier days pines were frequently used: white pine, scotch pine, austrian pine. All of these tend to lose their lower branches. They must be supplemented by something that will stay closer to the ground. It is known that many hereditary growth-forms occur in Europe in both of the foreign species. It is believed that the early collectors of seeds took them from the most accessible places, that is from low-growing, crooked and branching types. What with such a heredity and the rather unfavorable climate of Iowa these trees rarely show the fine erect boles that make them favorite timber trees in the cultivated commercial forests of modern Europe.

The Iowa State College (Campbell and Grau 1948) recommends at least three rows of evergreens for a windbreak, the rows 18 ft. apart, the trees 18 ft. apart in the rows, with "alternate spacing" (in quincunx). It is suggested to have pines in the middle row and

spruces on each side, or with Douglas tree on north and west. A temporary belt of deciduous trees may be planted adjacent to the evergreens, with rows and trees six feet apart. The evergreen species recommended are:

Pinus strobus
Pinus resinosa
Pinus ponderosa
Pinus sylvestris
Pinus banksiana
Thuja occidentalis
Juniperus virginiana
Picea glauca
Picea glauca albertiana
Picea excelsa
Picea pungens
Pseudotsuga taxifolia
Abies balsamea
Abies concolor

Even a narrow windbreak makes life impossible for prairie plants because of shade. There is neither opportunity nor a suitable microclimate for the sparse ground-vegetation of the coniferous forest. The surface under the low-branched trees is a bare mat of needles. In the deciduous windbreak the ground is taken over by weeds. The burdock likes the windbreak and is hard to control. Cocklebur may get in along the margins. Some weedy grasses and a spanish needle are to be expected. A thin mull develops, and the moss *Leskea gracilescens* may settle on the trunks. Beginnings of a shrub border are indicated by the appearance of black raspberry and elderberry, introduced by birds. But these developments are best carried out in groves and timber claims, to which we now turn.

3. Woodlots. The need of lumber for all purposes was a serious matter on the prairie. The smaller groves, as at The Lizard in Pocahontas County, were quickly cleared. It was obvious that sawlogs could not be produced in significant quantity, but each farmer might in a lifetime harvest a crop of fence posts and fuel. Barbed wire and wooden posts made possible the fencing of the prairie. The post-and-rail or "worm" fences of the woodland areas were impossible in most of Iowa.

Attention was early given to the planting of trees as a crop. In 1868 "An Act to Encourage the Planting and Growing of Timber, Fruit Trees, Shade Trees and Hedges" was passed by the State legislature. This was replaced by a second Act in 1872 which, as entered in the Code of 1873, provided "that for every acre of forest trees

planted and cultivated for timber within the state, the trees thereon not being more than 12 feet apart and kept in a healthy condition, the sum of $100.00 shall be exempted from taxation upon the owner's assessment, for ten years after each acre is so planted." For fruit trees not over 33 feet apart an exemption of $50.00 per acre was allowed. The board of supervisors could exempt from county taxation as much as $500.00 for each acre of forest trees less than three years old. (Brindley **1911**).

The Act was frequently amended, but the abuses in the application of it were so flagrant that all exemptions for tree culture were omitted from the Code of 1897. In 1906 an Act provided "a flat taxable valuation of one dollar an acre for forest reservations."

With these inducements many groves larger than windbreaks were planted all over the State. These can be seen today in many stages of growth and decay, of care and neglect. They have given rise to plant communities which deserve much more study than they have ever had. When mature groves of deciduous trees have lost their lower branches and become open, they are generally pastured, and a bluegrass meadow association covers the ground. The floristic composition of such communities is not on record.

Shimek (**1910**) tells of a flourishing grove of soft maples in Monona County grown from seed planted 1865 and "cultivated like any other ordinary crop." The maples were from eight to seventeen inches in diameter in 1910. Amongst them had come up spontaneously twenty-five species of woodland plants, "yet the nearest natural grove is several miles away. Not one prairie species was found in the grove."

A ten acre grove in Dickinson County, bounded on the west by virgin prairie, was planted about 1895. Some of the trees have matured and fallen down. The subordinate vegetation is that of the natural woodland along Marble Lake a half mile northeast. This grove would repay a detailed study.

A 20 acre grove of mature conifers — larch, spruce, pine — near Traer was completely cleared a few years ago. It has not been studied. Fine groves of pines in the Amana Colonies would amply repay detailed study. Recent plantings west of Tama should be studied continually for development of vegetation and soil.

B. COMMUNITIES OF HERBACEOUS PLANTS

The glorious garment of prairie vegetation that once clothed seven-eighths of Iowa has been almost totally obliterated, and in its place has come an equally magnificent and amazing vastness of associations of cultivated plants, controlled more and more precisely by the hand

of man. Even more pleasing to the eye than endless stretches of flowers and grass are the incredible expanses of grain crops and pastures, laid out by the compass in squares. The airplane view at the first of July presents a soul-stirring panorama of human effort and achievement. A checkerboard of striking colors lies below: golden yellow squares of ripened oats; dark emerald blocks of growing corn not yet in tassel; brown-green hayfields dotted with stacks of hay; grass-green pastures peopled with comfortable cattle; a farmstead with a dozen buildings and a sheltering windbreak of trees on every quarter section; at two mile intervals the country school house, and every six to ten miles a village with trees and dwellings, church, store and grain elevator. The landscape now serves the purposes of civilized man. The increased production of food as compared with native prairie is figured in millions and billions, beyond the grasp of our imagination.

Although the cultural associations are planted and controlled by man, the plants are not held in complete abeyance. Many unbidden guests share the favorable conditions created for the planted crops. Weeds of various kinds accompany each crop, and are often characteristic of it. By their abundance and luxuriance they indicate the kinds of soil as well as the care or carelessness of the landlord.

SHORT-TERM CROPS[7]

1. Portulacetum.—For example, the vegetable garden. It is usually cultivated continuously all summer, and year after year. Rotation is practised only as to changing the location of the species from year to year. Presumably this practice reduces the incidence of diseases of individual crops. In spite of my best efforts I have never had a garden entirely free from the weeds *Portulaca oleracea* and *Euphorbia supina*. Such an association is universal from Iowa to Long Island (Conard **1935**). It has been called Portulacetum oleraceae. In most of its area it now includes *Galinsoga hispida*. Very often *Mollugo verticillata* is a member of the community. Many other weeds are included according to care and proximity.

Galinsoga is an immigrant from Central or South America which disembarked at Chester, Pennsylvania, in 1888. The first report of it in Indiana was in 1911 (Deam **1940**). This writer saw it in Howard County, Iowa, in 1918 and in Grinnell in 1921. It was abundant in

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[7] "—il est possible et même indispensable de distinguer dans la végétation ruderale des associations et des alliances bien individualisées non seulement au point de vue floristique mais aussi au point de vue de leur écologie." Braun-Blanquet et al. (1936).

Dickinson County in 1945. It is not mentioned in Pammel's Weeds of Iowa, second edition, 1926.

Following is a table showing the composition of the Portulacetum in Grinnell, Iowa, from field notes by Ruth Gilman (Mrs. T. T. McClure).

Portulaca oleracea garden weed Association
Portulacetum oleraceae
Record of presence in seven stands on Muscatine Silt Loam in Grinnell, Iowa

	Name of plant	Stands						
		1	2	3	4	5	6	7
Th	*Portulaca oleracea*	x	x	x	x	x	x	x
H	*Oxalis "corniculata"*	x	x	x	x	x	x	x
Th	*Euphorbia supina*	x	x	x	x	x	x	
Th	*Capsella bursa-pastoris*		x	x	x	x		x
Th	*Stellaria media*		x	x		x	x	
Th	*Malva neglecta*			x				x
H	*Taraxacum* sp.			x				x
Th	*Amaranthus retroflexus*	x				x		
Th	*Galinsoga ciliata*					x	x	

In only one stand: *Hibiscus trionum, Euphorbia maculata, Panicum capillare, P. dichotomum, Digitaria ischaemum*, all Th.

2. Small grains. In the 1870's Iowa was a leader in the production of wheat. Now wheat is rarely seen in the State. With it has gone the "corn cockle"—we should say wheat cockle—with its inch-wide red-purple flowers. It was a harmless weed, never abundant but always present in wheat fields—always until more refined methods of cleaning seed wheat were effective in eliminating the weed. In recent years the early wheat is badly infected and impoverished by "scab," the fungus *Gibberella saubinetii*. The same fungus attacks corn and grows on old corn stalks; thus corn makes the growing of wheat unprofitable. Late wheat is seriously reduced by black stem rust (*Puccinia graminis tritici*). Neither of these diseases is subject to control by fungicides. So we have given up wheat as a major crop.

Oats and barley are similar in being annuals. They are very extensively grown in northern Iowa, where flax is also an important crop. All three of these crops are easily overrun by wild mustard. To the passing tourist a 20 acre sheet of golden bloom of mustard (*Brassica kaber*) is a beautiful sight. Pammel et al. (1928) found in Boone, Story and Hamilton Counties marsh cress, curled dock, wild mustard and milkweed in nearly all fields of oats.

3. Corn (Maize). The weeds of cornfields must be of a different type. They must be able to grow up after the corn is well started,

and to mature in spite of the partial shade cast by the corn. Major weeds, almost characteristic of the "Zeetum" are *Abutilon theophrasti* and *Xanthium*. Even more universal, but with lower fidelity, are the two *Setarias* (*S. glauca, viridis*), *Panicum dichotomiflorum*, *P. capillare* and *Polygonum pensylvanicum*.[8]

4. Soybean. The soybean is now second to corn as a major crop in Iowa. The beans are sown late in spring, after weeds have been killed by repeated stirring of the soil. This crop is therefore worth growing for the purpose of controlling weeds. It is a good renovator of the soil because the root tubercles add assimilable nitrogen, and the roots add humus. If harvested with a combine the tops also are incorporated into the soil. The market price of the beans makes them almost as lucrative as corn. It is said that erosion of soil by rain is more injurious under beans than under any other crop. The weeds of the soybean association are of any kinds that are left over from previous crops and have survived measures for control. There are none that are characteristic of this crop.

Experienced farmers can estimate the fertility of their land by the weeds that take possession of it. Warner (1945) gave suggestions concerning this so-called "indicator" value of vegetation. He recognized that "well established plant communities are more reliable as specific indicators (of soil conditions) than weedy or other temporary plant communities." He noted, however, that at Floris in Davis County *Plantago aristata* indicates severe drouth in summer in the upper six inches of soil. *Ambrosia artemisiifolia* occurs on disturbed soils with bare places during the first half of the growing season; the disturbance may be due to heavy grazing. *Erigeron ramosus*, *Rumex acetosella* and *Potentilla simplex* indicate soil poor in organic matter and highly acid. Aster and goldenrod indicate poor structure of soil, undisturbed for two or more years. Kentucky bluegrass indicates the presence of an A-horizon, moderate carbon content, and available moisture during nearly all of the growing season. *Rhus glabra* indicates well-drained, usually somewhat eroded soils, rather porous and of low to moderate carbon content. *Symphoricarpus orbiculatus* and hazel indicate sites suitable for forests. Black oak

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[8] An Iowa farm on approximately level ground with fertile soil may profitably have more than half of its area planted with corn. Under present controls the actual plantings are:

Acres	in corn	in oats	in soybeans
360	88	45	25
180	57		

As much as one quarter of the farm may well be planted with clover. But many other crops and combinations are used.

and shingle oak indicate lower water supplies than white oak or shagbark hickory. Sugar maple and linden indicate the most mesic conditions of the region; the soil profile is well developed and is of the gray-brown podsolic type.

Schmitz (Gembloux 1948) studied the relation of certain weeds to soil acidity. He reported that in Belgium *Scleranthus annuus* shows distinctly greater abundance at pH 3.5 to 5.0 than at less acidity, but it grows yet at pH 8. Abundance means more than mere presence. *Cirsium arvense* was most abundant at pH 6.5-8.0, with a maximum at 6.5-7. *Anagallis arvensis* had a broad maximum of abundance at 7 to 8. Wild mustard (*Brassica kaber*) had its maximum abundance in Belgium at pH 7.5 to 7.9, but German investigators reported it as not growing in soils of pH above 7. *Daucus carota* is an indicator of basic soils. *Rumex crispus* is weakly acidiphile.

Schmitz examined two fields of rye. A very poor field where weeds (40 species) had a total coverage of 35% showed pH 7 to 7.9. A much better field, with 20 species of weeds, had pH 4 to 4.4. The estimate of pH is derived from a consideration of all of the species found rather than from any one, according to Schmitz. Similar advices have been given by Boyko for Palestine and by Veloso for Argentina.

The pH requirements for individual crops have been given by various authors. The figures vary so widely as to be of very little value. Evidently other factors greatly modify the results. For example: Rye 4.5-7.8; 4-7; 5.8-7.2. Potato 4.7-6.5. Alfalfa 6.4-7.8. Flax 6-8. Wheat 5-7.5. Oats 5.6-8.9; 4.8-6.5; 5-6; 5-8. Alfalfa and flax appear to prefer alkaline soils, and oats is favorable to alkaline reaction. These European figures are in harmony with agricultural practice in Iowa.

Pavlychenko (1937) found that weeds can reduce the root development of crop plants by 20%, more or less, under field conditions, by sheer competition in the ground. The effect upon the harvest must be serious. The view is sometimes expressed, however, that a cover of weeds in a potato field after the tubers are mature is beneficial in that it keeps the soil cool and dry until harvest time. Instead of weeds it is desirable to use annual flowering plants in the home garden to cover the beds of tulips and narcissi in loess soils. Cool and dry are the proper conditions for the spring flowering bulbs during the summer.

Hanel & Dansereau (1949) have discussed at length the ecology and sociology of weeds, with a brief bibliography.

5. Haylands. For present purposes we may define haylands as biennial or perennial forage communities annually mowed and subject to periodical plowing and renewal as a stage in the rotation of crops. Pasture may be defined as perennial forage communities not mowed but more or less closely cropped by livestock, and either never plowed or only rarely renovated as a stage in rotation. When the pasture is thus rejuvenated it is preceded by a few years of grain communities and two or more years as hayland.

In Iowa alfalfa is an important hay crop. Since it is not long-lived here, we are considering it along with other rotated crops. Farther west the alfalfa field is more permanent than any other introduced forage, and might well belong among long term crops. Which shows that my classification, like many others, is not perfect!

The alfalfa plant grows 18 inches to two feet tall. Being of the Pea Family each flower is a miniature sweet pea, with a pollinating mechanism that must be tripped by a bee if seed is to be produced. Its roots are powerful collectors of nitrogenous foods by means of nitrogen-fixing bacteria. They also go to incredible depths to bring up water and mineral salts. So alfalfa is the very best crop for improving the soil. It yields two good crops of hay each season, and sometimes three.

A good stand of alfalfa in Iowa still has room for weeds. And as the years go on the weeds increase. So alfalfa cannot be a permanent community in this State. The weeds of alfalfa fields were listed by Hershey and Pammel (1930). The list is interesting, but I do not see any name in it that is at all characteristic of alfalfa fields. Sixteen fields were examined in eight counties. Weeds listed as important and occurring in 40 to 100% of the fields studied are:

First rank in abundance
- *Setaria glauca*
- *Setaria viridis*

Second rank
- *Poa pratensis*
- *Ambrosia artemisiifolia*
- *Rumex crispus*
- *Agropyron repens*
- *Tragopogon pratensis*
- *Echinochloa crus-galli*
- *Polygonum pensylvanicum*

Third rank
- *Hordeum jubatum*
- *Polygonum persicaria*

Fourth rank

Taraxacum officinale
Lactuca scariola
Oxalis "corniculata"
Erigeron ramosus
Chenopodium album
Plantago rugelii
Capsella bursa-pastoris
Erigeron canadensis
Lepidium densiflorum
Phleum pratense
Asclepias syriaca
Solanum nigrum

Sometimes bluegrass or quackgrass becomes dominant, killing the alfalfa.

The standard old-fashioned hayfield is a mixture of timothy, bluegrass, redtop, orchard grass, red clover and alsike clover. The universal weed is whiteweed, *Erigeron ramosus*. In the first year the clovers may be predominant. In the second year the clovers are less abundant, the bluegrass and whiteweed more abundant. If left-over roots and rhizomes of milkweed or canada thistle or field bindweed made a start in the first season, they make great advances during the second, for they regenerate quickly after mowing. Small ragweed may come up thickly after the second year's crop is removed. Bluegrass should take over in the second year and the community becomes a pasture. In most cases, however, the hayland is again plowed and the man-made succession begins anew. A common rotation in Iowa is corn 2 years, oats one year, hay and pasture 2 years or clover one year, corn. The pasture period may be lengthened for stock raising or dairying.

The rotation of crops, a man-made succession of communities, is useful in the control of weeds because, as just shown, the conditions favorable for one crop-community are unfavorable for the weeds of any other.

LONG TERM COMMUNITIES

The bluegrass pasture Association

The bluegrass pasture community is maintained for indefinite periods on hilly land or on bottomlands too wet for producing profitable seed crops. A study of bluegrass pastures in Poweshiek County is here presented from a report by Ruth Gilman under supervision of the writer.

This stand was formerly a bur oak-hickory woodland association which is now cleared out except for a few stumps and a stray goose-

berry bush here and there. It is used as a pasture for cattle and is therefore rather heavily manured. The soil is Tama Silt Loam (Brown et al. **1935**).

Symbols used in the table are adapted from Braun-Blanquet (**1932**), as follows:

Abundance shown by covergrade,

—sparsely or very sparsely present; cover very small.
1 plentiful but of small cover value.
2 very numerous, or covering at least 1/20 of the area.
3 any number of individuals covering ¼ to ½ of the area.
4 any number of individuals covering ½ to ¾ of the area.
5 covering more than ¾ of the area.

Vitality

1 occasionally germinating but not increasing; many ephemeral or adventive plants.
2 feeble but spreading, never completing the life cycle.
3 strong and increasing but usually not completing the life cycle; many mosses.
4 well developed, regularly completing the life cycle.

Sociability

1 growing one in a place, singly.
2 grouped or tufted.
3 in troops, small patches or cushions.
4 in small colonies, in extensive patches, or forming carpets.
5 in great crowds (pure populations).

ASSOCIATION TABLE

	Name	C	V	Soc.	Frequency in 14 quadrats
G	*Poa pratensis*	4	3	4	100%
H	*Trifolium repens*	2	3	3	100
H	*Cirsium altissimum*	2	4	1	50
H	*Oxalis "corniculata"*	1	2	2	57
H	*Verbascum thapsus*	1	3	1	50
Th	*Digitaria ischaemum*	–	4	1	78
Th	*Euphorbia supina*	–	4	1	93
Th	*Setaria glauca*	–	4	1	7
Th	*Acalypha virginica*	–	4	1	14
Th	*Erigeron canadensis*	–	4	1	85
H	*Taraxacum* sp.	–	1	1	71
	Outside of the first quadrat:				
Th	*Ambrosia artemisiifolia*				43
H	*Verbena stricta*				28

	Name	C	V	Soc.	Frequency
H	*Plantago rugelii*				14
Th	*Erigeron ramosus*				14
H	*Achillea millefolium*				14
H	*Nepeta cataria*				7
Th	*Cannabis sativa*				7
	Bovista plumbea				21
	small mushrooms				21
	Additional plants of high constancy:				
H	*Cirsium lanceolatum*	H	*Verbena hastata*		

Poa pratensis is the dominating plant with the highest cover-grade and a moderately high vitality. The latter was perhaps due more to the lack of care of the pasture than it was to the vitality of the plant under normal conditions. Its sociability was high. From the field record *Cirsium altissimum* and *Trifolium repens* are important members of the association. The thistle is a destructive element as it ruins the pasture economically, and if allowed to increase will shade out the bluegrass. The vitality of both is high, but sociability is high for only *Trifolium*. The frequency column shows two species present in all of the quadrats of Stand 1: *Poa pratensis* and *Trifolium repens*. Interestingly enough the next most frequent species was *Euphorbia supina* which was present in 13 of the 14 quadrats; its vitality is highest, but its covergrade and sociability are very low. It is a weed. Other plants which occurred in more than a third of the quadrats were *Erigeron canadensis*, *Digitaria ischaemum*, *Taraxacum* sp., *Oxalis corniculata*, *Cirsium altissimum*, *Verbascum thapsus* and *Ambrosia artemisiifolia*. All are weeds, and all except *Digitaria ischaemum* were found in another pasture which was studied.

The other pasture showed all of the above mentioned species except *Euphorbia supina* and *Digitaria ischaemum*. The following four species were found in both pastures:

Achillea millefolium	*Verbena stricta*
Plantago rugelii	*Verbena hastata*

In bluegrass pastures several of our largest fleshy fungi are found: *Lepiota morgani*, *Calvatia craniiformis* and *gigantea*, *Endoptychum agaricoides*. The small *Bovista plumbea* is also common.

The meadow mushroom (*Agaricus campestris*) and its kin, with pink gills becoming black, are autumn products of lawns and pastures, along with the pure white *Lepiota naucina*. These mushrooms are edible, as is also the shaggy mane, *Coprinus comatus*, in similar habitats. The vegetative mycelia of these must have something to do with dead tissues of grass.

Whether any of these fungi grew in virgin prairie in Iowa we do not know. All of the species named are native to Europe and may be immigrants here like ourselves and our crop plants. Whenever we make conditions favorable for crop plants we also make them favorable for a series of unbidden guests.

Dansereau and Gille (1949) have discussed at length the various kinds of pastures and their ecological and sociological characteristics in Quebec. Ours correspond to three of their types: those developed in a clearing, those which are steps in a rotation, and those which are occasionally plowed but are kept in grass for long periods.

The bluegrass lawn association

The clipped bluegrass lawn is a much beloved and most interesting association. Much effort is expended in making a home for it, from the irrigated lawns of California and Colorado to the limed and fertilized estates of Long Island. But we have no practical way of meeting its requirements south of Virginia or the middle of Missouri. Climate limits vegetation.

The care of lawns is intended to produce conditions in which bluegrass can prosper in spite of frequent mowing. This uniform care is just as favorable for certain weeds which up to now have always been a part of the lawn association. The use of 2-4-D may radically change the picture. The association is well described in a report by Ruth Gilman for Poweshiek County. Quadrat studies in Dickinson County give almost identical results, and studies on Long Island, N. Y. (Conard 1935), are closely similar.

The bluegrass lawn association is made up principally of *Poa pratensis, Plantago rugelii, Oxalis "corniculata," Digitaria ischaemum, D. sanguinalis, Taraxacum officinale, T. erythrospermum, Trifolium repens* and *Poa annua.*

Poa pratensis is the dominating plant, having the highest vitality and the next to highest sociability and covergrade, the latter two being higher than any other plants in this association. *Plantago rugelii* is found in all of the stands and in all of the quadrats surveyed in Stand 1. Its vitality was kept down to 3 because the flowering heads were mowed off. However, it is interesting to note that when *Poa pratensis* is allowed to grow to a considerable height *Plantago* and *Taraxacum* disappear, apparently from suffocation and lack of sunlight. *Taraxacum* was found in all of the stands, but in only a third of the quadrats in stand 1. The vitality in October is lower than in the spring when they seem to be everywhere. The same thing may be said of *Oxalis*, except that it maintains its vitality at top rank throughout the growing season.

The *Digitarias* were found in every stand and in over half of the quadrats in Stand 1. They are hardy annuals which reproduce prolifically, thus providing strong competition with *Poa pratensis* if they get a start. *Poa annua* was unusually prevalent at the time of our study, seeming to take advantage of a moist spring and early summer; in autumn it was found mostly in shaded areas.

Table of the Bluegrass Lawn

	Name	C	V	Soc.	Frequency in 12 quadrats
G	*Poa pratensis*	4	4	4	100%
H	*Trifolium repens*	3	3	3	100
H	*Oxalis corniculata*	1	4	2	33
H	*Plantago rugelii*	1	3	2	100
Th	*Polygonum aviculare*	–	4	1	25
Th	*Digitaria sanguinalis*	–	3	1	
H	*Taraxacum* spp.	–	1	1	33
	Outside of the first quadrat:				
Th	*Poa annua*				41
Th	*Digitaria ischaemum*				17
Th	*Panicum dichotomum*				8
Th	*Stellaria media*				8
Th	*Capsella bursa-pastoris*				8
	Bovista plumbea				8

Additional weeds of lawns in Grinnell are:

H	*Prunella vulgaris*	H	*Cirsium altissimum sll.*
Th	*Euphorbia supina*	H	*Glechoma hederacea*

Mosses occur in lawns only where the stand is thin and open. On a newly graded lawn with many flecks of bare raw soil I have seen hundreds of red-purple tufts of fruiting *Ceratodon purpureus*. In a year or two the grass association crowds out the moss. In shaded places where bluegrass is sparse for want of light four mosses may appear in Iowa. The oval-leaved *Mnium cuspidatum* indicates abundance of moisture and no direct sunlight. Less moisture and up to 50% sunshine accommodate *Brachythecium salebrosum* in lawns, *B. oxycladon* in margins of pastures. Shade, ventilation and moderate moisture, as under tall trees of lawns and parkings, are suitable for *Leptodictyum brevipes*, a little moss that still produces its characteristic leaves and cells and flourishes well when some accident places it in water. The species seems to be endemic in the upper Mississippi Valley.

The fungi of the open lawn are an occasional *Agaricus campestris*, the white *Lepiota* (*L. naucina*) and *Hypholoma incertum*. At the

end of a wet spell the grass may be covered for a square foot or a square yard with the little ash-colored sporangia of the myxomycete *Physarum cinereum*, often in fairy rings. The big stinkhorns are also products of the lawn: *Phallus impudicus* (very rare) and *Dictyophora duplicata* (common); *Mutinus* frequent. All of these fungi are found in lawns east of the Appalachians.

CHAPTER X

Vegetational Change

"Nothing that is can pause or stay"

Every plant, like every dog, has its day. It comes into being, grows to maturity and dies. Communities also come into being and grow to maturity. Some die. More of them are changed. And some persist through periods of geologic time. Hitherto we have described plant communities as though they were permanent entities, but they cannot be adequately described without a consideration of vegetational change.

The most interesting changes in vegetation are due to the plants themselves. Large herbs may restrain and kill smaller or slower species by over-shadowing them. Purslane (*Portulaca*) disappears promptly when tall herbs take the ground. This may be due to inability of the purslane plant to function in dim light, to inability of the seeds to germinate in dim light, or, more likely to lethal infection of the plants by the "white rust" fungus *Albugo portulacae*.

Shrubs make permanent shade, permitting only tolerant species to survive beneath them. Trees in dense sands restrain all light-loving species. Meanwhile the soil undergoes changes. The soil under herbs is different from that under shrubs or trees. So it often happens that a stand of annual herbs is followed by winter annuals and tall herbs. Among these shrubs may get a start and achieve mastery. Among these, trees may spring up and overtop all others.

If the trees of a community are able to reproduce within the stand the community may remain for untold centuries, even though no one individual lives more than a few hundred years. Such a community we call "a terminal community of great permanence." If trees are not able to reproduce under their own shade they will be succeeded by other species which can germinate and grow up in shade, if any are available.

The same story can be told regarding grasslands. In Iowa the Andropogonetalia are terminal communities. They have maintained themselves for thousands of years.

Croplands suffer from depletion of certain minerals by solution (leaching) and by removal of crops. Since it is the alkali and alkaline earth elements which are chiefly removed, cultivated soils in-

evitably become more and more acidic. Crops cease to be profitable. The land is abandoned. Vegetation attacks the problem and builds a community suited to the conditions. By successive steps the fertility of the soil will be renewed. The human problem is to hasten the steps. Under a prairie vegetation and climate leaching is nearly matched by capillary rise of salts, and the "crop" falls where it grew instead of being removed. By decay—the action of microorganisms—the salts are returned to the soil.

Changes in topography or climate cause changes of vegetation which are superimposed upon the effects of the plants themselves. Most of these changes require thousands of years. Minor topographic changes due to erosion and sedimentation may proceed quite rapidly. A landslide may expose new land in a few minutes. A flood may scour the land bare, or smother the landscape with sand or silt, or build a sandbar or cut off an oxbow lake in a matter of hours or days. In any such case the plant world goes to work to reclothe the earth with successive garments suited to the changed and changing situation.

We shall first describe some easily observed, short term changes, and proceed thence to "long term capital gains." The changes may be due to agencies quite independent of the plants themselves, or to the action of the plants on the environment.

SHORT TERM CHANGES

River banks are the most unstable of habitats for plants, for the rivers are forever cutting away the banks at one place and depositing at another. But even the most mobile banks are not entirely devoid of vegetation. The plants that occupy them are all annuals, ready to move to another place at a season's notice.

Of such nature is the low sprawling grass *Eragrostis hypnoides*, with which may be associated *Gratiola virginiana* and *Lindernia dubia* and/or *Eleocharis obtusa*.

On shaded silty banks that are not too steep, and are flooded at high water, a moss community usually develops. Being annuals the members fruit in autumn or not at all. Most conspicuous are clusters or extensive sods of the light green watery leaves of *Aphanorhegma serratum* and *Physcomitrium immersum*—very much alike. Little green films of protonema mark the place of the *Ephemerums*, two or three species. The tiny globular capsules of all of these are nestled down among the leaves.

Scattered over stretches of bare silt are the rosettes of *Riccia frostii* and *R. sullivantii*, up to the size of a dime, and the fat inch-wide rosettes of *Ricciocarpus*. All of these mosses and liverworts occur also on the bottoms of shallow oxbow ponds, wet only after floods.

But on the bottom of just one of these ponds, near the south line of Poweshiek County, there appears year after year at the same spot a patch 20 feet across or 60 feet across, according to the season, completely covered with the microscopic moss *Nanomitrium synoicum*. Millions of them! The patch lies just below a pile of slaty debris from a little abandoned coal mine. The nearest locality for *Nanomitrium* is at Emma, Mo., in the richest coal region of that state. I wonder if the moss is again at the edge of a mine dump!

Around these oxbow ponds there is a row of willow trees (*Salix nigra*) or a zone of *Polygonum pensylvanicum*. In one of them I can always find a few plants of the rare *Polygonum longistylum*. Other similar areas are covered with *Polygonum lapathifolium*, sometimes with its big smut *Melanopsichium austro-americanum*.

Now since all of the above named herbs are annuals, their communities cannot be called permanent in the sense that woody plants are permanent. These annual communities are renewed every year wherever conditions are suitable, often on the same spots for many years in succession, and so they will continue to be as long as floods renew the silt and water, and the depressions are not leveled up and made suitable for sedges and slough grass or trees,—or until the river turns backward toward them and eats away the entire bottomland. When I was traveling every road in Dixon County, Nebraska, according to a map, I came to a dead end where a whole square mile had been swept away by the Missouri River. So we can only say what will happen to these annual communities if—. Though they come back every year in the same places for as much as forty years, to my personal knowledge, they are destined to be of relatively short duration in any one place. They will certainly undergo vegetational change.

The Associations, however, as generalized ("abstract") biological units, will continue to recur throughout at least a geological period or a major climatic cycle, albeit shifting their locations from place to place as circumstances require (Shimek **1948**, 148-150). It is generally believed that the great earth-zones of Humboldt, broad-leaved evergreens, deciduous forest, boreal conifers, grasslands, achieved their present physiognomy and much of their present floristic composition in Pliocene times or earlier.

The permanence of our riverbank moss community is similar to that of a moss community described by Kerner (**1950**) nearly a century ago. In certain alpine cirques glaciers and avalanches bring down each year a layer of rock powder which overwhelms all vegetation except a big haircap moss. The extensive Polytrichetum sex-

angularis has continued for countless years because of its ability to survive the annual burial that kills everything else. This moss community has its own kind of permanence.

New land: origin and sequence of communities.

Land surfaces completely devoid of vegetation originate in various ways. To the plant sociologist and his beloved plants these are "new lands." The early stages of settlement on new lands are usually short lived and follow one another in quick succession. New lands are therefore especially favorable for the study of vegetational change.

All of the ecology texts refer to the settlement of plants on sandbars along rivers. Usually the first permanent settler is the sandbar willow, *Salix interior*. The hairy-tufted wind-blown seeds lodge during the first or second season of exposure of the bar. The seeds ripen over a long period in early summer when floods are past or are few. The seedling has two narrow cotyledons and then a rosette of pinnatifid leaves lying on the ground. From the center of the rosette a shoot with typical leaves arises, and should reach a foot in height by the end of the first season. When fully grown this willow spreads widely by underground shoots several feet in length. Beneath the willows species of knotweed (*Polygonum punctatum, hydropiper*) and spanish needle (*Bidens*) cover the ground, and the tiny moss *Aphanorhegma patens* is at home. If the bar remains, accumulating silt and humus, cottonwood, black and peach-leaved willows shade out the sandbar willow, and the Salicetum amygdaloidis ensues.

Two series of this sort at Iowa City were observed by Shimek (1948). In one case he wrote: "During the first season a heterogeneous mixture of plants appeared on the new bar. Farm crop plants, garden vegetables, cultivated flowers, introduced and native weeds, forest plants of both upland and alluvial types, prairie plants and plants of swamps and sandy areas were here associated in a confusing mixture. Then followed a gradual elimination of species, until, on that part of the bar not carried away by a subsequent lesser flood, by the end of the fourth year only an alluvial thicket dominated by young *Salix nigra* and *S. interior* was left."

The second area, now destroyed, was observed for over forty years. At first "the plants were remotely scattered over the surface of the rather moist sand and gravel bar, and consisted chiefly of *Cyperus diandrus, C. rivularis*, a few larger specimens of the *C. strigosus* type, and *Bulbostylis capillaris*. During the first summer the river flooded the bar several times during minor freshets. After each recession of the water a thin deposit of fine silt was left around and below each plant, and this formed a new soil which was promptly

occupied by other plants, the seeds of which had probably been brought by the same floods which carried the silt. By the end of the season, and especially during the season following, the bar was quite well covered by the ordinary flotsam carried by our streams, weeds, prairie, swamp and forest plants being indiscriminately mixed. As the years passed the forest vegetation took possession, and * * * an alluvial grove has been developed in which the most common trees are the cottonwood, soft maple, box-elder, green ash, American elm, black birch, black willow and sandbar willow."

Sandy areas which are dry enough to become the playgrounds of the wind are blown into high moving dunes and deep depressions, "blowouts," which may have intermittent or permanent open water. Such dune areas are most extensively developed in Iowa along the Missouri River west of Missouri Valley and California Junction. This area was described by Shimek (**1910, 1917**). The undulating surface of the fully stabilized dunes supports a thin stand of cottonwoods with closed canopy, a sparse ground cover of grasses and sedges, and scattered dense clusters of *Cornus racemosa* head high and 20 to 30 feet in diameter.

"The first plants to take possession of the new dune-surfaces" says Shimek, "are mostly members of the Pea Family, the Legum inosae." He names:

Astragalus canadensis
Cassia fasciculata
Crotalaria sagittalis
Dalea alopecuroides
Dalea enneandra
Desmanthus illinoensis
Desmodium canescens
Glycyrrhiza lepidota
Lespedeza capitata
Melilotus alba
Petalostemum candidum
Petalostemum purpureum
Strophostyles helvola
Strophostyles pauciflora
Vicia americana

Neither Professor Shimek nor the writer has seen any evidence of any other woodland association to follow the Populetum in this area. Under the local conditions the Populetum is a terminal stage of indefinite duration. Shimek wrote: "In the few cases observed in which the cottonwoods had died there were no forest plants left, but new dunes were formed and the cycle is being repeated."

Very ancient dunes, perhaps half a million years old, may be seen

on the east side of glacial lake Calvin in Muscatine County (Schoewe 1920). A rich field awaits the plant sociologist in this region. The lake was caused by the encroachment of the Illinoian glacier, which blocked the Mississippi River. Into the lake thus impounded the Iowa and Cedar Rivers emptied. After the recession of the ice the rivers took their present courses, draining the lake.

The coming and going of plant communities on dune sand have fascinated all ecologists who have seen them: Kerner, Cowles, Clements. So conspicuous are the new lands of dunes and blowouts, so diagrammatic is the relation of plants to evaporation, soil water and amelioration of soil by the plants themselves, with corresponding changes in the vegetation, that Cowles and Clements based their ecologic systems upon vegetational change, "Plant Succession." Plant sociologists recognize that many of the "seres" (successions) that have been proposed are so highly speculative as to be unsuitable for a sound foundation of a reasonably exact science. (Biological science is never exact in the sense of mathematics, physics or chemistry). The successionists classify communities without adequately defining the community; they put embryology ahead of anatomy. Sociologists believe that the structure of the community is the immediately available datum on which an objective (not speculative) classification must be based, pending knowledge of development. The development of some of these empirical units can be observed and described. Of others the development can only be determined by observations extending over several lifetimes, or by piecing together various existing putative stages. But, as has been shown above, the development of any one kind of community is not always the same.

Landslides and newly made cuts and embankments of roads and railroads are similar in that the instability of the steep banks is the first hazard for any settlers. And since they occur in all kinds of soil and exposure and vegetation, they illustrate especially well the dictum of a British ecologist. When vegetation is depleted by any agency "replenishment follows from what is most suitable that is nearest at hand" (Pallis 1939). There is no one way at present in which vegetation begins on new land.

Communities of road banks in Iowa do not begin with a blanket of the white mycelia of the pink-headed lichen *Baeomyces roseus*, nor with the green perennial protonema of *Pogonatum pensilvanicum* as in eastern Pennsylvania and New York. On the side of an east-west road south of Searsboro the north-facing bank consists of a thin veneer of loess, six feet of leached and oxidized drift, and two feet of unleached drift rich in carbonates and greenish ferrous salts.

This unleached stratum was settled with a dense, luxuriant sod of the little moss *Barbula unguiculata*, covering several square yards and fruiting abundantly. After three or four years flowering plants became more and more prevalent, shading out the moss.

An 18 inch clayey bank of a woods road under red oaks was settled first by a thin stand of *Ditrichum pusillum*. After two or three years the vigorous matted growth of *Atrichum angustatum* began spreading downward from an old stand above the bank. In a few more years *Atrichum* had completely covered the bank to the exclusion of *Ditrichum*. But on a nearby vertical bank, exposed by a little landslide, the settlers are *Ditrichum pusillum*, *Brachythecium oxycladon* and *Anthoceros laevis*. This bank is damp and stony. Still farther up stream a ten-foot clayey bank has been continually slumping for the last 20 years. It has never had anything but clumps and thin stands of *Ditrichum*.

The course of events is quite different on a landslide 50 feet high north of Homestead, in Iowa County. This slide breaks into a steep hillside with 100% cover of red oak and linden, and a ground cover of *Bartramia pomiformis*, *Aulacomnium heterostichum*, *Anomodon attenuatus*, *A. rostratus* and *Brachythecium oxycladon*. Other plants are *Solidago flexicaulis*, *Aralia nudicaulis*, *Diervilla lonicera*, *Ribes missouriense*, etc. I first found this bank feebly stabilized by *Ditrichum* and *Barbula* on the upper ten feet, while the lower part already had some willows, dogwoods and tall herbs, including *Gentiana andrewsii*, *G. quinqueflora*, *Solidago gigantea*, *Aster sagittifolius*, grasses and sedges. Later there were saplings of aspen (*Populus tremuloides*) and willows farther up the bank and *Brachythecium oxycladon* amongst these. At present *Brachythecium* has entirely replaced the other mosses, but the neighboring oaks, elms and lindens have not yet taken hold. There is as yet very little humus in the soil.

An extremely interesting sequence was described by Thone (1915-18) on a levee of raw earth thrown up by dredges in southeastern Des Moines. The levee was finished in May 1914, and left practically bare. By the end of the growing season 56 species had appeared. Pigweed (*Amaranthus retroflexus*) reached the abundance and luxuriance of a dominant. There were tall ragweeds (*Ambrosia trifida*) and wild sunflowers as high as a tall man, sods of grass, a *Cyperus* (*C. esculentus*), waist high jimson weeds (*Datura stramonium*), sprawling amaranths six feet in diameter, and some lamb's quarters (*Chenopodium album*). At one end of the levee tall ragweed was dominant on a small area.

In the following year lamb's quarter germinated much ahead of

pigweed and became dominant, with specimens of pigweed "few and far between." A few specimens of wild lettuce (*Lactuca scariola*) appeared, bore seed, and established an abundance of rosettes before winter. The stand of tall ragweed became larger.

In the third season *Lactuca scariola* was overwhelmingly dominant, and *Ambrosia trifida* had spread as far as the margin of the area of *Lactuca*. *Erigeron canadensis* was a strong newcomer amongst the *Lactuca*. The upper end of the levee was again denuded by grading operations early in the third season, and on this area pigweed immediately became dominant, in spite of the proximity of the lettuce and ragweed. "It would seem as if the cycle would repeat itself." In the next season *Chenopodium* over-ran *Amaranthus* and became dominant. After that the levee was destroyed.

The three steps in this succession seem to be due to the early start of lamb's quarter and wild lettuce in spring, following the initial heavy seeding with *Amaranthus*.

Warner (**1945**) studied the actual changes of vegetation on one small tract near Floris in Davis County, through four years. On this site corn and oats had been grown for a number of years without fertilization. It was abandoned in 1934 because of low yields The tract was basin-listed in July, 1936, leaving the ground entirely bare. It was sown with rye in autumn. A dense cover of *Plantago aristata* developed before winter. In the spring of 1937 clovers and grasses were sown. By July the rye and plantain were dying out, ragweed was conspicuous and seedlings from the spring sowing were present. In the summer of 1938 sweet clover was dominant. In 1939 redtop grass was dominant over most of the area. The different stages of vegetation showed regularly increasing control of runoff and erosion, but changes in the soil were insignificant except for a great increase of vegetable matter (roots) in the upper foot. It does not appear that the sequence of plants was due to any amelioration of the soil in the short period under observation. Kucera and Aikman (**1951**) report considerable amelioration of soil at Floris, induced by suitable crops and cultural treatments.

A point not mentioned in the studies just cited is the addition of humus on a microscopic scale by root-hairs. These tiny one-celled structures are the actual absorbing organs for water and mineral salts. Each hair lives only a few days or weeks. New ones are constantly growing out. Dittmer (**1938**) estimated that oats would have 150,000 root-hairs in every cubic inch of soil, and bluegrass one million. The loosening and softening effect must be considerable, and a quantity of dead tissue (humus) is added to the soil.

LONG TERM CHANGES

Restoration of Prairie

It was the firm belief of Professor Shimek that when prairie vegetation is disturbed in a prairie habitat it will inevitably return if left to itself. He studied over several years an abandoned plowed field at Mason City (**1925**). "At the beginning the area was occupied chiefly by native and introduced weeds, but by the fifth year it was dominated largely by four species of Compositae, *Solidago rigida, Aster multiflorus, Aster azureus, Aster laevis.*" Twelve native and 7 introduced weeds were present.

At the end of another five years "the physiognomy of the area was changed to resemble very closely that of the adjoining prairie." Thirty-two prairie plants had come in, including 5 principal prairie grasses. The area was bounded on the north and east by woods, and on the south and west by unbroken native prairie. There were no other cultivated tracts nearby to supply seeds, and the prairie was on the most favorable side for seeding. Nevertheless the weeds that dominated the area at the beginning were definitely reduced to insignificance or completely destroyed by the prairie plants.

Another area repeatedly examined by Professor Shimek (**1925, 1948**), is along the Rock Island Railroad between Wilton and Summit. The slopes of the deeper cuts were originally left entirely bare. Whatever may have been the first settlers on these slopes, by 1925 the flora was "indistinguishable from that of the adjacent native prairie."

A different development of prairie was recorded by Shimek (**1913**) at Homestead. Here a roadway was cut in 1856 through a forest of bur oak and hickory, and so much of the 66 foot right of way as was not denuded for vehicles was kept free of woody growths. "The flora covering this road-strip was originally the typical flora of the forest, such as now (1912) appears in the bordering woods, but this has been completely replaced by a typical prairie flora." Shimek's list of "prairie plants" in this strip has 59 dicots and 13 monocots.

In 1925 this roadway was abandoned in favor of a new route and the plant population that developed on the central strip of bare ground was studied for three years by R. P. Adams (**1929**). He reported finding along the sides about the same list of plants that Shimek had found in 1912. On the bare strip a thicket of weeds sprang up. In 1928 several conspicuous pioneer weeds had disappeared: *Amaranthus retroflexus, Polygonum pensylvanicum*, etc. Plants from the prairie strip and the adjacent woods were present. "It is evident that a forest flora, if allowed to pursue its course, will

be completely established." At present (1950) the conclusions of Adams are more and more justified. The prairie had persisted only through human intervention.

An experiment in progress at Iowa Lakeside Laboratory was initiated by Shimek. A forty acre tract of rolling pasture land, once rather heavily pastured but never plowed, has been fenced and left to itself. Most of the area carried, and still carries, a dense sod of bluegrass. Anderson (**1936, 1946**) studied permanent quadrats in this forty over a period of fifteen years. His conclusion was that if prairie is returning to this tract it is at a very slow pace. Miss Sylvia Rudman re-examined Anderson's quadrats in 1950. She reported a perceptible increase of prairie grasses in the upland areas (verbal comm.).

The lower levels of this tract have such a dense mat of living and dead culms and leaves of bluegrass that no seed can reach the ground, and the grass is so smothered as to be unable to bloom. Sandbar willow is invading from the lake shore by means of rhizomes. And box-elder is crowding in from a ravine along the south side of the tract.

Another portion of the Lakeside property is so densely covered with *Bromus inermis* and *Cirsium arvense* that no herbaceous plant can get a foothold.

Hayden (**1918**) showed the restoration of prairie in Story County by comparison of the lists of plants found on 1. uncultivated prairie, 2. prairie land formerly cultivated but uncultivated for 21 years, and 3. uncultivated for 36 years.

	1	2	3
Andropogon gerardi	x	–	–
Andropogon scoparius	x	x	x
Bouteloua curtipendula	x	–	x
Bouteloua hirsuta	x	–	–
Elymus robustus	x	–	x
Koeleria cristata	x	–	–
Sorghastrum nutans	x	–	–
Stipa spartea	x	–	–
Comandra umbellata	x	–	–
Anemone patens Wolfgangiana	x	–	–
Rosa arkansana suffulta	x	x	x
Amorpha canescens	x	–	–
Petalostemum candidum	x	–	x
Petalostemum purpureum	x	–	x
Lithospermum canescens	x	–	–
Lithospermum incisum	x	–	–
Artemisia ludoviciana	x	–	–
Aster azureus	x	–	–
Aster sericeus	x	–	–

	1	2	3
Cirsium lanceolatum	x	x	–
Coreopsis palmata	x	–	–
Heliopsis helianthoides	x	x	–
Silphium laciniatum	x	x	–
Solidago missouriensis	x	x	–
Solidago speciosa angustata	x	x	–
Helianthus laetiflorus rigidus	x	x	–
Equisetum kansanum	–	x	–
Agrostis alba	–	x	–
Panicum oligosanthes scribnerianum	–	x	x
Poa pratensis	–	x	x
Anemone cylindrica	–	x	x
Potentilla arguta	–	x	x
Linum sulcatum	–	x	x
Euphorbia corollata	–	x	x
Oenothera biennis	–	x	x
Convolvulus sepium	–	x	–
Verbena hastata	–	x	–
Ambrosia artemisiifolia	–	x	–
Helianthus grosseserratus	–	x	–
Lactuca canadensis	–	x	–
Lepachys pinnata	–	x	–
Liatris squarrosa	–	x	–
Onosmodium occidentale	–	x	–
Monarda fistulosa mollis	–	x	–
Pycnanthemum virginianum	–	x	–
Physalis lanceolata	–	x	–
Garardia aspera	–	x	–
Veronicastrum virginicum	–	x	–
Aster ericoides	–	x	–
Liatris pycnostachya	–	x	–
Eryngium yuccifolium	–	x	x
Panicum virgatum	–	–	x
Rubus "villosus"	–	–	x
Astragalus caryocarpus	–	–	x
Baptisia leucophaea	–	–	x
Desmodium illinoense	–	–	x
Rhus radicans	–	–	x
Ceanothus americans	–	–	x
Asclepias syriaca	–	–	x

With the exception of *Cirsium lanceolatum, Agrostis alba, Poa pratensis, Oenothera biennis, Verbena hastata, Ambrosia artemisiifolia* and *Rubus "villosus"* all of the species named are typical prairie plants. These strips seem to have fully returned to prairie in the allotted time. Number 2 has the most weed species and might be considered less completely restored. It is notable however that the lists for the three strips are very different. Either the strips were

at different levels and represent different types of prairie, or the strips were not large enough to make adequate samples. All three taken together give the best picture of a prairie flora.

In general Hayden concluded that reversion takes place very slowly, and that bluegrass and sweet clover are able to prevent reversion.

It seems likely that Shimek was right in saying that prairie will rejuvenate itself against ordinary weeds of farm and garden. But that our native plants can outdo the sturdiest steppe plants gathered by explorers from all over the world is not so certain. Indeed it is not likely. It may be that smooth bromegrass and Canada thistle and sweet clover and bluegrass can hold their own against the prairie in all arable soils.

INVASION OF PRAIRIE BY SHRUBS

An interesting example of succession was observed at the historic ghost town of Hardin City in Hardin County. When I first saw the town site the only trace of settlement was an exactly square pure and vigorous stand of *Andropogon scoparius*, the size of a city block. This had been the public park of Hardin City. Presumably *Andropogon* had replaced some other vegetation. On my next visit several years later the square was covered 100% with *Rhus glabra*, well grown and of even height. The next time the square was—*miserabile dictu*—a gravel pit!

On the property of the Lakeside Laboratory there is a little triangle of land between two stands of bur oak, which was in 1923 a beautiful fragment of *Andropogon scoparius* prairie. There was *Petalostemum candidum* and *purpureum*, *Lepachys pinnata*, *Delphinium virescens*, *Allium stellatum* and other prairie plants. In 1948 the tract was completely covered with *Rhus glabra*. Beneath the canopy of this shrub *Andropogon* still made a feeble ground cover, and an occasional *Delphinium* bloomed beside the path. The prairie cannot long survive.

Hayden (1918) found in Story County evidence that forest was spreading from bottomland woods out into prairie along tributary ravines. In small ravines *Crataegus mollis*, *Pyrus ioensis*, *Populus deltoides* and *Ulmus rubra* were established. On the brow of one of the bounding hills thickets of *Rhus glabra* were found, with young specimens of *Ulmus americana*, *Crataegus mollis*, *Pyrus ioensis*, *Vitis riparia* and *Celastrus scandens*. Remnants of prairie were found under the farthest outliers of forest, indicating invasion. It would appear that trees spread directly from the bottomlands into the lower parts of ravines, but profit by the mediation of *Rhus glabra* on the higher, drier sites.

Whether and how often *Rhus* marches out into the prairie with destructive effect under wholly natural conditions we have no records for Iowa. The Nebraska ecologists have abundant evidence that it does encroach on prairie under mesic conditions, and that prairie may encroach on *Rhus* under more xeric conditions. Similarly they find that *Quercus macrocarpa* grows big, shades the Rhoetum, weakens it, and then acorns planted by squirrels or blown a few feet by the wind can sprout and grow up into trees. Thus a regular succession takes place: Andropogonetum—Rhoetum—Quercetum macrocarpae. This is, however, also a reversible reaction.

Warner (**1945**) stated succinctly the effect of plants upon the environment. "As successive plant communities develop on a site, climatic factors are ameliorated, organic matter is added to the soil, and microclimate and soil structure are gradually modified to favor plant growth until finally the climax vegetation is developed as the fullest expression of climate and soil." McComb and Loomis (**1944**) point out that shingle oak and blackjack occur on Marion soils, white oak and shagbark hickory on Weller soils, while red oak and basswood occur on Clinton soils, all as found in southeastern Iowa. The plants make the soils and the soils maintain the plants.

In this paper it is stated that 1,000 to 2,000 years have been required to produce any major changes in prairie soil profiles when invaded by forest. Specifically it has taken more than 2,000 years to develop the profile of the Ames type of soil. McComb and Loomis further state that at present all of Iowa has a forest climate. The persistence of prairie is due to the fact that this type of climate has been in effect for only 500 to 1,000 years—too short a time for trees to possess the land, and obviously when forests are found on prairie soils they must have invaded recently. Forests are found on such soils, even in western Iowa (McComb and Loomis **1944**).

Consideration of such long term changes is extremely interesting, even though it leads us into nebulous regions of speculation. The reality of these long slow changes is beyond reasonable doubt. Actual records rarely extend over more than 100 or 200 years—much less than that in Iowa. Longer sequences can sometimes be well assured by inspection of numerous stands. The attempt to give to every community a place in a definite sequence induces us to make unwarranted assumptions and to give too free rein to the imagination.

The best charts of sequences for Iowa that I have been able to find are those of Aikman (**1935**) for Ledges State Park and Warner (**1945**) for southeastern Iowa (**Figs. 14** and **15**). The successive communities are called "stages" in the development of the final

ROBERT M. WARNER

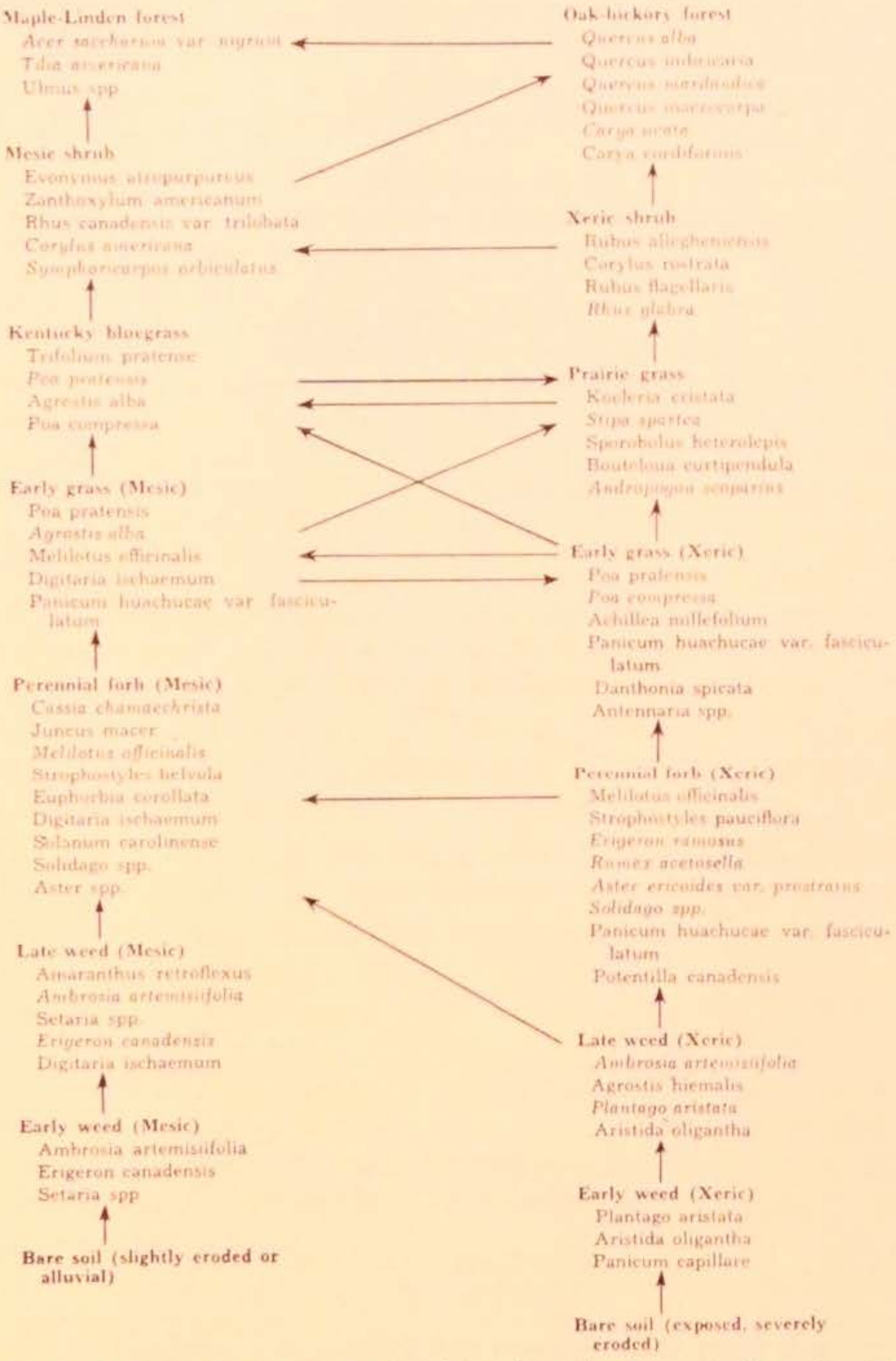

FIG. 10. A diagrammatic representation of secondary plant succession in southeastern Iowa under severely eroded soil conditions (Xeric) and under slightly eroded or alluvial soil conditions (Mesic). The plants most frequently dominant are shown by italics.

Fig. 14. Secondary succession in southeastern Iowa, after Warner 1945.

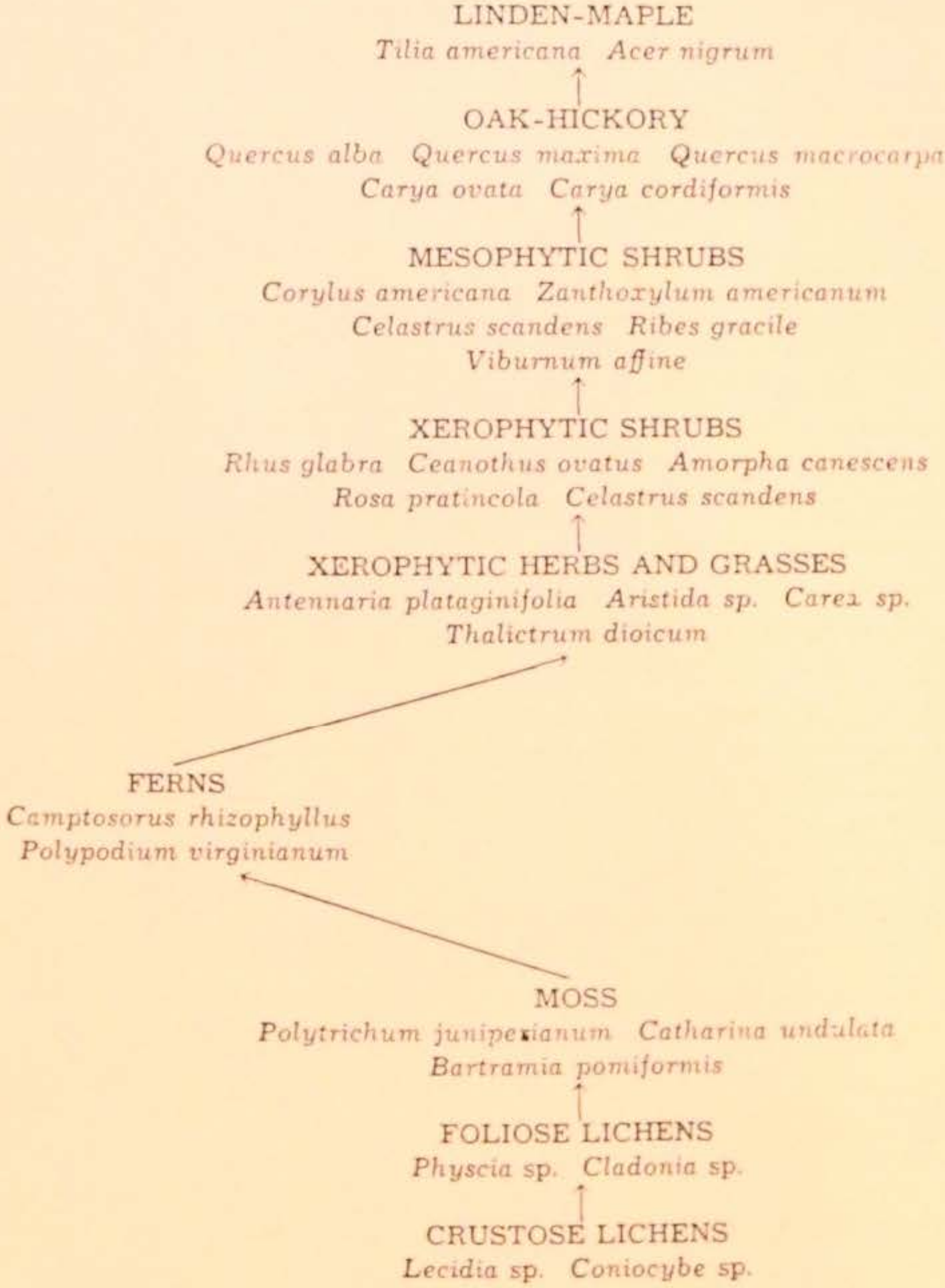

Fig. 1. Stage of the xerosere with the dominant species of each stage.

Fig. 15. Xerosere in Ledges State Park, after Aikman 1935.

association. The inference is that on one square foot or acre or square mile of land the vegetation has gone or is going through one or another of the stages or transitions as indicated by the arrows. Warner actually observed his first three stages. Under "short term changes" we have given several examples from other sources—no two alike! The later stages of Warner's paper are arrived at by inspection of stands and by their proximity. The argument from proximity we have considered under the title of zonation (below). We find that proximity is not adequate evidence for genetic relationship.

Concerning Aikman's chart, the following remarks seem to be pertinent. In Ledges State Park the upland is made up of glacial drift. It is cut by deep gulleys that lead down to the Des Moines River. The lower thirty feet of these gulleys is, in places, bounded by vertical walls of brown porous Pennsylvanian sandstone. On these sandstone ledges Aikman finds the crustose and foliose lichen communities and the moss communities indicated in his chart. On the overlying geest and drift, mostly drift, the other associations are found. Dr. Aikman does not assume that all of the park area was first populated by crustose lichens, to be followed in succession, from place to place, by the other stages of his chart, even though all of these communities are now in proximity in the area. Perhaps less than one per cent of the area was ever populated by lichens as now seen on the most recently exposed ledges.

The one thing certain is that the park was covered with drift before the gulleys with their ledges were exposed. The most certain inference is that coniferous forest and mixed forest or grassland covered the drift long before the gulleys were cut down to bedrock. Another certainty is that crustose lichens do not grow on loess or drift, though fruticose forms may do so.

What then does such a "chart of succession" mean? It means that the area in question has a number of plant communities differing in complexity and permanence. These may be listed in the order of their complexity or advancement, just as we would list the species of plants from Alismaceae to Orchidaceae, or the animals from fishes to amphibians, reptiles and mammals. We consider these taxonomies to be evolutionary sequences, but no one thinks that any orchid of Iowa is descended from any Iowa lily. Thus understood the chart of succession is useful, the more so because it bristles with problems for investigation. Lacking such an explanation, charts of succession are likely to deceive the uninitiated. Of one which I published many years ago (**1935**) Miller & Egler (**1950**) have recently said, and rightly so, it would be excellent "if the arrows were all reversed."

It would seem much more truthful and objective to say frankly what we mean, and to list our communities by classifying them according to floristic and biological complexity. In the next chapter I shall proceed to an attempted classification of the plant communities of Iowa.

The myth that life begins on new land with a growth of lichens, followed by mosses, and then by vascular plants is of ancient origin, and is faithfully reproduced in textbooks and in some otherwise scholarly papers. Humboldt in 1805 (**1807**, p. 290) noted that lichens are pioneers in cool climates but not in warm. "Wo jetzt hohe Waldbäume ihre Gipfel lustig erheben, da überzogen einst zarte Flechten das erdenlose Gestein. Laubmoose, Gräser, krautartige Gewächse und Sträucher füllen die Kluft der langen aber ungemessenen Zwischenzeit aus. Was im Norden Flechten und Moose, das bewirken in den Tropen Portulaca, Gomphrenen und andere fette niedrige Uferpflanzen." Keever et al. (**1951**) explicitly state that on granite rocks in North Carolina "crustose and foliose lichens are present on bare rock surfaces but do not initiate succession."

ZONATION

The causes of vegetational change are many. We have cited the destructive effects of erosion by rivers, by landslides, by various human interventions. Thone's (**1915-1918**) levee showed how one species of plant can crowd out another by starting off earlier in the spring.

The agency of shrub borders is of another sort. The plants in such a case influence the environment in many ways. In the series Quercetum — Rhoetum — Andropogonetum light is strongest in the prairie, weakest under the trees, intermediate under the shrubs. Humidity of air and moisture of soil are greatest in woodland, less in shrubland, least in grassland. Temperatures of air and soil and total evaporation are least in woodland, greatest in grassland. Thus three microclimates lie side by side, determined by the vegetation. Each microclimate is unfavorable to plants of the others. But the less sensitive members of each community can live in the borders of the adjacent ones, and may be able to change the environment to their own advantage. If they do, one community crowds out the other.

So common and widespread is this kind of vegetational change that one is tempted to regard every strip of vegetation lying between two others as a transitional stage, and to assume a universal change from A to B to C.

When such strips of vegetation are arranged concentrically around a pond, or in parallel bands along a stream, the strips are called

zones, and the phenomenon zonation. The communities have been called zone-associations. Clements (**1916**) has stated that zonation is always a sign of succession, and that the zones are stages in a sere.

The woodland associations along our river valleys form a series of zones and may be assumed to be stages of succession: 1. Salicetum interiis on new bars—2. Salicetum amygdaloidis—3. Ulmetum—4. Quercetum rubrae—5. Quercetum macrocarpae. The assumption is that each of these will give place to the next in the course of time. The most certain event is that the first three associations will be swept away by the river, and the fourth will be broken by landslides. Then the lowland cycle will begin anew at a slightly lower level. On the completion of this cycle of meanders Quercetum rubrae may move two or three feet nearer to sea level. Repetition of this cycle will continue until geologic base level is attained, a period much too long to admit of any speculation on the probable climate and vegetation at that distant time. All of the zones are permanent in the sense that they continually recur. But even a local stand of bur oak on the top of a hill may be undercut and may slide down into the river. You never can tell!

Zone-associations are very conspicuous around the glacial ponds of the Wisconsin Drift. They are often made up of short-lived plants, each zone with a color and texture of its own. As the seasons are wet or dry the zones move back or forward from year to year. Each pond has its own unique vegetation, a situation completely baffling to the ecologist, but quite universal with glacial ponds. The conditions are varied and changing, and the vegetation follows.

Over long periods, however, these ponds accumulate more and more of dead plant tissues. The bordering plants encroach upon the pond, making for themselves a congenial peaty soil. Finally the open water is entirely covered over, and the vegetation may even pile up at the center, forming a raised bog or fen, around which a lower, wetter ring or moat may appear. Submersed aquatic communities are entirely crowded out. While no one has observed all of these processes in any one place, the various stages can be seen and the conclusion seems to be altogether certain. All of these changes are brought about by the plants themselves in a uniform environment. The process is slow, humanly speaking. It takes from 1,000 to 20,000 years.

An interesting zonation was observed by Lewis (**1949**) in two artificial lakes at Chariton in Lucas County, known as Red Haw Lake and East Lake. The overflow from Red Haw runs directly into East. East Lake was constructed in 1915 for the city water supply and is

regularly treated with copper sulfate to keep down the growth of algae. Red Haw has waterbloom almost continuously, but there is very little algal growth in East. The pH runs about 7.6. Red Haw Lake was constructed in 1935 and stocked with fish in 1936. Each lake covers about 80 acres. The following zonation was recorded (**Fig. 16**).

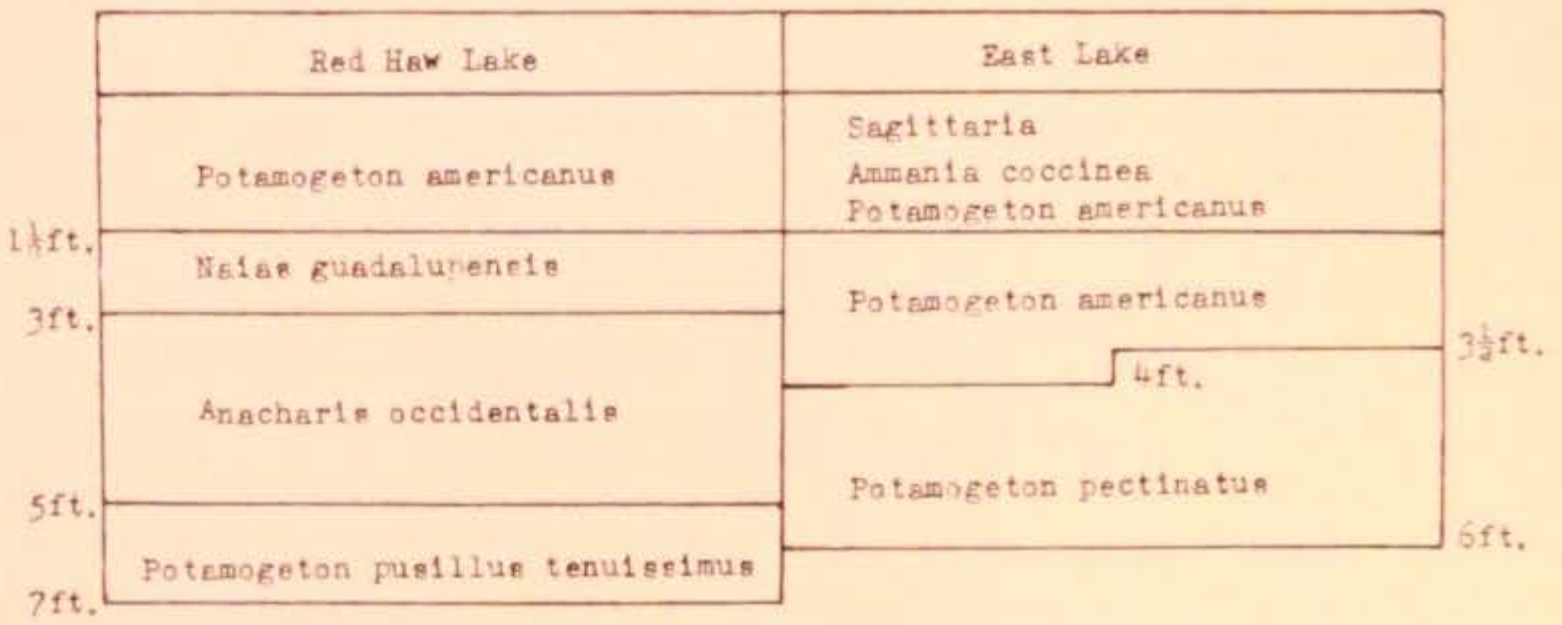

Fig. 16. Zonation at Chariton, after Lewis 1949.

Whether these two lakes will finally settle down to an identical zonation one can only guess. Nor is there any assurance that other species will not come in, completely altering the picture. In actual fact these zones are due to differences in habitat. One did not follow another, but all were settled practically simultaneously by "whatever was suitable that was nearest at hand." One zone may displace another as the lakes fill up with silt. The present status is the only datum we have. It seems futile to speculate upon what will happen next, but it is very desirable to keep accurate records and find out.

CONTINENTAL ZONATION AND SUCCESSION

Imagination runs riot in contemplating the changes in vegetation resulting from the several glacial incursions. Geologists tell us explicitly of the four glacial stages and various substages. Rather scanty fossil remains make certain that vegetation returned to the State after each icy erasure. The details of these tremendous movements of plant and animal life have been much written about and disputed about. The broad facts are indisputable. Within about 25,000 years the area of the "Mankato Lobe" has changed from a sheet of ice to its present condition. The stages and processes can only be conjectured (cf. Gleason **1923**).

Cowles (1901) in his physiographic plant ecology has discussed the development of river valleys and the changes of relief leading toward peneplanation, with presumptive changes in vegetation. This is projecting plant ecology over millions of years. Doubtless Iowa may undergo such changes.

Others have considered changes of climate and vegetation in Wyoming owing to the rise of the Rocky Mountains and the Cascade Range, covering many millions of years. The climate of Iowa must have suffered many accompanying changes (Peattie 1941).

Neither geologic nor physiographic change has much interest for the present day plant ecologist, though recent glacial incursions are often cited in explanation of the occurrence of fragments of boreal vegetation in Iowa. These long term gains and losses have little influence on the problems of today. As Transeau has said: "There is not much to be gained by assuming that all of the 'subclimax prairie' would be succeeded by forests 'if present climatic conditions continue'. The thing of which we can be surest is that it will not continue as it is."

CHAPTER XI

Classification of Communities

A classification of communities should achieve at least three aims: 1. It should arrange the list of communities in a logical sequence. 2. It should serve to show similarities or relationships between communities. 3. It should facilitate the comparison of the communities of different parts of the world.

Rübel (1930) has proposed a classification of world-wide application. It is based on the physiognomy of the vegetation from place to place. Though it smacks somewhat of the arm-chair, it offers an extremely useful guide for the correlation of vegetations. Certainly no one knows more about the plant communities of the world and no one is better qualified to classify them than the widely traveled, profoundly learned and delightfully humorous Dr. E. Rübel.

Braun-Blanquet (1932) has proposed a classification according to the complexity of the communities. Proceeding from simple to complex we have in Iowa:

1. Floating communities with no fixed habitat.
   Lemnetum minoris (*Lemna*, *Spirodela*, *Wolffia*)
   Aphanizomenetum (*Microcystis*, *Anabaena*, *Aphanizomenon*)
   Gleotrichietum
   Ceratietum tripodos

2. One-layered communities without roots.
   Protococcus on bricks, boards and bases of trees.
   Oscillatoria, *Phormidium*, *Lyngbya* on wet stones or mud.
   Ulothrix on rocks just below water level.
   Spirogyra, etc., in shallow water.
   Achlya, *Saprolegnia*, etc., in shallow water.
   Crustose lichens. Diatorelletum, etc.
   Grimmia and *Orthotrichum* communities.
   Dematodon obtusifolius communities on ledges.
   Conocephalidetum conici on moist earth or rocks, etc.
   Ceratophylletum

3. One-layered communities with roots.
   Submersed aquatics.
      Charetum
      Potameta

   Emersed aquatics
      Potametum americanae

Nupharetum advenae
Nymphaeetum tuberosae
Nelumbonetum
Typhetum latifoliae
Zizanietum aquaticae
Scirpetum validae
Myriophyllum-Ranunculus community
Terrestrial
One layer of roots
Caricetum filiformis of peat bogs
Caricetum strictae. Szombek communities.
Pellaeetum glabellae
Secalinetalia—wheat, oats, rye
Portulacetum
Polygonum persicaria communities
Two layers of roots
Poetum pratensis arvense. Hayfields
Poetum pratensis pratense. Pastures
Poetum pratensis domesticum. Lawns

4. Two layers above ground.
Herbaceous
Triglochinetum of fens
Caricetа
Tridentetum flavae Froelichietosum
Phalaridetum arundinaceae
Phragmitetum communis iowense
Calamagrostidetum canadensis
Spartinetum pectinatae
Woody
Rhoetum glabrae
Cornetum racemosae
Coryletum americanae

5. Three or more layers above ground and as many under ground.
Woody
Salicetum interiis
Salicetum amygdaloidis
Ulmetum
Quercetum rubrae
Quercetum macrocarpae
Quercetum imbricariae
Aceretum saechari nigri
Pinetum strobi
Abietetum balsameae
Herbaceous
Andropogonetum scoparii iowense
Andropogonetum gerardi
Boutelouetum curtipendulae
Stipetum sparteae
Panicetum virgati

Since the names used above have no technical diagnosis they are tentative and temporary, with no claims to permanence or priority. Corresponding communities have been described in Europe in many cases.

It must be clear from what has been said in this essay that the prairie is the most complex community or group of communities in the temperate zone. The layering of roots and tops is highly developed along with seasonal aspects. Texture and moisture of soil are intimately expressed by the vegetation. The stands are more closely "closed", that is, more dense, than in any other communities, with a far greater number of species. Each species is especially and uniquely fitted by structure and behavior for life in a relatively dry habitat.[9] Each species fills its own particular niche. The number of species indicates the number of niches. The prairie collects its own substrate of soil by catching the dust of ages. It mulches itself in winter but does not smother. It is able to maintain itself without significant change for centuries and millenia. It is a terminal stage of great permanence.

The Zürich-Montpellier school of plant sociologists uses a taxonomic system of classification based wholly upon the species that make up each association and the role of the species therein (Braun-Blanquet **1932, 1951**).

The Association, with the ending -etum corresponds to the species in ordinary taxonomy. The Alliance (-ion) corresponds to the genus. The Order (-etalia) corresponds to the family. The Class (-etea) corresponds to the order in taxonomy. We may have then, for example: Class Secalinetea. Association of grain crops.

Order Secalinetalia. Small grains.

Alliance Secalinion

Association Secalinetum secalis, a field of rye.

The most important associations of Iowa may be arranged provisionally according to this plan. It must be borne in mind that none of these associations has been sociologically examined in North America. The names used are merely suggestive. Many of the corresponding associations in Europe have been studied and described. A Prodromus of plant associations is in preparation. Several parts have already been published.

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[9] To dwellers east of the Great Plains the prairie climate is xeric (dry). It is the driest climate in that area. To dwellers in the Great plains and southwestward the prairie climate is mesic. It has more moisture than those areas. Rübel (**1915**), as a globe-trotter, says "Die ursprüngliche Prärie hat einen nur schwach xerophytischen Character" (only weakly xerophytic).

Some Plant Associations of Iowa arranged taxonomically according to floristic composition, with geographic distribution and reference to some corresponding European and North American Associations.

1. Phragmitetalia. Eurosibiric-North American.
   Phragmition. Eurosibiric-North American.
      Phragmitetum communis. Europe
      Phragmitetum communis iowense. Iowa
      Zizanietum aquaticae. Eastern North America
      Scirpetum validi
      Typhetum. Cosmopolitan.
      Phalaridetum arundinaceae. Europe and North America
      Spartinetum pectinatae.
   Magnocaricion. Eurosibiric-North American
      Caricetum strictae. Iowa to Pennsylvania.

2. Andropogonetalia. Eastern half of United States.
   Andropogonion
      Andropogonetum scoparii Blizz. New England to Pennsylvania
      Andropogonetum Hempsteadi Cain. Long Island
      Andropogonetum scoparii iowense. Prairie
      Tridentetum flavae. Eastern Pennsylvania
      Tridentetum flavae Froelichietosum. Southeastern Iowa.
      Andropogonetum gerardi. Prairie
      Andropogonetum virginici. Missouri to Virginia and southward
      Stipetum sparteae. Prairie
      Spartinetum pectinatae. Iowa, etc.
   Buchloion. Short-grass Plains
      Buchloetum. Nebraska, Kansas, Colorado
      Boutelouetum curtipendulae. Central and western Iowa
      Boutelouetum oligostachyae. Fragmentary in Iowa
   Spartinetalia
      Spartinion
         Spartinetum glabrae, Atlantic coastal salt marshes.
         Spartinetum patentis, Atlantic coastal salt marshes.
         Spartinetum Townsendii, southern England salt marshes.
   Potametalia. Eurosibiric-North American
      Potamion americanum. Northeastern North America
         Potametum zosterifolii. Also in Europe
         Potametum americanae.
         Ceratophylletum demersi. Also in Europe
         Charetum contrariae
            nitellosum Cain. Michigan, Iowa
         Myriophyllum-Ranunculus community
         Nymphacetum tuberosae. Iowa to New York
   Populetalia. Eurosibiric-North American
      Populion deltoidis. Eastern United States
         Populetum deltoidis

Ulmetum
Salicetum amygdaloidis
Populion albae. Europe

Quercetalia
Quercion rubrae. Iowa to the Atlantic coastal plain
Quercetum rubrae
Quercetum macrocarpae. Northern Mississippi Basin
Quercetum imbricariae.Southern Iowa and adjacent Missouri
Quercetum albae
Quercion montanae. Massachusetts to Georgia on the Piedmont

Aceretalia
Acerion sacchari. Northeastern U. S. and adjacent Canada
Aceretum sacchari. Quebec to Ontario and New England
Aceretum sacchari nigri. Fragmentary in Iowa. Cf. Dansereau 1943, 1946

Class Vaccinio-Piceetea
Order Gaultherio-Piceetalia. Northeastern North America
Alliance Gaultherio-Piceion. Quebec to New England and Alberta
Suballiance Abieto-Piceion canadensis. Northeastern United States and adjacent Canada
Abietetum balsameae. Fragmentary in northeastern Iowa

Pinion
Pinetum strobi. Fragmentary in northeastern Iowa; outliers in Hardin and Muscatine Counties

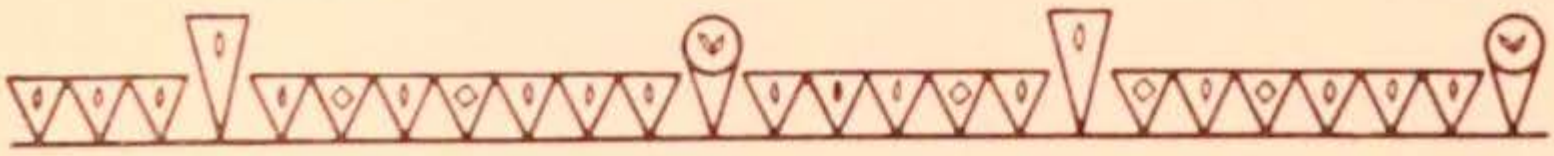
The composition of some of these units is described on previous pages.

Recalling the proposed objectives of a classification, the above scheme permits (1) arrangement of communities in a logical sequence, in this case from aquatic to grassland and woodland; (2) showing relationships between communities on the basis of floristic composition; (3) comparison of communities of different parts of the world.

The classification of communities according to observed or inferred sequences in the course of vegetational change (succession), as maintained by Clements and his followers, has proven helpful where the inferences are not too far-fetched. Such a project is a powerful challenge to research. The dunes of Lake Michigan present the most perfect examples in America of the concurrent development of vegetation and soil, supported by conclusive geological evidence. The sand hills of Nebraska are almost equally suggestive. Many similar sequences are on record from other parts of the world. They are important locally as guides to the use of land. I am not aware, however, of any attempt to coordinate the associations of the world on a genetical basis. Nor do I see how that could profitably be done. Succession does not furnish a satisfactory basis for a classification

of the associations of the world, much less for a comparison of them (Cf. Braun-Blanquet **1951**).

In presenting "a system based predominantly on structure" Dansereau (**1951**) evaluates sympathetically the advantages and limitations of previous systems. (Egler **1951** has criticized prevailing american practices very justly, if too polemically). **Fig. 17** copied here is an example of Dansereau's scheme, proposed for worldwide usage. The figure and formulae would be identical for the grasslands of Hungary and Bessarabia in Europe, and for southwestern Manchuria in Asia.



ANDROPOGONETUM IOWENSE

Hmdgzb. Fldvzb. Hldg(a)zc.

Fig. 17. Andropogonetum scoparii iowense, after Dansereau 1951. The first sign on the left is a gramineous herb of low stature. The fourth is a tall gramineous herb. The sixth is a medium- or small-leafed forb. The twelfth is a compound-leafed shrub. F means shrub; Hm, herb 0.5-2m. tall; d, deciduous; g, graminoid; z, membranous (as opposed to fleshy); b, coverage sparse; v, compound leaf; c, coverage continuous.

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