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THE PLANT GEOGRAPHY OF IOWA

BY

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of the Herbarium

State University of Iowa

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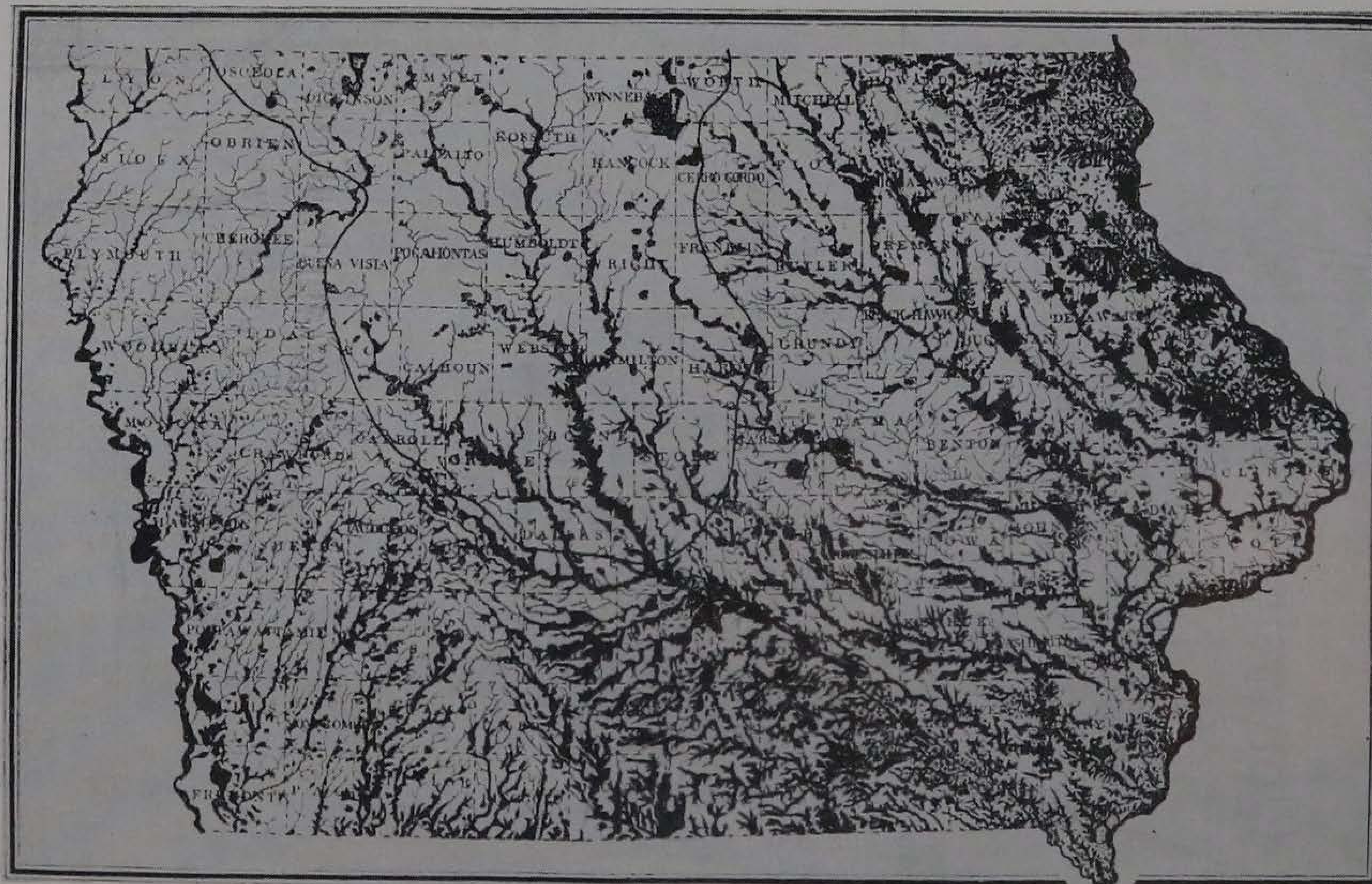

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THE PLANT GEOGRAPHY OF IOWA

Bohumil Shimek

Preface

In 1931 the legislature of the State of Iowa appropriated $2000.00 for the publication of a projected essay on the plant geography of Iowa by Professor Shimek. The project had the enthusiastic support of the Iowa Academy of Science, for Professor Shimek was the last living botanist who knew Iowa while much of the State was little affected by settlement. By 1930 nearly all of the vegetation of the State had been radically changed.

At the end of the biennium of the appropriation the essay was not forthcoming. The task which Professor Shimek had laid out for himself could not be completed in the two years allotted to it.

Eight years after the death of Shimek a manuscript came into the possession of the Botany Department of the State University of Iowa. All evidences and testimony indicate that this manuscript is to be regarded as an exact reproduction of that which Shimek wrote with his own hand, or caused to be tabulated under his direction.

As a testimony of the esteem in which Professor Shimek's scholarship is held, and of confidence in his faithful recording of plants and places, and as a record of data concerning the natural vegetation of Iowa, now gone forever, the words of Professor Shimek's uncompleted manuscript are here reproduced just as he left them. The portion of the projected essay dealing with the vegetation proper was never written. "The Plant Geography of the Okoboji Region" (135) indicates the kind of treatment that Professor Shimek evidently planned to follow. It is a matter of everlasting regret that Professor Shimek did not write down more of his observations and conclusions on the original plant life of Iowa.

The Editor

THE PLANT GEOGRAPHY OF IOWA

Foreword

This plant geography of Iowa is based on personal studies and observations which have extended over a period of more than half a century. Beginning as early as 1873, they continue and systematize general observations extending back to early childhood.

A native of Iowa, the writer had an opportunity to observe many of the earlier natural conditions which have become a mere tradition. Born and reared at the edge of the woods extending north from Iowa City, the contact with the earlier conditions of this really fine piece of inland woods became an intimate part of his earliest experience.

Even these very early observations were made quite definitely, for the writer spent much of his boyhood wandering about in the woods, along the water courses and in all other types of our area, observing the outdoor world, and before he was eleven years of age he had accumulated a collection of several hundred species of local insects. The specimens were mounted on common pins, on strips of corn-pith fastened to the bottoms of cigar boxes. There were then still miles upon miles of almost undisturbed timber, fine white oaks predominating on the uplands, the hard maple occasionally dominating the river-bluffs, and the red cedar finding an anchorage on the limestone ledges, while the black walnut and various softwood trees occupied the narrow bottomlands. The upland woods were carpeted in early spring with hepaticas (chiefly on the steeper slopes) and the rue anemone, while the ravines were decked with beautiful ferns, interspersed with pink and yellow ladies'-slippers and many other wild flowers, all in great profusion, while the lowland woods displayed their gorgeous raiment of spring-beauties, *Mertensia,* buttercup, *Phlox* and *Isopyrum*, the whole making a wonderful flower garden.

Nor did plant-life furnish the only interest. The wild turkey persisted, at least as late as 1886, the drumming of the ruffed grouse, now almost extinct, was one of the most familiar sounds in our woods, and the passenger pigeon still came in great clouds to seek shelter amid the oaks of our uplands. (The writer saw the last pair of passenger pigeons in 1887. The male was shot.)

Nor were primitive conditions displayed in the forests alone. There were still remnants of prairies, even in eastern Iowa, and in the year 1882 the writer found large areas of native prairie in the counties north and northwest of Wright County, and for more than twenty years thereafter (in constantly diminishing amount) in the northwestern part of the state.

These larger undisturbed tracts gave an early opportunity to study the native prairie, and to form a basis for the understanding of the prairie remnants which persist to this day. Numerous comparative observations were also made in eastern Nebraska, South Dakota, North Dakota, Oklahoma, and elsewhere.

The waters, too, were largely unchanged. The mania for draining every wet spot had not fully developed, and there were ox-bow lakes along our streams, then still undisturbed and unpolluted, and the "thousand-lake" region of north-central Iowa, with the countless kettle holes and lakes, was still true to the name bestowed upon it by the early pioneers.

Something of the primeval conditions of that region is suggested further by the fact that in 1882 the writer still found much of the territory north and northwest from Wright County without roads other than uncharted prairie trails, and that not only was the flora of the prairie and the prairie "sloughs" and lakes but little affected by the white man's invasion, but bird-life still occurred in old-time profusion. Prairie-chickens were found in countless thousands and their nests often covered acres of the prairie; the long-billed curlew, now unknown in Iowa, everywhere hovered over the prairie, an easy mark for every pot-hunter; great clouds of golden plovers or "prairie-pigeons" swooped down seemingly out of nowhere, apparently to alight, but only to sweep away again like a turbulent wave; the white and the sand hill cranes danced merrily (and awkwardly) before their mates; the borders of swamps and "sloughs" were often lined with the nests of ducks of several species; pelican eggs could be collected in favored spots by the boat-load; and practically every muskrat house supported the nest of a wild goose.

But with the influx of new settlers and the extension of drainage projects all this was soon undergoing rapid transformation, and it became apparent that these earlier conditions would soon disappear, or at least be preserved in mere mutilated fragments.

The writer therefore early resolved to concentrate his chief attention on the preservation of a record of the flora of the state. For this purpose every county of Iowa has been visited repeatedly and in each typical surface area one or more counties were selected for more continuous studies.

Earlier observations were checked, locality and habitat lists were prepared, and illustrative material was collected. In many cases these lists, and to some extent the collections, were repeated at the same locality at various seasons of the year and through many years. This makes a record of the flora of the state, which despite its inevitable incompleteness, can never again be duplicated or equalled.

For many years, despite the advance in the settlement of the state and the consequent increase in cultivated areas, many areas were preserved in unchanged or but slightly altered condition. Then some thirty or more years ago the influence of the extension of drainage projects began to be felt. The wet meadows, which had furnished the chief pasture lands since the closing of the public prairie ranges, were given over to cultivation and many of the groves were cleared or partly cleared for pasture. Thus cultivation destroyed most of the natural water surfaces and the groves.

Hope was entertained by the original promoters of our state parks that in them, at least, types of our natural areas could be preserved for future study, and for the information of coming Iowans. But there has been so much of artificial improvement, and so much transplanting without regard for the natural or original condition of the areas that they, too, have lost their value to the student of natural plant distribution, introducing an element of uncertainty which is fatal to both observation and conclusion.

There is no effort made in the present work to include every species of plants known to the state, — that is left to a subsequent effort. The purpose is rather, to set out the dominant or characteristic types of each flora and to indicate the group characters of the various floral areas. The native flora, however, will be quite fully set out in the course of this discussion.

No attempt is made, therefore, to discuss questions of nomenclature or the fine points of distinction of a few species. The nomenclature of Gray's Manual of Botany, 7th edition (71), is accepted in the main. The few exceptions will be noted specifically. It will undoubtedly be necessary to change some of the names, with the definite designation of certain plants, and not with refinements in synonymy. The systematic botanist will have no trouble in understanding the names used, and those who are not taxonomists will find it much more satisfactory to follow a definite reference, like Gray's Manual, than to flounder about among the niceties of nomenclature.

The verification of the species listed in this report is possible in the Herbarium of the State University of Iowa, where the collections are deposited. Unfortunately, portions of some of the earlier collections were destroyed by an invasion of mice in inadequate quarters in the Old Science Hall, where they were stored. Fortunately the species were practically all restored from the same localities by later collections.

The names of authors of species are omitted to save space. They are not essential for our purpose, and those who want them can get them from Gray's Manual. Scientific names are used in all the lists because they are definite, specific, and international in usage.*

English units are used throughout for dimensions, etc. (excepting in a few special tables), and temperature is recorded in degrees Fahrenheit. The writer personally prefers decimal systems, but recognizes that we here face "a condition and not a theory," for the decimal systems are not in general use in this country. Even our research students all too frequently tend to reduce metric measurements to English units for a better concept of their magnitude.

As many of the problems herein discussed have a distinct economic bearing, some attention is given to the latter phase. Instead of setting out these economic features in a separate chapter, however, the writer prefers to deal with them in direct connection with the scientific facts or conditions on which they rest.

Throughout the ecological discussions the writer has attempted to avoid unnecessary and cumbersome terminology. In the formative phases of any science new, or at least modified, nomenclature is necessary, but this has been rather overdone in plant ecology. So many factors enter into the determination of the ecological

* The Reader will find common names and families in Gray's Manual. Professor Shimek intended to add in appendices a list of families and genera, and a list of species with common names, alphabetically arranged. — Ed.

fitness of any area for the development of its characteristic flora, and the many larger sections of the earth's surface, as well as their minor subdivisions, present these facts, and their consequent floras, in so many combinations that an endless series of possibilities presents itself for new and varied ecological classifications. Such classifications, as a rule, set out the peculiarities of particular regions or areas, but they usually fail as a basis for generalizations.

The unfortunate multiplication of classifications, groups and terms has had a disastrous effect upon the advancement of this branch of botanical science, as well as on its appreciation by those interested in other fields. The result has been the comparative neglect of that fascinating subject towards which not only the various branches of botany, but all biological and physical sciences, should converge. Terminology should be an aid, not a hindrance, and excessive refinements of classification are not desirable until there is a closer correlation of the diverse studies which have been (and are being) made in various parts of the world. Until such correlation is effected, new terms and new classifications should be offered with great reserve. The writer's experience has been limited to our own country, to portions of Canada, Mexico and Tropical America, and to Central Europe, but it has been sufficient to show that while there are certain fundamental principles which govern the development of floras everywhere, the details of both conditions and responding floras are so varied, that much more careful study will be required for their proper correlation and ultimate classification.

Plant ecology has been largely discredited by the torrents of innumerable terms, and even more so by the shifting of terms to other conditions than those which they originally expressed.

The writer strongly approves the fundamental principles of phytogeographical nomenclature as set out by Flahault and Schröter (57) in their report to the Brussels International Botanical Congress (1910), and particularly the first, which reads as follows: "Nomenclature is an auxiliary of science, whose progress it is intended to facilitate; its function is essentially and solely practical. Those who work at the same science ought to try to understand one another; pedantic pretentions to erudition are useless or dangerous." Incidentally, this statement should also be taken to heart by those of our botanists who have burdened our literature with useless synonyms, and who have brought systematic botany into disrepute by endless contention over rules of nomenclature.

In the following pages the writer attempts to present a record of conditions as they existed, or still persist, in Iowa, without in any way contributing additions to the confused terminology covering the wide field.

The topics throughout are discussed with special reference to Iowa floral conditions, and an attempt is made to present the picture of Iowa flora as it was, and also to emphasize the lessons which this flora teaches.

THE PLANT GEOGRAPHY OF IOWA

Introduction

The flora of Iowa has received the attention of numerous students, particularly on the taxonomic side. The earlier papers were wholly restricted to this phase of the subject, and dealt mostly with local floras or with restricted groups of plants. Arthur early (4) published (5-9) a list of the vascular plants of the state known to him, while other authors have given lists or accounts of various lower groups. The only attempt at a presentation of the entire flora is Green's "Plants of Iowa" (72), a useful but by no means complete compilation of the flora of the state.*

The ecological papers are fewer in number and deal with special or local problems, as is shown in the ecological bibliography. No attempt has been made thus far to set out the phytogeography of the state as a whole, and the purpose of this treatise is to present a view of the entire field which will serve both as a record of our fast vanishing flora in relation to habitat, and as a basis for future more detailed work on the numerous special problems which it will naturally suggest, or which may develop in the future. Many of these problems are not only of genuine scientific interest, but also of great economic importance in an agricultural state whose main employment must continue to be the growing of crops. Botanists would do well to turn aside from the pursuit of elusive philosophical questions, or the elaboration of petty details, to the consideration of the great problems involved in the relation of plants to their environment.

It had been the author's original intention to include the nonvascular plants in these discussions. Much information covering a period of more than forty years has been gathered but the more exact determination of many of the species would require so much additional time that it might endanger the completion of the main part of the work.

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* Since this was written, an excellent list of the plants of Iowa has appeared: Cratty, R. I., The Iowa Flora. Iowa State Coll. Jour. Sci. 7: 177-252. 1933. — Ed.

It is worthy of note, however, that, in the main, ecological conditions are sufficiently fully typified by the vascular plants.

The non-vascular cryptogams may be grouped into three divisions according to their ecological relationships.

1. The Bryophytes (mosses and liverworts) and lichens (and the very few algae) which often play an important part in the initial establishment of floras on bare areas; or they form mats (especially in forested areas) which locally modify surface ecological conditions. They are most commonly found in conspicuous numbers on clay banks and more recently bared earth-surfaces, on ledges, blocks of stone and boulders, on fallen logs, — on trunks of standing trees, and less frequently in sandy areas.

2. The non-chlorophyll-bearing Thallophytes, bacteria, fungi and slime-moulds, which are all parasitic and saprophytic, and hence dependent on materials and conditions furnished by the higher plants. They constitute important biotic factors in modifying normal floras, and in bringing about reaction resulting from decay. They are not as a whole, however, of value in determining or designating floristic areas.

3. The chlorophyll-bearing Thallophytes or algae, etc., which are locally sometimes dominant in true hydrophytic associations. The latter, however, are also more commonly dominated by vascular hydrophytes, excepting for the (usually) inconspicuous plankton.

While the practical omission of these groups will leave inevitable gaps in our flora, the discussions of the vascular plants will present a sufficiently clear concept of the prevailing floristic conditions in our state.

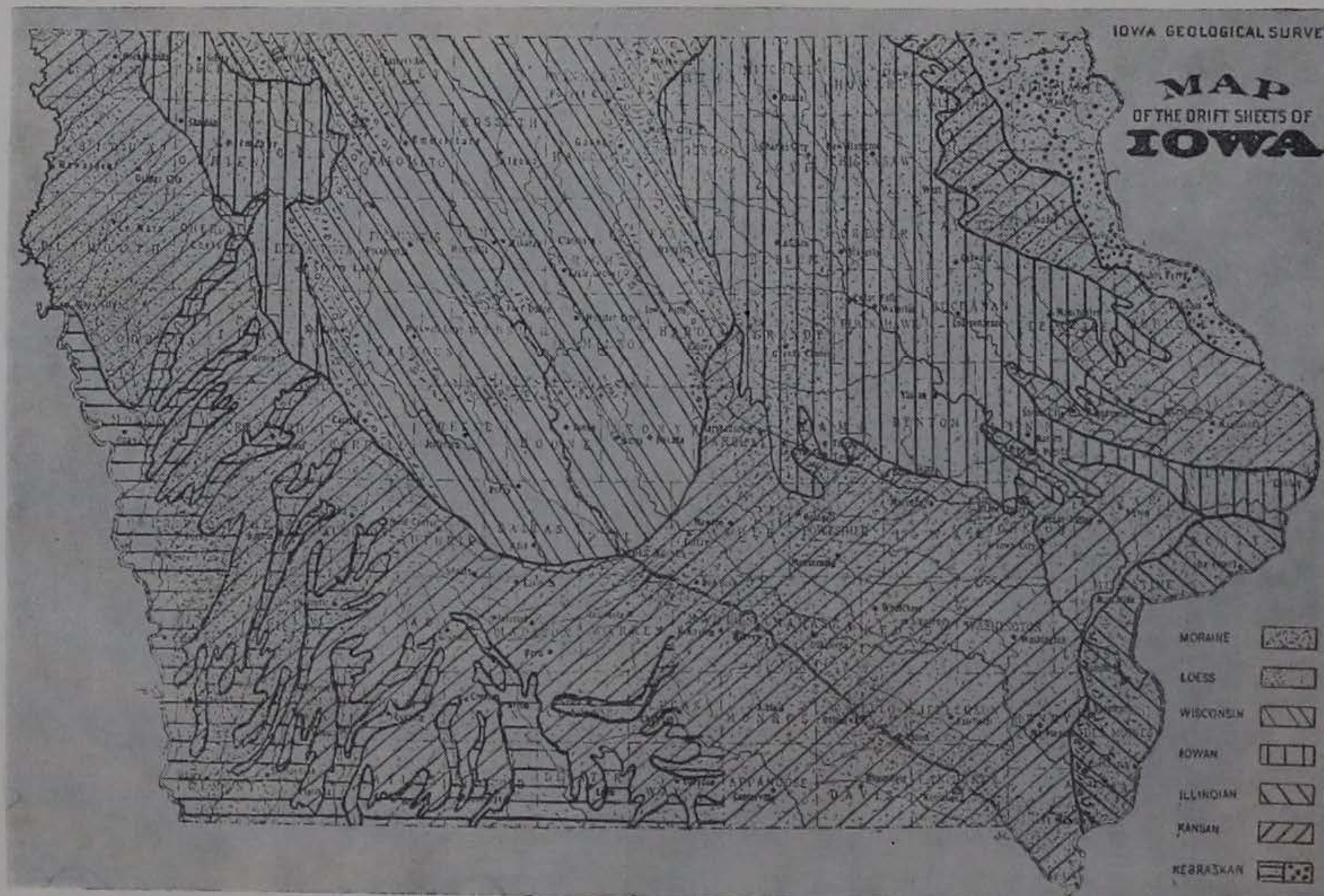

Plate II. THE GLACIAL DRIFTS OF IOWA

Courtesy of the State Geological Survey

CHAPTER I

SURFACE FEATURES

A. Changes in Surface Features

The natural flora of Iowa is disappearing so rapidly, and its remnants are being readjusted so generally, that soon practically all traces of its original character will have disappeared. Even now it is difficult for the newcomer to determine what may properly be designated as natural conditions and those which represent change.

These changes have been brought about primarily through the rapid and very complete settlement of the state by the white man. Groves were cleared or pastured, prairies were broken, and swamps and lakes were drained, and each of these processes was followed by a readjustment of the flora peculiar to each regional type.

There is now no exact record of floristic conditions as they existed at the time of the first white settlers, and even if it existed, it could not represent conditions which were purely natural as distinguished from those which have been induced or influenced by man. For the red man dwelt in the groves, roamed and hunted over the prairies, and plied his canoes over the waters of the state, frequently shifting his location in search of food or warfare. These constant migrations must have brought about the transfer from one location to another of many plants, especially such as were used for food or other purposes, to say nothing of those which would be carried incidentally and unintentionally in the form of seeds.

Then when the white hunters and trappers came, before the settlement of the state, they, too, must have contributed to early changes in noticeable degree.

There was, therefore, no time when the flora of the state was subject exclusively to natural conditions. The early changes brought about through man's influence, however, were minor, and did not materially affect the natural floral regions. These retained their characteristics even long after the white settlers came. It is within the easy recollection of the writer that numerous groves, large expanses of prairie and countless swamps, ponds, streams and lakes in Iowa showed no visible effect of man's influence up to forty or fifty years ago.

The groves were the first to suffer. The early settlers had occupied many of them not only because they needed shelter, building materials and the water of springs, but because they entertained the widely prevalent belief that the soils of the forest were better suited to agriculture than those of the open prairies. In consequence the forests were cleared, burned, and finally their remnants were pastured, until almost nothing remains of the primeval forest.

When the richness of the prairie soils came to be appreciated, the vast treeless areas were quickly occupied and broken until no large area remains to give a full concept and understanding of the prairies as they once existed.

Finally the search for more land resulted in the draining of innumerable swamps, ponds and lakes, and the third of our major regional types was almost completely changed.

The student of the Iowa flora must recognize the fact that today he is no longer dealing with strictly natural conditions, excepting in very restricted localities, and that even the latter are fast disappearing under the general tendency to "improve" them. This is greatly to be regretted, for there is no better measure of the conditions which are suitable to man's existence than that which is furnished by the native flora, which represents the final product of physical conditions operating through long periods of time, and reflects most clearly the sum total of these conditions. We should have preserved, we should even now preserve, some of the remnants which present the several natural floral types for future scientific study, and they should be preserved in a truly natural condition, free from any danger of the "improvement" mania. The little steppe remnants along the Rhine, and elsewhere in Central Europe, have become highly valued ground for scientific investigators, but they are wholly inadequate for satisfactory study because of their small number and size. We should take the lesson to heart before it is too late, and preserve especially those areas which are not of high agricultural value, and which merely delude their victims into the belief that they are suitable for profitable farming. Such are, particularly, some of the rougher forested areas, the western rugged prairie ridges, the sandy areas of Harrison, Muscatine and Louisa Counties, and several swampy areas, particularly along the Mississippi River and in the northern lake region. The small areas of relatively poor lands desirable for this purpose would not materially affect the total agricultural output of the state, and would save some of our citizens from the folly of attempting to make a satisfactory living on them.

Iowa presents floristic areas of several types, and we commonly recognize the floras of the prairie, the forest and the waters, with secondary groups belonging to sandy areas and rock-ledges. This grouping is not wholly satisfactory, as will be noted later, but is obvious, and forms a satisfactory basis for general discussion.

Each of these type areas contains a flora which is wholly, or in conspicuous part, characteristic of it, as is brought out quite conclusively in the plant lists which follow, and as is shown also on the forest map (Pl. I),* which becomes almost a topographic map.

* For many years the writer has made use of the notes of the government surveyors who subdivided the land in Iowa into sections. After the land was subdivided into townships six miles square, deputy surveyors were appointed, under a system of bids, to subdivide them into sections, one mile square. Under the instructions of the U. S. Interior Department, they were required to begin at the southeast corner of the township, retrace the first mile westward, thus testing both the course and the length of the chain. Thence the line was run northward one mile, the intermediate half-mile (or half-section, or quarter) corner being marked on the way. Then a trial line was run due east to the section corner one mile north of the southeast corner. This was usually missed, but the error was measured, and on the return towards the northwest corner the pro rata correction was made for the half-mile post on the trial line. This process was repeated for each section northward, and finally for all the sections of the township. The surveyor thus travelled around every section of the township by the time the survey was completed.

Under the federal instructions the surveyors were required to note at what distances they entered and left any prairie, swamp or grove, and to sketch in the outline of all groves and swamps. This makes the most complete record of the location and extent of our original groves which is available, and was employed in the preparation of the Forest Map (Pl. I, cf. Shimek, 132). In some cases the records are inaccurate because of the carelessness of the surveyors (as for example, in the northeastern part of Madison County), but in innumerable cases their accuracy was avouched by the writer by observation in the field.

The surveyors were also required to describe the land over which they passed, and in this connection some of them named the most conspicuous plants, especially of the groves and prairie. They were also required to establish "witness-trees" for the government corners where possible, and some of these records are useful in indicating the location of former groves. They will, however, scarcely come up to the expectations expressed by Kenoyer, nor do they equal in value the general field notes of the surveyors. In several years experience as a land surveyor and engineer, 40 or 50 years ago when witness trees were still quite generally preserved, the writer found that not infrequently they were incorrectly identified, and that all too frequently they were designated by general or meaningless names, such as ash, oak, jack-oak, etc. These general designations do not admit of accurate application or interpretation, and since such trees were widely separated and have been mostly removed, their evidence is of but secondary value, though in special cases

This peculiarity of grouping is not an accident, but is directly related to physical environment and to the ability of plants to exist under its varying moods.

The principal environmental factors which influence our flora and determine its distribution and behavior are the following:

- I. Edaphic or local factors.
  1. Topography and drainage.
  2. Soils.
- II. Climatic or meteorological factors, often locally greatly modified by the edaphic factors.
  3. Light.
  4. Temperature.
  5. Moisture.
  6. Winds.
- III. Biotic or living factors.
  7. Plants.
  8. Animals, including man.

It is the purpose of the writer to discuss these rather elementary subjects only so far as they have a distinct bearing on the character, occurrence and distribution of our own floras. The discussions are stripped so far as possible of all technical verbiage which is not necessary for clear understanding, for such scientific facts and conditions as are here discussed may well be presented in simple, generally understandable language.

1. Topography and Drainage.

One of the most obvious of these relations is that to topography. Iowa is comparatively a plain. The difference between the highest and lowest points within the state is a little less than 1200 feet, the

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they may be helpful. The surveyor's field notes are usually a much better index to his accuracy in identifying the trees.

Kenoyer's (84) suggestion, however, forcefully calls attention to the extensive, or even complete, obliteration of the evidence bearing on the natural condition of our floras, and on our ecological problems in general. Students of these problems should make haste to study what little remains, and there should be a concerted effort made to preserve certain judiciously selected natural areas, untouched by the blight of "improvements," for future careful and protracted study. Such studies should be prolific of valuable practical results which would add to our present knowledge, for it must ever be remembered that the environmental factors which determined the nature of our native flora are still operating on our cultivated plants, and that the former are by far the best index of these factors and the conditions under which they operate.

lowest being the low-water level in the Mississippi River at Keokuk, about 477 ft. above sea level, and the highest* on Ocheyedan Mound, Osceola Co., 1670 ft. above sea level. The general level of the state, however, shows much less variation in altitude, the differences scarcely exceeding 1000 ft.

This comparatively level plain often suggests to those who are not familiar with the state a uniformity of conditions which would produce little variety in our flora. This, however, is not borne out by a study of the state, for the surface over large areas is more or less broken, and presents a much greater variety of conditions than would be suggested by the presence of the general plain. This will be more clearly shown by a more detailed description of the topography.

Iowa has been scoured and levelled over its entire area, or in part, by five glacial ice-sheets. The two oldest, the Nebraskan and the Kansan, passed southward beyond the limits of the State, and left no notable morainic irregularities of surface. The three remaining sheets, the Illinoian, Iowan and Wisconsin, left not only the characteristic plain, but also more or less prominent moraines. These moraines, however, did not give to the state that ruggedness which characterizes some of its parts, and which has been produced by agencies other than ice.

The most rugged and most picturesque part of the state lies in the north-eastern part, constituting the area which was formerly considered driftless. Its surface has been exposed to erosion longer than any other part of the state, and in consequence it is scarred by numerous valleys and ravines.

Each of the glacial plains has also been more or less broken by erosion, the older sheets naturally suffering most. In addition, the surface in the western part of the state, and elsewhere to lesser extent, has been modified by wind-action, the wind-blown loess deposits, which along the Missouri River are often more than 100 feet in depth, forming prominent ridges. Less prominent irregularities are also formed by the wind-blown sand-dunes of Harrison, Muscatine, and Louisa Counties, and elsewhere in lesser degree.

Thus the surface of the state has been quite extensively modified by the action of ice, water and wind to produce conditions sufficiently varied for a very diversified flora.

The main topographic areas may be defined as follows:

* The highest point is 1675 ft., northeast of Sibley. — Ed.

The Wisconsin Drift Plain.* This plain occupies the northern and central part of the state, (map, Pl. II) and is the highest and most level part of Iowa. Its surface is varied chiefly by the narrow and deep valleys of the Des Moines River and its tributaries, which drain it. The plain itself is quite level, excepting for occasional kames, — gravelly rounded knobs, — and for slight depressions, or "kettle-holes," which were occupied by swamps, ponds, or even lakes, formerly most abundant in the northern half of the area. The plain was covered with a prairie flora, while the kettleholes harbored an aquatic and marsh flora, entirely different in character.

The valley of the Des Moines River within this area is a narrow canyon, whose lower half reaches a depth of a hundred feet, or more, and which has been carved out of the general level plain by erosion. Its sides are steep bluffs, often cut by short lateral ravines, and with occasional rock-exposures forming ledges and cliffs. This valley is largely wooded, both on the narrow alluvial flats and on its rugged sides, and in the rougher parts, as below Ft. Dodge and Boone, it provides for the inland "islands" which contain a number of plants belonging to the forest and rock-ledge flora of northeastern Iowa.

The valleys of the two forks of the Des Moines above Humboldt are less deeply cut, often wider, but with occasional steep wooded bluffs, as at Humboldt, Algona and Estherville. These bluffs also present a well-developed forest flora of the more easterly type, but lack the flora of rock-ledges.

The border of the Wisconsin drift area is occupied by morainic ridges, which are mostly rather low in the southern part, but northward the moraine on both sides becomes more rugged. On the east side its highest and most conspicuous point is Pilot Knob, while on the west side it contains a series of knobs and ridges, of which those bordering the Okoboji Lakes, and those lying west of Spirit Lake, are most conspicuous.

These morainic knobs and ridges, as well as the higher kames which occur occasionally within the border, furnish a habitat for the more xerophytic prairie-steppe flora of the northwest, thus forming another set of detached floral "islands."

The Iowan Drift Area. This is an irregular area lying between the exposed Kansan strip in northeastern Iowa and the Wisconsin lobe, and possibly extending west of it, as shown on the map (Pl.

* See note at beginning of Chapter IV.

II). It presents a gently rolling surface somewhat broken by long shallow draws which are usually somewhat swampy, especially towards their heads, which are evidently remnants of former kettle-holes.

The general plain is broken chiefly by the valleys of the Cedar and Wapsipinicon Rivers, which drain the area. These valleys are quite deeply cut, and are in part bordered by rugged bluffs which are usually wooded. Striking examples of these rougher areas are found along the Wapsipinicon in Linn and Buchanan Counties, and along the Cedar in Linn, Benton, Black Hawk, Floyd and Mitchell Counties. The intervening bluffs are lower, usually bordering broader parts of the valleys, and are wooded. The broader parts of the Cedar valley are usually quite sandy.

The Iowan area is also broken by large islands of Kansan drift, as in southern Butler and northern Black Hawk Counties, and in southern Bremer Co. (see map, Pl. II), and by smaller similar islands, lying mostly along and within its eastern border. These islands are elevations which the thin Iowan sheet was not able to cover, and which sometimes rise more than 100 feet above the plain. They are often capped with loess and sometimes covered with forest, especially when larger and more broken. The smaller rounded or elongated knobs of this kind are known as pahas. They were often treeless, especially where isolated, and were then covered with dry-prairie flora.

The morainic border is also somewhat roughened, and was often timbered, but it does not form a very prominent topographic feature. As a matter of fact the rougher borders are frequently but a part of the Kansan rising above the Iowan plain.

The Kansan Drift Area. Surrounding most of the Wisconsin lobe, and enclosing the irregular Iowan area on both sides, is another drift-plain which occupies a large part of the southern and western parts of the state, and forms its largest topographic unit. Its surface has been cut by erosion in varying degree until it ranges from the very rough topography of the Devil's Washboard in Appanoose and adjacent counties and the rough northeastern strip, to the much less eroded parts in the northwest and the remnants of the glacial plain which still remain, north of Washington, near Fairfield, west of Ottumwa, near Udell, near Corydon and Allerton, and elsewhere in the southern part of the state. These latter areas at their borders show clearly that outlying rougher areas have been produced by the carving of stream valleys out of a great plain, for they do not rise above its level. These remnants of the glacial plain will be recognized on the forest map (Pl. I) in the localities noted, by the fact that they were (and are) treeless.

Limited rougher areas, such as are found in Lucas and Clarke Counties, may represent an older topography which was not materially influenced by the Kansan. They do not, however, differ in their floral characteristics from the rougher southern Kansan area.

The northeastern strip of the Kansan area is deeply cut, particularly by the valley of the upper Iowa, Turkey, Volga, and to a lesser extent by the Wapsipinicon Rivers and their tributaries, and its surface and floral characteristics are similar to those of the adjoining northeastern area which was formerly regarded as a part of the Driftless Area of Wisconsin. The valleys are deeply cut, with numerous rock exposures, and the rough lands adjoining them were quite generally wooded.

The Kansan area of the southern nearly half of the state is also cut by numerous stream valleys. In the southeastern part the Cedar, the Iowa, the Skunk and the Des Moines have all carved out valleys with rugged bluffs and rock ledges at more or less frequent intervals. Where these rougher areas occur they are uniformly more or less wooded, and the conditions for plant life are similar to those of the northeastern part of the state.

The Kansan in the south-central and south-western part of the state is also more or less dissected, its roughest parts being in the counties near the southern border of the Wisconsin, where cut by tributaries of the Des Moines. Southward the streams are mostly the upper courses of larger Missouri streams, and their valleys are less deeply cut, though frequently penetrating through the Kansan. Even their occasional more abrupt slopes, however, are timbered, but there are almost no rock exposures.

The inland portion of the Kansan area to the west and northwest is rather less deeply cut, and there are almost no rock exposures. The peculiar Nishnabotna River system, with its numerous creek-like branches, has cut out broad valleys which are bordered by rounded, mostly treeless bluffs. The remaining streams of the western slope are similar, with the exception of the Little Sioux, which has cut a deeper valley, bordered by higher rounded bluffs which are more or less wooded, excepting where exposed to the west or southwest. All these streams, however, cut through the loess-covered bluffs which border the valleys of the Missouri and the Big Sioux. Their broad valleys are treeless, excepting for a fringe along their immediate banks, and the bluffs are wooded only where sheltered from exposure to the west and southwest. The rolling areas between these valleys were originally upland prairie.

The Loess Areas. The Kansan has been modified by other than water-action. In the vicinity of the eastern streams, and more notably along the Missouri River, there are extensive loess deposits which have been piled up by wind-action. In the eastern part of the state they seldom exceed 15, and very rarely 35 feet, in depth, and they modify the topography somewhat only by accentuating the roughness of the Kansan surface, as they cap the hills instead of filling the hollows.

In this part of the state they are distributed over the Kansan chiefly near the margin of the Iowan. This has given rise to the widely prevalent belief that loess is closely connected with the Iowan, when in fact its source and distribution are accounted for more satisfactorily in relation to the streams of this part of the state. The Iowa River skirts most of its southern boundary, and the Cedar and other more northerly streams cut through it. In the vicinity of the main deposits the valleys are broad and with numerous sandbars at low water, from which the loess-dust was evidently derived. Loess deposits are also found along the Iowa, Des Moines, and other streams well below the Iowan, and also over the Illinoian drift in southeastern Iowa, along the bluffs of the Mississippi, and along the Upper Iowa River within the ''driftless'' area. The Iowan furnished much sand for the bars of most of these streams and that perhaps was its greatest contribution to the formation of loess.

The western deposits of loess have affected topography in a much more marked degree. Here also the loess caps the hills, and is distinctly deepest on their summits, sometimes reaching a depth of more than 100 feet. Its main body spreads out quite to the Wisconsin lobe, in the main within the lines indicated on the map, (Pl. II) and its greatest depth by far is not on the side nearest to the Iowan, but on the Missouri River bluffs. The peculiar topography of the crested hills of these bluffs, resembling huge snowdrifts, is evidently due to their eolian origin.

The abrupt hypsometric changes in this bluff region bring about conditions which are favorable to forest growth in the sheltered valleys at one extreme, and which only confirmed xerophytes can survive on the crests at the other.

The Nebraskan Drift. This drift is exposed only along the western border, and in river valleys in the southern part of the state. Its topography presents nothing different from the Kansan in its relation to plant growth.

The Illinoian Drift. This occupies only the southeastern part of the state (See glacial map, Pl. II). Its narrow treeless uplands do not differ materially from the Iowan surface, but on the side adjoining the Mississippi Valley the depth of that valley has brought about extensive erosion which has produced a surface not unlike that of the rougher Kansan areas in the northeast. In Muscatine County the upland plain is varied by numerous sand-dunes, derived from glacial Lake Calvin and the valley of the Cedar River.

The moraine bordering this area on the west side also presents some rough features, but ecologically it does not differ from the adjacent Kansan.

The "driftless" Area. This area occupies the northeastern part of the state (See map, Pl. II), and constitutes a botanical region of great interest because it makes possible the existence of many plants which have few or no suitable abiding places in other parts of the state.

This is the only extensive area of the state which has not been notably modified by drift. It was formerly included in the Driftless Area of Wisconsin, and while traces of drift may be found on its higher elevations, it may still be regarded as "driftless" in the sense that no material amount of drift remains upon it, and that its surface has been practically uninfluenced by it. For this reason, and for convenience in reference, it will be designated as the "driftless" area in this paper.

While it contains remnants of what is evidently an ancient plain (probably the remnant of the old Nebraskan glacial plain), especially in Clayton and Winneshiek Counties, the greater part of its surface is deeply cut, even the smaller streams usually occupying deep gorges.

The effect of erosion on its long-exposed surfaces is well shown in these numerous narrow canyons, which in many cases cut through the country rock to the depth of 300 to 500 feet, exposing vertical cliffs and forming prominent head-lands, the whole constituting a topography so rugged and picturesque that this section has become known as the "Switzerland of Iowa."

Cliff-dwelling plants, and those requiring much shelter, find an abundance of suitable habitats, — the former especially being favored by the numerous exposures of limestone, sandstone, and even shale, often in the same bluff. Thus, in ascending the bluffs below McGregor one encounters the St. Croix sandstone at the base, followed successively by the Lower Magnesian limestone, the very friable St. Peter sandstone and the Plattville limestone, each presenting its peculiar characteristics on the same general slope.

The sheltered valleys and slopes were well wooded, while the exposed faces and the uplands were covered with prairie.

The principal streams which drain the area are the upper Iowa, Yellow and Turkey Rivers. Their valleys are deep, and mostly narrow, that of the Upper Iowa, however, widening in Allamakee County to about a mile. Sandbars are few and mostly quite small and habitats suitable for marsh and aquatic plants are limited.

Sandy Areas. Sandy areas are scattered, and mostly of rather limited extent in Iowa. They present two general topographic types: They appear as dunes (or sandy caps on drift or loess ridges) ; or they are comparatively flat beaches and bars along the shores of lakes and streams.

The dune areas are comparatively few and cover a small percentage of the area of the state. The largest of these areas in the western part of the state extends along the Missouri River in Harrison and Monona Counties, and breaks the level of that part of the broad alluvial plain bordering it. The dunes here seldom rise to a height of over ten feet, and most of them are fixed for the time being by growing vegetation.

In the eastern part of the state dunes appear both along some of the larger streams, and to more limited extent, at or on the border of the Iowan. One area of considerable extent caps the great Sand Mound on Muscatine Island in Muscatine and Louisa Counties. This was regarded as a remnant of a terrace by Udden (146, p. 256).

The Mound itself presents the appearance of an elongated rounded dune, and is nearly three miles long, nearly a mile wide at the widest part, and rises scarcely 35 feet above the alluvial plain on which it stands. The western sandy slope was fixed by a well-developed prairie flora, but the top and eastern side consists of more or less shifting sand, piled up occasionally in low dunes.

A distinct dune region also occupies the Illinoian drift plain east of the Cedar River in Muscatine County. In places it extends five or more miles east of the river valley, and before the attempted cultivation of parts of the area the dunes were fixed (excepting in very dry seasons) by a prairie flora.

Sandy areas occur along almost the entire course of the Cedar River, and occasionally the sand is piled up in dunes in minor areas, as along the west side of the Cedar in Muscatine County and just south of Cedar Rapids; in northwestern Black Hawk County, and at other points along the Cedar; and in the northern part of Johnson County, on the south side of the Iowa River.

Sandy caps on ridges, sometimes dune-like, are usually quite limited and local, and may be observed especially near the southern and eastern border of the Iowan drift. Conspicuous examples may be found in Iowa, Johnson, Dubuque and Delaware Counties.

Sand flats occur in two forms: As beaches along the shores of some of our lakes, as Spirit Lake, the Okoboji Lakes, Clear Lake, Iowa Lake, and others in varying degree; or as alluvial flats and bars along many of our streams.

The latter are best illustrated along the Missouri, Mississippi, Cedar and Iowa Rivers, though they may occur along most of our streams, particularly in the southeastern quarter of the state. They sometimes appear as terraces which are remnants of older alluvial plains at higher levels. Such terraces may be observed along the Big Sioux and Missouri Rivers on our western border, and along many of the tributaries of the latter, particularly the Little Sioux, the Maple, and Boyer, and the larger branches of the Nishnabotna.

They are also well shown along the Mississippi River at intervals along almost its entire course in the state, and are especially prominent in Muscatine, Louisa and Lee Counties.

These terraces are usually 30 to 50 feet above the stream, quite flat, with sandy and gravelly slopes where cut by erosion, and they were originally chiefly covered with a xerophytic flora of the prairie and sand type, excepting in some cases where a finer alluvium covered a part of the terrace.

Finer alluvial flats also occur along the more sluggish courses of all our streams, and topographically these are similar to the alluvial sand-flats, with which they alternate or intermingle. These alluvial flats reach a width of 15 to 20 miles in Harrison and Monona Counties, and they were originally covered in the main with prairie.

Summary. The major topographic features of the state, as they are related to the distribution of its native flora, may be summarized as follows:

1. The "driftless" area, with the adjacent part of the northeastern Kansan strip, which is characterized by a surface deeply cut by mostly narrow stream valleys, with numerous rocky ledges and cliffs exposed in the high and precipitous bluffs.

Somewhat similar "island" areas of more limited extent, and with floras of the same type, in outlying parts of the state, as at the Palisades on the Cedar in Linn County; along the Iowa River in Johnson and Hardin Counties; along the Des Moines River in Wapello County, at the "Bluffs" in Mahaska County, Red Rock in Marion County, the "Ledges" in Boone County, and the vicinity of Ft. Dodge in Webster County; and at the "Devil's Backbone," now a part of the Pammel State Park, in Madison County.

Surfaces of this type were mostly heavily wooded, excepting on the highest points, and on surfaces with a southwesterly exposure.

2. The Rolling Topography of the main body of the Kansan drift, together with the morainic borders of the Wisconsin and Iowan, and the valleys of many of the streams cutting their plains. This is characterized by rounded contours offering less shelter and also greater exposure than in the preceding type, with a consequent diminution in forest and increase in prairie, the ratio varying with the roughness of the surface. The surfaces may be modified drift or loess; that seems to make little difference. Rock exposures are limited, and the rock flora is poorly represented.

3. Flatter drift areas, including the plains of the Wisconsin and Iowan drifts, and the lesser flat areas of the uplands of the Illinoian and the remnants of the Kansan drift plain. These areas, excepting where cut by river valleys belonging to the preceding group, are quite uniformly exposed and were originally prairie, excepting on the undrained parts, especially of the Wisconsin, which contained a marsh and aquatic flora.

4. The Missouri River Loess Bluffs and the Northwestern drift knobs and ridges, which are characterized by numerous steep slopes with almost no rock exposures, and offer rather scant shelter for a limited forest vegetation, but are covered mostly with prairie.

Their most exposed parts are of the prairie-steppe type with quite a number of westerly more xerophytic plants.

5. The Sand-dune Areas, which are more limited in extent, but present noteworthy ecological conditions.

6. The Alluvial Flats along our streams, which also present distinctive ecological features, but the character of their flora is largely determined by the nature and position of the bordering highlands.

7. Rock Exposures, which are found chiefly in area (1) and in the scattered ''islands'' to which reference has been made. In these areas the rocks are older Cambrian and especially Silurian limestones, sandstones and some shales, in the northeastern area (1), Silurian limestones also appearing at Anamosa in Jones County and at the Palisades in Linn County; Devonian limestones in Johnson, Floyd, Cerro Gordo and Mitchell Counties; Lower Carboniferous limestones in Lee, Des Moines and Hardin Counties; Upper Carboniferous sandstones and shales in limited areas in Muscatine, Scott, Johnson and Iowa Counties, and in mostly larger exposures, including some limestones, in the ''islands'' already cited along the Des Moines and in Madison County. Among the exposures at Ft. Dodge are also Permian gypsum ledges.

Insignificant Cretaceous exposures also occur along our northwestern border, and there are two small areas of Algonkian Sioux Quartzite, about two miles apart, in the northwest corner of Lyon County.

B. Elevations

While the surface of Iowa thus presents some variety, the differences in altitude are not great, and the state as a whole may well be regarded as a great plain. Though the Wisconsin area is the flattest in the state, containing many normally undrained wet areas, it forms the highest part of the larger topography, as is shown by the drainage of all streams away from it, and by the upper three east and west cross-sections of the state presented in the upper three of the following tables of elevation above sea-level.

These elevations are taken chiefly from Dr. J. H. Lees' paper on ''Altitude in Iowa'' (87), but the Gannett (63) and Marshall (102) reports, published by the U. S. Geological Survey, and the railway profiles published by the Iowa Railway Commission (79) were also consulted. A few of the approximate elevations were determined barometrically by the writer.

The elevations are those of railway stations. Excepting at the terminals of each section, the stations were selected as nearly as possible on the level of the general plain, but in most cases the surface rises somewhat higher in their immediate vicinity. The figures, nevertheless, indicate the altitudes of the general surface very satisfactorily, with stream valleys cutting below the general level, and moraines and other knobs and ridges rising above it.

Each section of the table contains one tier of counties, beginning at the east end. The name of the county in each case is followed by the name of the station, with its elevation above sea-level in feet. Fractions of a foot in elevations are omitted (For location of these sections see map Pl. II).

The terminal stations in each section, with one exception, are located on the alluvial flats, respectively, of the Mississippi and Missouri Rivers, — at or slightly above high-water mark. The exception is at Granite, Lyon County, where the station is probably 50 feet, or more, above the narrow alluvial plain of the Big Sioux River.

County	Station	Elev. ft.
Section 1		
Allamakee	Lansing	632
Allamakee	Waukon	1216
Winneshiek	Ridgeway	1211
Howard	Cresco	1300
Mitchell	Riceville	1232
Mitchell	Osage	1168
Worth	Manly	1205
Winnebago	Thompson	1272
Kossuth	Swea City	1187
Emmet	Gruver	1311
Dickinson	Superior	1501
Dickinson	Spirit Lake	1465
Osceola	Ocheyedan	1555
Osceola	Sibley	1516
Lyon	Larchwood	1468
Lyon	Granite	1313
Section 2		
Dubuque	Dubuque	608
Dubuque	Dyersville	943
Delaware	Delaware	1078
Buchanan	Independence	917
Black Hawk	Raymond	884
Grundy	Wellsburg	1058

Hardin	Buckeye	1154
Hamilton	Kamrar	1115
Webster	Duncombe	1110
Webster	Tara	1150
Calhoun	Rockwell City	1221
Sac	Early	1332
Ida	Holstein	1445
Woodbury	Sioux City	1103
Section 3		
Scott	Davenport	569
Cedar	Durant	713
Johnson	Iowa City	671
Iowa	Homestead	861
Poweshiek	Grinnell	1007
Jasper	Newton	942
Polk	Ankeny	998
Dallas	Dallas Center	1073
Guthrie	Guthrie Center	1070
Audubon	Ross	1354
Shelby	Panama	1248
Harrison	Missouri Valley	1005
Harrison	Blairbridge	1007
Section 4		
Lee	Ft. Madison	520
Lee	Donnellson	703
Van Buren	Milton	804
Davis	Bloomfield	857
Appanoose	Centerville	1002
Wayne	Corydon	1083
Decatur	Garden Grove	1114
Decatur	Leon	1019
Ringgold	Mt. Ayr	1217
Taylor	Gravity	1151
Page	Yorktown	1038
Fremont	Hamburg	911

It will be noted in the first section that there is an abrupt rise from 632 feet in the Mississippi Valley at Lansing to 1216 feet at Waukon. The rise is greater than these figures indicate, for the station at Waukon is somewhat below the general level of this area. Most of this change takes place near Lansing, where the bluffs rise quite abruptly from the valley. Westward the elevation becomes less on the Iowan Drift area, being 1168 feet at Osage, and 1205 at Manly, which is just east of the Wisconsin Drift border.

The Wisconsin Drift area then shows a somewhat greater altitude, ranging from 1272 feet at Thompson to 1311 feet at Gruver and 1501 feet at Superior, with a noticeable depression in northern Kossuth County, which seems to follow the Des Moines Valley southward. Superior, which shows the greatest altitude in this part of the section, is on the divide between the Missouri and Mississippi watersheds, and should, perhaps, be considered as within the irregular and more or less indefinite morainic area which occupies the western side of the Wisconsin lobe in northwestern Iowa.

It will be noticed that the general slope of the Wisconsin plain is southeastward, as is shown by comparing the altitudes within it along the first three sections. At the north the altitudes run from 1272 feet at Thompson to 1311 feet at Gruver with a depression to 1187 feet at Swea City. In the second section the altitudes range from 1154 feet at Buckeye, to 1221 feet at Rockwell City, with a drop to 1115 feet at Kamrar, and 1110 feet at Duncombe, — both within the Des Moines Valley depression.

At the southern extremity of the lobe the third section shows an altitude of 998 feet at Ankeny, and 1073 feet at Dallas Center. Thus, on the east side of the Des Moines depression the altitudes drop from 1272 feet at Thompson, to 1154 feet at Buckeye and 998 feet at Ankeny; on the west side the drop is from 1311 feet at Gruver, to 1221 feet at Rockwell City and 1073 feet at Dallas Center; while the Des Moines depression drops from 1187 at Swea City, to 1110 feet at Duncombe and 998 feet at Ankeny.

Another striking elevation is revealed by the watershed which extends from Dickinson to Appanoose County, with a branch extending from Adair to Decatur Counties, and other elevations between. At Superior its altitude is 1501 feet and drops to 1354 near Ross, in Audubon County (not quite at the top of the divide) and to 1217 feet at Mt. Ayr, which is also below the highest part of the west fork of the divide.

At Moravia, in Appanoose County, near the east fork of the divide, the elevation is 1009 feet, and at Corydon, Wayne County, which lies between the two forks, it is 1083 feet, and 1114 feet at Garden Grove in Decatur County. Both east and west the surface drops quite regularly, with local exceptions, as at Holstein in Ida County and the vicinity of the border of the drift in Osceola County. There is also a dip upwards towards the northeast, much of the "driftless" area rising above the glacial plain to the west.

A comparison of the elevations in the four sections (best observed in the map, Pl. II) shows clearly that the general slope of the state is southward. It is interesting to note particularly that while the Mississippi alluvial plain drops from 632 feet at Lansing to 508 feet at Keokuk, a difference of 124 feet, the corresponding alluvial plain of the Missouri drops from 1103 feet at Sioux City, to 911 feet at Hamburg, a difference of 192 feet in scarcely two-thirds the distance. In about one-third the distance, the Big Sioux River alluvial plain drops from about 1260 feet near Granite, to about 1100 feet near Sioux City, — a difference of about 160 feet.

In addition to the general levels here discussed, we must take into account elevations rising above them. Thus all the elevations given along the Missouri Valley are those of the alluvial lowlands. Along the entire valley in Iowa the loess-covered bluffs rise to a height of from 150 to 400 feet above the level of the valley. The glacial knobs and ridges which are especially prominent near the northern extremities (in Iowa) of the Wisconsin lobe rise considerably above the general levels which are given in the sections.

Thus, some of the morainic knobs in the Okoboji Lake region rise 100 feet or more above the level at the town of Spirit Lake; Ocheyedan Mound in Osceola County has an elevation of 1670 feet and rises over 100 feet above the surrounding plain; Pilot Knob in the northeast corner of Hancock County has an altitude of 1450 feet above sea-level while the Wisconsin plain to the northwest is about 180 feet lower; the Kansan drift islands (including paha) on the Iowan drift uniformly rise from 40 to more than 100 feet above the drift plain; and in northeastern Iowa the ridge which extends from Waukon to Lansing, and the numerous erosional hills and knobs, rise well above the altitude of Waukon, — in a few cases more than 100 feet. These restricted or isolated elevations bring about more xeric conditions by their exposure, and the flora on their summits, especially westward, approaches or develops the prairie-steppe type.

Drainage. Drainage is determined primarily by topography, and its general direction and character in Iowa have already been presented. The depth of the stream valleys is usually related to the age of the surface formation, but it may be greatly modified by the stream gradient, and by the volume of water carried.

Thus, the Kansan strip in northeastern Iowa is much younger than the adjacent "driftless" area, but its contiguous parts have been quite as deeply eroded in many places because the rapid run-off from the increasingly steeper slopes, and the abrupt drop from the Kansan uplands to the lower valleys of the "driftless" area, resulted in a volume of water and a rapidity of current which greatly increased the rate and amount of erosion.

Another illustration is furnished by the Des Moines River, which has cut a gorge often exceeding 100 feet in depth in the lower half of the Wisconsin lobe, — the youngest of our surfaces. The explanation is to be found in differences in altitudes, and the consequent increase in the stream-gradient. The Wisconsin plain east of the Des Moines River in Emmet County has an altitude of 1311 feet at Gruver, while at Ankeny, in Polk County, the same plain reaches an altitude of but 998 feet, a fall of 313 feet; the fall from the Wisconsin plain at Ankeny to the alluvial plain near the mouth of the river, an almost equal distance, is from 998 to 508 feet, a drop of 490 feet.

Of this total of 490 feet, the drop in the short distance from Ankeny on the Wisconsin plain to the alluvial plain of the Des Moines River at Des Moines is 202 feet, still leaving 288 feet for the fall of the alluvial plain from Des Moines at the edge of the Wisconsin to the mouth of the river. When we consider that the Missouri River alluvial plain drops but 192 feet between Sioux City and Hamburg, a distance about equal to either of the two sections of the Des Moines noted above, we can appreciate the steeper gradient of the Des Moines, and the consequent more rapid erosion along its course in the lower part of the Wisconsin lobe.

The width of the eroded valleys is also determined by the kind of material through which the stream has cut. Thus, in northeastern Iowa most of the stream valleys are narrow because cut in solid country rock, but the lower part of the valley of the Upper Iowa is much broader (reaching a mile in width) because it has been cut out of more friable sandstones which were easily removed.

Where the material is loose, as over much of the drift area, and where the fall and the volume of water are sufficient, the valleys may be both deep and broad, particularly on older areas, as in the western and southern parts of the state.

The depth and direction of the stream valleys bear an important relation to the distribution of our natural flora. The valleys in northeastern Iowa with a southeasterly trend, and the irregular valleys in the southern part, had both their alluvial valleys and bluffs well wooded, excepting where local exposure prevented it.

On the other hand the alluvial valleys of the western streams having a southwesterly trend were mostly treeless excepting for a narrow fringe along the immediate banks of the stream, and the bluffs were also largely treeless, excepting in sheltered lateral ravines. The significance of this phenomenon will be discussed in connection with the prairie problem.

C. Soils

It is a widely prevalent belief that soils are all-important in determining the possibilities of plant growth. As a matter of fact in Iowa they are of but very secondary importance in determining the distribution of our native flora, and where they do seem to exert an influence it is due chiefly to their water-absorbing and water-holding qualities.

The chief reason for this lies in the fact that our own Iowa soils differ comparatively little in chemical composition, all having the mineral ingredients necessary for plant growth. Since the soils are mixtures, these ingredients appear in varying quantities, but they are always present and more or less available for use by plants.

Our Iowa soils are all practically of drift origin, with the exception of small areas near rock exposures, and in portions of the "driftless" area in the northeast. Even the latter, however, are similar, for they consist of materials derived from limestones, sandstones and shales, similar to those which were ground by glacial ice and water to form our glacial soils, and in our territory there are always at least traces of glacial granitic boulders, and pebbles.

Four groups of soils may be recognized, based on the origin of their mineral constituents, namely glacial, alluvial, loess and geest soils.

The glacial soils and subsoils cover the greater part of the state, and are derived directly from the finer materials of the several drift sheets.

The alluvial soils are found chiefly in narrow strips along our streams, only occasionally widening out into plains from 5 to 20 miles in width, as in Harrison and Monona Counties along the Missouri, and on the Green Bay bottoms along the Mississippi, below the mouth of Skunk River, in Lee County. Their materials have been washed down chiefly from the uplands covered with glacial drift or loess. The much less extensive lacustrine soils along the shores of our lakes are of similar origin.

The loess soils, which chiefly occupy the uplands in large sections of the state, are made up of finely comminuted rock materials which were ground by the glaciers, washed down to the bars of streams, and from them blown back to the uplands in the form of dust which was lodged among the plants of the uplands.

The geest soils, composed of local rock materials, are of least extent, and in most cases are so mingled with soils of the other types that they are indistinguishable, especially since they are very similar in chemical composition to the soils of glacial origin.

The similarity in chemical composition of these several types of soils, which are also present in Wisconsin, was brought out very clearly by Chamberlain and Salisbury (25, pp. 250, 282). All contain all the minerals essential to plant growth, such as iron, manganese, sodium, potassium, calcium, magnesium and, in lesser amounts, sulphur and phosphorus, and with them silicon in large amount for the purpose of diluting the nutritive materials.

These minerals do not of course, appear as distinct elements, but are found in the form of quartz (silicon dioxide), limestone (calcium carbonate) and the polysilicates of most of the members mentioned, which form feldspars, hornblende and mica. Quartz is always abundant, forming from about 40% to about 74% of the mineral content, the remaining elements trailing downward until only a fraction of one percent appears in some cases. They are, however, always present, and as a plant requires a very small amount of each (the total amount of all solid materials varies in different plants from less than 10% to 40%, and the carbon, which forms a little more than one half of it, comes chiefly from the air), the amount in our soils is usually sufficient to meet the demand.

Of course these mineral constituents are not sufficient to form a fertile soil, for if taken alone they would be quite sterile. Other essential elements, such as nitrogen, are necessary, and these are derived from the humus of the soil which results from organic decay, or they result from the activities of various plant and animal organisms in the soils, such as the nitrifying bacteria in root-tubercles, and others. These additions, however, are made normally to all our soils and hence they constitute no distinction.

Because of this similarity the question of the chemical composition of any particular soil becomes of minor importance in Iowa, and the differences in our soils are to be sought chiefly in their composition, which will vary with the relative percentages of the constituents, but especially with the coarseness of the particles and the consequent compactness of the soil. The latter quality will largely determine the readiness with which water may be taken up or drained (or evaporated) away, and the fineness and compactness of the soil become more important in determining differences between our soils than the chemical composition.

It must also be remembered that the roots of many of our plants, especially those of the prairie flora, penetrate to great depths, and often pass through strata which differ greatly in compactness and water-holding power. The nature of the surface soil may therefore be of importance only, or chiefly, in germination and initial growth, for beyond that the roots penetrate to the subsoil strata which thereafter determine the continued existence of the plant so far as the soil is related to it.

Our soils have little to do with the natural distribution of our native floras. They may influence the vigor of the plants and the amount of their organic product, but they do not determine the kinds excepting in a very limited degree. Repeated efforts have been made, however, to delimit certain portions of our flora on the basis of soils and surface formations.

Thus Whitney, (154) regarded fineness of soil as responsible for the prairie, though our prairie flora seemed to prosper on soils of all types, from the finest to those which were sandy or even gravelly. McGee, (93, p. 198; 94, p. 115; 95, pp. 296-298) repeatedly declared, and he has been widely quoted, that the loess was covered with timber, and the drift with prairie, though there are enormous areas of loess, especially in western Iowa, which were covered with prairie, and numerous places where groves appeared on the drift. We have both prairie and forest on almost every type of soil in the state, and the same is true of our swamp and water areas. Thus, in what is now West Iowa City there were several ponds and boggy places on upland loess, and traces of some of them still remain; the Wisconsin drift was dotted with numerous lakes, ponds and swamps resting directly on the drift; ox-bow lakes and ponds are still frequent along our streams on both fine alluvium and sand; and our sand-dune areas in Harrison and Muscatine Counties contained numerous ponds and sloughs, some of which still persist.

Topography is a much more potent factor in determining distribution, as will be especially shown in the chapter on the prairies.

CHAPTER II

OTHER FACTORS AND PLANT ADAPTATIONS

A. Climatic or Meteorological Factors

1. Light

Since light is essential to the photosynthetic processes by which green plants produce their organic constituents, it must be recognized as one of the most important of the ecological factors. Since it is an exceedingly variable factor owing to diurnal changes, including the clearness of the sky, and seasonal changes affecting the length of the day and the angle at which light is received, plants require certain adjustments or adaptations* which will tend to assure the reception of light in the proper degree of intensity. Many of these adaptations are universal, and are shown in the greater development of chlorophyll on the more exposed sides of leaves (which is causative); the arrangement of leaves on the stem and branches and their elevation on tall or climbing stems, or exposure by floating in water; the form and size of the leaf; the flexibility of the stem and leaf which permits a swaying by wind and consequent change of position; the turning of leaves towards the light; the shifting of chloroplasts; etc., — all resulting in a better exposure of the chlorophyll-bearing parts to light.

There are also adaptations by which the intensity of light is increased, as by the convexity of epidermal cells; and other adaptations by which its intensity is diminished, as by hairs, scales, spines, wax, thick cutin, sclerenchyma cells, elongated and closely-packed palisade cells and other devices by which a portion of the light is cut off before reaching the chloroplasts. These adaptations are chiefly useful in enabling plants to secure the necessary amount of light amid surrounding plants, or under diverse topographic conditions. They do, however, undoubtedly influence the distribution of our larger plant formations to a greater or lesser degree, but it is often difficult to ascertain which is the governing factor, — the

* Much objection has been made to the use of the term ''adaptation'' in ecology. These objections, however, are hypercritical. The term is convenient and expressive when used with reference to fitness and not, as has been assumed, to express causative adjustments. It first came into general use in its proper sense in connection with pollination studies, and its use in that sense should be continued. It will be so used by the writer.

light or temperature (especially through its influence upon moisture), for both come to us from the same source. There are general adaptations of our prairie and forest floras, for example, which serve to adjust the plants to both light and moisture. Thus, the (usually) reduced, strongly cutinized leaves of prairie plants protect the plant both against the intense light of the prairie and the excessive loss of water which its exposure would invite; while the broad, sprawling, thin, slightly protected leaves of the forest are benefited by the broader, unhampered surfaces, both for receiving the dimmer light in sufficient amount, and permitting freer transpiration.

Two striking features of our floras seem to be related chiefly to light, though some relation to moisture is also evident.

The first is the stratification of vegetation, noticeable especially in the forest. Our groves have been disturbed to such an extent, especially by the clearing or pasturing of the undergrowth, that this interesting feature has been almost wiped out. Formerly in the denser groves the larger trees formed one distinct stratum; below this appeared a stratum of large shrubs or small trees, such as *Cornus alternifolia*, *Corylus americana*, some of the hawthorns (*Crataegus*), *Prunus virginiana*, and *Zanthoxylum americanum*, and a few very tall herbs, such as *Cirsium altissimum*; then followed smaller shrubs, such as *Ribes*, and a large number of rather large herbs, such as our taller ferns, *Actaea alba*, *A. rubra*, *Aralia racemosa*, *Aster Drummondii*, *Cryptotaenia canadensis*, *Heliopsis helianthoides*, *Solidago ulmifolia*, and many others; a still lower stratum, usually merging somewhat with the preceding group, consisted of *Circaea lutetiana*, *Dicentra Cucullaria*, *Mertensia virginica*, *Phlox divaricata*, *Polemonium reptans*, *Uvularia grandiflora*, etc., and beneath these appeared still smaller plants, such as *Anemone quinquefolia*, *Anemonella thalictroides*, both forms of *Asarum*, *Carex pennsylvanica*, *Claytonia virginica*, *Erythronium albidum*, *Hepatica acutiloba*, *Isopyrum biternatum*, *Trillium nivale*, etc.

These plants did not flower at the same time, but, with the exception of the last group of early flowering species, they were usually well in evidence by or before early August.

The second striking feature is the seasonal development of parts of the flora. Thus the last of the preceding groups appears in the spring before the foliage of the trees and shrubs, and the undergrowth of larger herbs, develops. There is then an abundance of light in the woods, and these plants can function and get out of the way for the season before their light is cut off by the overshadowing foliage of the larger plants.

Somewhat the same seasonal progression may be observed on the prairies. The earlier plants, like *Anemone caroliniana*, *A. patens* var., *Antennaria neglecta*, *Astragalus caryocarpus*, *Ranunculus fascicularis*, *R. rhomboideus*, *Sisyrinchium campestre*, *Viola fimbriatula*, *V. pedatifida*, etc., are small or prostrate, and appear well before they are overtopped by the more robust vegetation which follows.

The latter also comes by successive steps. The low early vegetation is followed by a stratum of somewhat taller plants, such as *Anemone cylindrica*, *Castilleja coccinea*, *Dodecatheon Meadia*, *Koeleria cristata*, *Lithospermum canescens*, *Panicum Leibergii*, *P. Scribnerianum*, *Phlox pilosa*, *Senecio plattensis*, etc.; these in turn are followed by a group of usually taller plants, including *Achillea Millefolium*, *Amorpha canescens*, *Cirsium Hillii*, *Coreopsis palmata*, two species of *Brauneria*, two species of *Petalostemum*, *Potentilla arguta*, *Rudbeckia hirta*, etc., and later by *Aster azureus*, *A. laevis*, *A. multiflorus*, *Solidago nemoralis*, etc., and finally these are displaced or overtopped by the taller plants of later summer such as *Andropogon furcatus*, *Coreopsis tripteris*, several species of *Cirsium* and *Helianthus*, *Rudbeckia subtomentosa*, *Silphium integrifolium*, *S. laciniatum*, *Solidago rigida*, *S. speciosa* var. *angustata* and many others forming the seasonal climax of the prairie flora.

We finally have in this case a stratification of vegetation often quite as clear as that of the forest.

In both cases moisture (with associated temperature) is a factor quite as manifest as light.

2. Temperature

The direct effect of temperature upon plant distribution in Iowa is difficult to estimate, but it has probably not been very decisive. There is a marked difference in the ability of plants to resist cold and undoubtedly some plants have been exterminated locally by late frosts in the spring, or early frosts in the fall, but on the whole this direct effect has probably been limited.

The difference in latitude between northern and southern Iowa is not great, and there are no great natural barriers, or marked differences in altitude, yet the shortening of the season by three to six weeks in the northern part of the state results in a delay of the spring vegetation, and in the course of time has brought about an earlier maturity of plants in that section in the fall.

The diurnal and seasonal variations in temperature (ranging from about 30° F. below zero to about 112° above, though both extremes are quite rare), however, are so great that no doubt the very existence of many plants is determined by it, since either extreme is injurious, if not fatal. The injury may be produced either by the coming of late or early frosts which destroy many plants in an immature state, or by such a lengthening of the opening season that its midsummer portion suffers from excessive heat and accompanying drouth.

Unlike the ability to resist other climatic factors, that to withstand extremes of temperature is not revealed in the structure of a plant. Thus it does not suggest why the tender rosettes of the delicate winter annual *Houstonia minima* survive a severe winter even when not thoroughly covered, when the sturdier looking peach tree often succumbs; or why the flowers of witch hazel (*Hamamelis*), *Aster sericeus* and *Gentiana puberula* remain uninjured even after heavy frosts in the fall, while so many others perish at the approach of even the lightest early frosts; or why blue grass (*Poa pratensis*) remains green long after the otherwise hardy bluestems (*Andropogon*) have turned brown by frost in the fall.

A report on killing frosts published in the Report of the Iowa Crop and Weather Service (80) for 1902, throws some interesting light on the appearance of killing frosts within the period from 1873 to 1902, inclusive. The extreme variability of the length of the period between the last killing frosts of the spring and the first frosts of fall is illustrated by the following table.*

Locality	Average	Maximum	Year	Minimum	Year
Keokuk	190	235	1882	160	1888
Davenport	174	216	1900	133	1883
Dubuque		218	1878	138	1888
Des Moines	171	210	1879 1880	120	1890
Sioux City	145	182	1891	129	1890 1895

* In the main the older meteorological records are quoted because they present conditions more nearly as they existed before the drastic changes in surface conditions of more recent years.

The records at Keokuk and Dubuque are for the years 1873-1902, inclusive; for Davenport for 1872-1902; for Des Moines for 1878 to 1902, and for Sioux City for 1889 to 1902. The first column after the name gives the average number of frost-free days in this period; the second contains the maximum number of such days, followed in the third column by the year in which the maximum occurred; the fourth column contains the minimum number of days, followed by the date of the minimum number.

It will be observed that the difference between the longest and shortest seasons between frosts amounts to 75 days at Keokuk, 83 days at Davenport, 80 days at Dubuque, 90 days at Des Moines and 53 days at Sioux City. As the difference in the length of these extreme seasons at the same place amounts to nearly 3 months in most of the cases, it is evident that the effect on the native flora must have been marked. The longer season does not, however, always result in advantage to the flora, for the longer seasons are almost invariably divided by long, hot and dry midsummers which interfere seriously with plants.

It is not the length alone of this open season, however, which is of importance. If it begins unusually late, or ends unusually early, much greater harm is done. In the period under consideration the latest killing frost occurred on May 22, 1882, in Des Moines and Davenport, and on the same date in 1883 in Davenport. The earliest frosts in the fall during this period came on September 12, 1878, in Des Moines, and September 18, 1875, in Davenport.

Killing frosts, or at least a distinct lowering of temperature, are of almost annual occurrence during the second week of May, but spring often opens long before that time. Thus, in 1879 twenty species of native plants in flower were collected in the vicinity of Iowa City, on the 19th of February. A striking illustration of the variability of our seasons is furnished by the delayed spring of but two years later, 1881, when snow and ice remained in wooded ravines in the same vicinity until the first week in May.

Undoubtedly a more consistent influence, however, is exerted upon plants through the effect upon precipitation and evaporation, both extremely important factors in their relation to plant welfare, and this will be considered more fully in connection with the moisture problem. It will also be shown that much of the difficulty in perpetuating many cultivated plants, which is usually ascribed to cold, should be charged to drouth.

3. Moisture

Moisture is not only one of the most essential factors in the development of plants and floras, but it also forms the basis of the most satisfactory ecological classifications. Light serves the forester as a basis for his grouping of trees as tolerant and intolerant (of shade), but the requirements and adaptations of plants in relation to moisture are so many and so varied that light is most unsatisfactory for ecological grouping.

Plants vary greatly in their water requirements. All require a relatively large amount, and the continuity of this supply depends largely on the plants' surroundings, though in a measure this may be controlled or determined by the plant itself. Some plants must be wholly submersed; some have at least the roots submersed; many grow in places in which both soil and atmosphere are merely moist; while many are exposed to periodic drought resulting in insufficiency of moisture, both in the soil and the atmosphere.

The following grouping based on these differences in habitat is generally recognized:

I — Xerophytes, plants exposed to periodic drought, with us plants of the prairie, rocks and sand.

II — Mesophytes, plants requiring moist soil and air, with us chiefly those of the forest.

III — Hydrophytes, plants in part or wholly submersed, with us those of the swamps and waters.

That these plant groups persist in their various habitats is not a matter of accident, but results from structural and other modifications, or adaptations, by which each group is fitted for its particular environment.

The adaptations to moisture conditions are mostly quite obvious, although even here there are differences in behavior which cannot be ascribed wholly to structure. Thus, some of our rock lichens may become so dry (despite any protective structure) that they may be crumbled almost to dust, but will revive on the addition of moisture, though the exposed parts of most other plants would perish under like conditions. Some of the desert ferns of the southwest show the same power of recuperation.

The structural adaptations, however, are usually quite distinct, and they may serve a variety of purposes. They may consist of a reduction or expansion of the leaf surface of the plant, the former reducing and the latter increasing transpiration; they may consist of a protective covering of cutin, sclerenchyma, hairs, scales, etc., by which transpiration is checked, and an absence of which permits it to take place freely; storage tissue for water to be used in brief emergencies may be present; the root system may be greatly enlarged, thus enabling it to draw water for the plant from greater depths in dry periods, or serving for the storing of prepared food for quick growth in early or short growing seasons; and the tissues may be loose in texture, with large intercellular spaces which facilitate transpiration, or they may be compact and thus reduce it.

The adaptations which check loss of water from the plant are rarely all present in the same plant, excepting in extreme xerophytes, the leaves especially being usually well provided with them. To such an extent is this true, that it is usually possible to determine much concerning the habits of the plant from a microscopic section of the leaf, or sometimes of the stem or root.

These structural adaptations, together with the conditions under which they benefit the plant, as well as certain peculiarities of habits which enable the plant to meet the conditions under which it can grow, will be considered more fully in connection with the discussion of the three great habitat groups of plants represented respectively by the flora of the prairie, the forest, and of the swamps and waters.

It need not be assumed that the plants of these several groups have been modified in a purposeful way to meet their needs in the places in which we find them, though some are modified directly by their environment. They are found in their respective habitats simply because they possess adaptations which enable them to meet the extremes of their environment, and plants of the same ecological type finally occupy each habitat exclusively because all plants not adapted to it have been (and are being) eliminated.

An intelligent appreciation of the characteristics and distribution of the flora of the state is conditioned on an understanding of both the environmental factors which influence plants, and the adaptations which permit the latter to meet them successfully. Both should be kept in mind in connection with all floristic studies.

In considering the relation of plants to moisture it is necessary to take into account both soil and atmospheric moisture. The former is of great importance, but even professional botanists usually exaggerate its relative ecological value, for the moisture of the air is just as important to plants. The former must insure a continuous supply of food-laden water, while the latter should prevent excessive drainage of the plant by transpiration if the plant is to succeed. Both are equally essential.

It is therefore necessary that we consider not only precipitation, for the primal source of the water supply, but the persistence and continuity of this supply as determined by run-off, evaporation and transpiration.

a. The source of the water supply.

Rainfall. The total amount of rainfall is commonly regarded as the chief factor in determining the distribution of our floras. In Iowa, however, the annual rainfall, even in the driest years, is sufficient for the successful maintence of our floras if it were favorably distributed. The average for the state is a trifle over 30 inches for the year, but it fluctuates greatly, the extremes which have been noted being 15.74 inches at Rock Rapids, Lyon County, in 1894 and 74.50 inches at Muscatine in 1851. While such extremes are rare, the extent of these fluctuations is well illustrated by the following table, prepared from the reports of the Iowa Crop and Weather Service (80) for 1902.

In this table the first column contains the names of the stations, with the counties in which they are located; column II gives the number of years covered by the report up to and including the year 1902, excepting that of Muscatine, which ends with 1890, and that of Hopkinton, which ends with 1898. Column III gives the average annual rainfall for the number of years indicated in the preceding column; column IV and VI contain respectively the maximum and minimum annual rainfall at each station named, followed in columns V and VII by the respective years in which they occurred.

Station	II years	III av.	IV max.	V year	VI min.	VII year
Cresco, Howard Co.	32	30.43	43.86	1881	22.52	1877
McGregor, Clayton Co.	27	33.32	48.73	1881	20.77	1895
Algona, Kossuth Co.	30	29.51	40.01	1873	16.56	1886
Sac City, Sac Co.	26	30.21	46.55	1881	21.68	1886
Onawa, Monona Co.	24	32.07	49.93	1881	16.01	1894
Logan, Harrison Co.	36	33.80	56.60	1881	16.63	1894
Ames, Story Co.	27	31.29	51.90	1881	20.61	1887
Des Moines, Polk Co.	24	32.52	56.81	1881	19.77	1901
Independence, Buchanan Co.	36	33.84	51.82	1876	19.61	1901

Monticello, Jones Co.	48	35.12	52.30	1876	18.57	1895
Hopkinton, Delaware Co.	64	29.67	52.00	1878	19.79	1886
Clinton, Clinton Co.	30	35.55	52.85	1868	22.07	1901
Davenport, Scott Co.	31	32.92	46.82	1876	17.33	1901
Muscatine, Muscatine Co.	45	39.22	74.50	1851	23.66	1854
Iowa City, Johnson Co.	44	36.95	50.60	1869	24.48	1886
Keokuk, Lee Co.	31	35.35	52.48	1898	22.51	1879
Fort Madison, Lee Co.	53	37.79	54.14	1849	22.32	1894

These stations are well distributed over the state. It will be observed that while the average rainfall to 1902 at these stations varied from 29.51 inches to 39.22 inches, the maxima ranged from 40.01 inches to 74.50 inches, and the minima from 16.01 inches to 24.48 inches.

The year 1881 was exceptionally wet, and the year 1894 exceptionally dry in Iowa, yet during these two years there was much diversity in rainfall, as is shown by the following table giving the total annual rainfall at widely separated stations.

For 1881 (wet year)

Des Moines	56.81 in.	Osage	39.90 in.
Logan	56.50 in.	Davenport	37.28 in.
Dubuque	55.15 in.	Ft. Madison	38.34 in.

For 1894 (dry year)

Onawa	16.01 in.	Iowa City	27.22 in.
Logan	16.63 in.	Keosauqua	29.04 in.

It will be noted that in the wet year 1881 three widely separated stations had almost the same high rainfall, while the three intermediate stations in the second column show a rainfall but a few inches above the average.

In the dry year 1894 the two western stations had extremely low precipitation; while the record for the two eastern stations was but little below the average.

The great variation in rainfall in Iowa is further emphasized in Table B* following, which brings the record up to 1930 for several widely scattered stations, four of them being the same as in Table A. The record for Logan begins with 1910, following that in Table A, while the records for Keokuk, Onawa and Algona include those given in Table A for these stations but extend them to 1930.

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* Compiled from the "Climatic Summary of the United States" published by the U. S. Weather Bureau (147).

B. Rainfall table, averages, maxima and minima to 1930.

I Station	II years	III av.	IV max.	V year	VI min.	VII year
*Keokuk, Lee Co.	60	33.67	51.65	1876	21.82	1910
Afton, Union Co.	60	33.81	50.61	1915	18.50	1894
Clarinda, Page Co.	59	32.43	51.73	1902	18.18	1894
Glenwood, Mills Co.	56	30.35	45.95	1878	19.90	1894
*Logan, Harrison Co.	21	27.51	38.27	1915	18.69	1930
*Onawa, Monona Co.	56	31.35	50.53	1903	21.32	1930
Sioux City, Woodbury Co.	72	26.57	56.37	1881	15.07	1864
Le Mars, Plymouth Co.	55	27.72	41.70	1884	16.49	1879
Rock Rapids, Lyon Co.	38	25.60	36.63	1905	11.53	1910
Fort Dodge, Webster Co.	78	31.91	44.03	1900	23.25	1910
*Algona, Kossuth Co.	70	29.40	42.90	1875	15.73	1910

It will be observed that the average annual rainfall at the four stations marked by asterisks is diminished by the extension of the record from 1903 to 1930, though the minimum decrease, that at Algona, amounts to but 0.11 of an inch.

The flora of any given region is not wholly determined by the character of any one season, but is the result of eliminations and additions which have been going on for many seasons. It must also be remembered that the absence of certain plants is not brought about by averages and totals of rainfall, etc., but by extremes which may be fatal. This is particularly true of moisture, the absence of which so often destroys plants. The damage may be done by one season, but more frequently a single season results in merely checking certain species, and it is only by frequent repetitions that complete elimination is accomplished. It is therefore important that we note the frequency of occurrence of exceedingly dry seasons in the state.

The following lists give the number of years during which the precipitation was less than 20 inches at the stations named. The total number of years covered by the record is also given.

None below 20 in.		1 or 2 yrs. below 20 in.		
Keokuk, Lee Co.	60 yrs.	Afton, Union Co.	60 yrs.	1 yr.
Keosauqua, Van Buren Co.	55 yrs.	Clarinda, Page Co.	59 yrs.	1 yr.
Knoxville, Marion Co.	55 yrs.	Glenwood, Mills Co.	56 yrs.	1 yr.
Mt. Ayr, Ringgold Co.	55 yrs.	Council Bluffs, Pottawattamie Co.	44 yrs.	1 yr.
Thurman, Fremont Co.	56 yrs.	Oskaloosa, Mahaska Co.	55 yrs.	2 yrs.
Onawa, Monona Co.	56 yrs.	Spirit Lake, Dickinson Co.	27 yrs.	2 yrs.
Ft. Dodge, Webster Co.	55 yrs.	Ames, Story Co.	55 yrs.	2 yrs.
		Boone, Boone Co.	60 yrs.	2 yrs.

*Compare with Table A.

The stations in the second list which have had but one year with less than 20 inches of rainfall are all in the southern part of the state. Those with two such seasons are central or northern, with the exception of Oskaloosa, which is in the southeastern part.

The stations which have had from three to eight years with less than 20 inches are in the following list:

Des Moines, Polk Co.	54 yrs.	3 yrs.	Algona, Kossuth Co.	70 yrs.	7 yrs.
Estherville, Emmet Co.	38 yrs.	4 yrs.	Sioux City, Woodbury Co.	72 yrs.	8 yrs.
Logan, Harrison Co.	65 yrs.	4 yrs.	Sibley, Osceola Co.	52 yrs.	6 yrs.
Le Mars, Plymouth Co.	55 yrs.	3 yrs.	Rock Rapids, Lyon Co.	38 yrs.	5 yrs.

The record of each of these stations also shows a number of dry years during which the total rainfall was between 20 and 26 inches. These range from 5 for Le Mars and Des Moines to 28 for Sioux City.

It will be noted that, with the exception of Des Moines, these stations are all in the northwestern part of the state. That Des Moines and Le Mars have had the same number of dry years in nearly the same length of time does not indicate that they are equally dry, for the average annual rainfall for Des Moines for that period was 31.90 inches, while that for Le Mars was 27.72. The difference in evaporation between the two stations, with its marked effect on plant life, will be considered later.

The increase in the number of dry years towards the northwest is closely linked with the diminution in rainfall in the same direction. The following record of annual rainfall to 1930 for stations selected from the U. S. Weather Bureau reports is worthy of note in this connection. The first line of stations extends across the state from southeast to northwest. In each case the name of the station is followed by the number of years covered by the record, and this in turn is followed by the average annual rainfall in inches.

Keosauqua, Van Buren Co.,	55 yrs.	35.73 in.
Ottumwa, Wapello Co.	54 yrs.	33.16 in.
Des Moines, Polk Co.	54 yrs.	31.90 in.
Ft. Dodge, Webster Co.	55 yrs.	31.91 in.
Algona, Kossuth Co.	70 yrs.	29.40 in.
Sibley, Osceola Co.	52 yrs.	27.26 in.

A second line of stations across the southern part of the state shows the following remarkably uniform records:

Keokuk, Lee Co.	60 yrs.	33.67 in.
Afton, Union Co.	60 yrs.	33.81 in.

Clarinda, Page Co.	59 yrs.	32.43 in.
Thurman, Fremont Co.	56 yrs.	34.52 in.

A similar line of stations across the west end of the state is also of interest. It extends from the southwest to the northwest corner of the state.

Thurman, Fremont Co.	56 yrs.	34.52 in.
Glenwood, Mills Co.	56 yrs.	30.35 in.
Onawa, Monona Co.	56 yrs.	31.35 in.
Sioux City, Woodbury Co.	72 yrs.	26.57 in.
Le Mars, Plymouth Co.	55 yrs.	27.72 in.
Rock Rapids, Lyon Co.	38 yrs.	25.60 in.

Here there is a distinct and rather uniform diminution in total rainfall as we go northward. Some allowance may be necessary because of the difference in the length of the periods covered by the record, but this cannot materially modify the general result.

That part of the northwest corner of the state which is cut off by a line drawn from Sioux City to Emmet County shows the lowest record of rainfall for the state. The record for four stations within this area, namely, Sioux City, Le Mars, Sibley and Rock Rapids, has been given in preceding tables. At all these stations the average total annual rainfall falls below 28 inches. The following are additional records:

Washta, Cherokee Co.	34 yrs.	28.73 in.
Sheldon, O'Brien Co.	36 yrs.	28.43 in.
Spirit Lake, Dickinson Co.	27 yrs.	27.56 in.
Estherville, Emmet Co.	38 yrs.	27.74 in.
Sioux Center, Sioux Co.	32 yrs.	27.72 in.

These additional records do not, however, materially change the result.

The great variations in total annual rainfall in different parts of the state are further emphasized when we consider the monthly differences during the open months from April to September, inclusive. The records for these months in the years 1893-1896, the former quite dry and the latter quite wet, are given in the following tables, preceded in each case by the average, the maximum, and the minimum for the state.

In 1893, for 46 stations in Iowa.

Maximum rainfall 33.27 in. at Clarinda
Minimum rainfall 19.19 in. at Algona
Average 27.31 in.

But during the open months of this year the maxima and minima varied in Iowa between the following extremes in different parts of the state:

April —	Maximum 7.01 at Eagle Grove, Wright Co.
	Minimum 1.24 at Villisca, Montgomery Co.
May —	Maximum 5.82 at Carroll, Carroll Co.
	Minimum 1.37 at Le Claire, Scott Co.
June —	Maximum 7.56 at Atlantic, Cass Co.
	Minimum 1.36 at Rock Rapids, Lyon Co.
July —	Maximum 8.84 at Clarinda, Page Co.
	Minimum 1.49 at Oskaloosa, Mahaska Co.
August —	Maximum 6.32 at Villisca, Montgomery Co.
	Minimum 0.40 at Algona, Kossuth Co.
September —	Maximum 5.49 at Seymour, Wayne Co.
	Minimum 0.74 at Rock Rapids, Lyon Co.

In 1896, for 75 stations in Iowa.

Maximum rainfall	51.60 in. at Waterloo, Black Hawk Co.
Minimum rainfall	24.07 in. at Cresco, Howard Co.
Average	37.45 in.

During the corresponding months the rainfall varied between the following extremes:

May —	Maximum 11.79 in. at Mt. Ayr, Ringgold Co.
	Minimum 3.40 in. at Mt. Vernon, Linn Co.
June —	Maximum 7.89 in. at Atlantic, Cass Co.
	Minimum 0.81 in. at Vinton, Benton Co.
July —	Maximum 11.93 in. at Greenfield, Adair Co.
	Minimum 1.61 in. at Rock Rapids, Lyon Co.
August —	Maximum 9.18 in. at Knoxville, Marion Co.
	Minimum 0.86 in. at Sioux City, Woodbury Co.
September —	Maximum 9.04 in. at Keosauqua, Van Buren Co.
	Minimum 1.82 in. at Iowa City, Johnson Co.

These differences between different localities are, however, by no means constant, for any one locality will show almost as much variation from year to year and month to month as is displayed by the state at large. The annual variation was brought out in the Tables A and B of Annual Averages, Maxima and Minima, and the monthly variation is quite as striking. Thus, in the 44 years from 1866 to 1909, inclusive, the rainfall at Logan, Harrison Co., during the critical month of July, ranged from 0.41 of an inch in 1894 to 13.0 in 1878, and many similar cases could be pointed out for each of the months of the open season.

The extreme irregularity in the periodic distribution of precipitation is shown at a glance in any series of the precipitation maps published by our State Weather Bureau.

Thus during the months of April to August, in 1924, the relative amount of rainfall shifted from month to month and place to place as shown in the following reports:

For April — Several areas of low precipitation (less than 1 inch for the month) were distributed over the state. The largest formed a belt across the western part of the state. A smaller area occupied all of Benton and adjacent parts of Buchanan, Black Hawk and Iowa Counties; another covered parts of Dallas, Polk and Madison Counties; and a still smaller area was located in Butler County.

The area of high precipitation (more than 4 inches for the month) was limited to parts of Franklin, Wright and Hardin Counties.

For May — There were three widely separated areas of low precipitation (less than 1 inch) distributed as follows:

Parts of Sioux and Plymouth Counties; parts of Audubon and Guthrie Counties; and parts of Jones, Cedar, Scott and Clinton Counties.

There were four areas of high precipitation (more than 2 inches), of which the largest occupied nearly all of the northeastern quarter of the state; another covered parts of Cherokee, Crawford, Sac, Carroll and Calhoun Counties; another covered parts of Jefferson, Van Buren, and Davis Counties; and a small area extended across the western end of Pottawattamie County and the northwest corner of Mills County.

For June — One large area of low precipitation (less than 1 inch) occupied nearly all of the northern third of the state.

There were four areas of high precipitation (exceeding 12 inches): one occupying Cass and adjacent parts of Adams, Montgomery, Pottawattamie, Shelby, Audubon and Adair Counties; one in parts of Marshall, Tama, Poweshiek and Jasper Counties; one in parts of Cedar and Muscatine Counties; and one in parts of Des Moines and Louisa Counties.

For July — There were three areas of low precipitation (less than one inch): one in parts of Lyon, Sioux and O'Brien Counties; another in Dickinson and adjoining parts of Emmet, Palo Alto, Clay and Osceola Counties; and a smaller area in Polk County.

There were several areas of high precipitation (more than 7 inches), all in the eastern third of the state. The largest extended from Poweshiek to Des Moines County; one covered a part of Van

Buren County; one occupied nearly all of Black Hawk County, and small adjacent parts of Butler, Grundy, Benton and Buchanan Counties; and one covered most of Jones County and adjacent parts of Delaware, Dubuque, Jackson, Clinton and Cedar Counties.

For August — Several widely separated areas showed less than 1 inch for the month. The largest occupied the southwest corner of the state, extending from Pottawattamie to Wayne County; one covered most of Henry County and small adjacent parts of Washington, Louisa and Des Moines Counties; another extended from Polk to Marshall County; and another covered most of Lyon County and parts of Osceola and Sioux Counties.

There were three areas of high precipitation (more than 9 inches) : one occupied Clinton and parts of Cedar and Jones Counties; another covered parts of Hardin, Franklin, Butler and Grundy Counties; and a third extended from Winneshiek to Floyd County.

It will be observed that the areas of low and high precipitation do not at all coincide for the several months of one year, and a similar variation would be found in other years.

These constant shiftings of the centers of low precipitation exert a direct influence on our floras, for they bring about periodic droughts in every part of the state, thus eliminating many plants, especially of the mesophytic forest type, which do not receive special local protection.

Too great emphasis cannot be placed on the fact that it is not the total annual, or even monthly precipitation which determines the success or failure of plants, but that the distribution within the month, and particularly within the months of the open season from April to September, is usually much more important.

This is well illustrated by a further analysis of the local record for Logan, Harrison County.

In 1887 the total rainfall was 23.6 inches, and 7 inches below the average for the state, but 17 inches of this was precipitated rather evenly between the months from April to September, making a rather favorable season.

In 1889 the total was 29.87 inches, — a little below the state average, but 22.57 inches fell in the four summer months, May to August, making this a rather wet season.

In 1893 the total was 43.82 inches, of which 29.65 fell during the four months, from April to July, and this was evenly distributed, making the season quite favorable to plant growth.

In 1896 the total was 43.82 inches, of which 29.65 fell during the four months, from April to July, and this was so evenly distributed that all these months were quite wet, the rainfall ranging from 6.70 inches to 7.93 inches per month.

In 1907 the total was again very low, being 22.73 inches, but 15.28 inches fell in the period from April to August, and this also was quite evenly distributed with June and July somewhat in the lead, again making the season much better than the total would indicate.

Another excellent illustration of the irregularity in the distribution of precipitation in the state, both geographic and periodic, is furnished by the two following monthly records in total number of inches for three summer months in 1918.

Station	*June*	*July*	*August*	*Total for 3 mo.*
Lake Park, Dickinson Co.	3.02	5.44	6.70	15.16
Winterset, Madison Co.	2.60	2.00	2.63	7.23

This record also illustrates the importance of the distribution of precipitation within the month. Apparently the three months in both localities had the rainfall fairly evenly distributed, though the total at Lake Park was more than twice as much as at Winterset. The difference between the seasons at the two localities was much greater, however, than is indicated by the total monthly record.

During this season the morainic hills near Lake Park remained green throughout the summer, though during the average season they are dry and brown by the latter half of July. The vicinity of Winterset, on the other hand, suffered from destructive drought, especially in the southern half of the county. The difference was not due wholly to the difference in total rainfall, but in large part to its distribution, particularly in the months of July and August. May was quite favorable in both localities, the total rainfall in each slightly exceeding 6 inches, with a fairly even and equal distribution in both. June was less favorable with a total of 3.02 inches at Lake Park, and 2.60 inches at Winterset, the greater part of which, in both cases, was precipitated during the first six days of the month.

In July and August, however, there was not only an increased difference in the total, but also in distribution. In July there were seven rainy days at Lake Park, with the precipitation favorably distributed, occurring on the 4th, 7th, 14th, 24th, 26th and 28th of the month, with a total of 5.44 inches. At Winterset there were eight rainy days, the 4th, 6th, 15th, 17th, 23rd and 26th, for a total of 2.60 inches. This would also appear to be an even distribution, but unfortunately 1.23 inches of this fell on the 4th, and the remainder was distributed among the remaining dates in small amounts of 0.01 to 0.32 of an inch. August was similar, with seven rainy days at Lake Park with a total of 6.70 inches, favorably distributed between the 7th, 8th, 13th, 15th, 20th, 21st and 30th; while the total of 2.63 inches at Winterset was distributed between the 11th, 13th, 14th, 15th, 18th, 23rd, 28th and 30th, but with 1.17 inches falling on the 18th, with fractions of 0.05 to 0.55 of an inch for the remaining days.

The result of these differences was an even, favorable season in Dickinson County and a destructive drought in Madison County.

The deceptive character of totals is still further illustrated by a part of the record for Dickinson County, at and near Lake Park.

In 1912 the total rainfall was 21.08 inches, much below the average, for the state, but 16.11 inches of this were precipitated during the open months, April to September, making the season much less severe than the total would indicate.

In 1913 the total was 26.42 inches, still quite low, but 24.00 inches of this fell during the six months of the open season, a liberal amount.

In 1922 the total was very low, being but 19.08 inches, but of this 11.37 inches fell in the open season, making it much less destructive than the total suggests.

In 1924 the total was but 21.17 inches, but 16.55 inches was precipitated in the open season, — again a fairly generous supply.

In 1928 the total was somewhat higher, being 28.56 inches, of which 21.84 inches was delivered within the six months of the open season. As this was quite well distributed, with a minimum of 8.59 inches in August and a maximum of 11.16 inches in July, the season was very favorable and the native vegetation was in a flourishing condition.

An additional fact still further emphasizes the unreliability of total amounts of precipitation. At times the apparently favorable totals include larger amounts precipitated during short periods, as in 1890 at Logan, when 14.09 inches (nearly half the average for the state) fell in June, or in 1900 at Primghar, in O'Brien County, when 13 inches were precipitated in the 24 hours including parts of July 14 and 15. In the case of such great and sudden precipitation the apparently favorable total may be brought up, but the resulting floods do much more harm than good. The heavy run-off injures the vegetation on the slopes by washing, floods the bottom lands and after doing much damage, runs away from the territory, leaving no beneficial results behind.

Another marked effect is produced on the flora by a succession of wet or dry seasons. Thus at Logan the years 1890-1892 were quite favorable, the total precipitation ranging from 34.95 to 35.39 inches, while the years 1893-1895 were very dry, the precipitation having been reduced to 16.63 to 26.12 inches per year. During the wetter continued periods many swamp plants, especially perennials, advance to higher ground, usually merely in small numbers, while during the more protracted dry periods many prairie and sand plants, especially perennials, will encroach on the drying swamps.

A striking illustration of the first type of advance was observed on the rather low morainic ridges southwest of Miller's Bay, West Okoboji Lake. These ridges rise about 30 to 40 feet above a low draw which produces a typical swamp flora, and they are normally covered with a dry prairie flora, portions of it of the prairie-steppe type. In 1918, however, a few specimens of *Haberaria leucophaea*, *Cicuta maculata*, *Steironema quadriflorum* and *Lathyrus palustris* (all also occurring on the low ground) were found on the area quite near the top, while *Lilium canadense* [*L. Michiganense* Farw.] and *Lycopus americanus* were found on the normally dry slopes. All excepting the *Lathyrus* were in flower. The open seasons from May to August during the years 1915 to 1918, inclusive, were quite favorable, though the total rainfall during the first two years was rather low. The rainfall was well distributed in the four months of this period during each of the years noted, and totalled (for these months) the following amounts for each year:

1915 — 16.52 in.	1917 — 15.92 in.
1916 — 13.43 in.	1918 — 21.86 in.

During this continuous series of favorable seasons the swamp perennials noted above were able to establish themselves temporarily in this unusual (for them) habitat, but they disappeared again during the drier seasons following 1919.

Illustrations of the second type of advance may be found at the border of any swamp during the drier periods.

Sometimes the wet and dry seasons alternate, as at Logan during the following years:

1872, 32.10 inches	1875, 42.00 inches
1873, 43.20 inches	1876, 28.20 inches
1874, 28.40 inches	1877, 45.10 inches

During such alternating periods there is little advance of either type of flora, excepting on the part of the comparatively few species of annuals. Alternating periods, however, whether long or short, tend to destroy the stability of both floral types, and frequently temporarily shift the line of demarkation between them.

Since every plant requires a rather limited but continuous supply of water, it is evident that the oft-recurring extremes which bring both drought and floods, eliminate many plants which are not equipped to resist the frequently changing conditions.

Precipitation during the growing months, from April to September, exerts a direct and decisive influence on vegetation, but precipitation during the remaining months may also become an influential ecological factor.

It may result in direct injury to woody plants by ice and sleet, or by extreme drought during the resting period; it may make possible the storing of water in the form of snow or soil-water for use during the early part of the growing season; and an abundant precipitation of snow will protect seeds and underground perennials by preventing deep freezing and excessive drying of the soil.

b. The disposal of precipitated water.

The amount of precipitation, however, is not alone the determining agency in relation to our floras, no matter how favorable in amount, or how well distributed. Several factors may aid in either the conservation or rapid dissipation of moisture, and they frequently determine the success or failure of individual plants, or even floras. The most common of these factors are, the rate and amount of run-off; absorption by the soil; rate of evaporation; the floral covering in its relation to the temporary retention of surface films of water above the soil to facilitate evaporation, to absorption of soil-water by the plants, and to transpiration.

The run-off. — The rate and amount of run-off is determined by the rate and amount of precipitation (or thawing), the slope of the surface, the amount and nature of the plant covering, and to some extent by the porosity of the soil.

The amount of the run-off must be an extremely variable quantity from the very nature of the differences in precipitation and in surface characteristics, but unfortunately we have no exact data in Iowa on this point. Such information as is available for other parts of our country, however, is of interest, though it is by no means sufficient to meet all of our conditions.

Thus Rodhouse's* observations in Missouri, covering a period of seven years, showed the run-off to be 30.2% of the total rainfall; Professor Tarbe's* report on some of the streams of Illinois indicates a run-off from 21.5% to 37.9%; Lynde's* observations in North Carolina over a period of five years showed a run-off of 41.8%; Norton* found the Ohio River carrying away 30% of the rainfall, while the Missouri carries but 15%; and in drier regions the run-off is said to be even less than 5%.

It is evident that Illinois and Missouri present conditions most nearly like those in Iowa, and it is probable that 30% represents our average, though even in our state the variation must be great. This percentage, however, like all averages, may be very unsatisfactory for specific cases, for the run-off must vary for the same locality, being greatly augmented by heavy increases in both volume and rapidity of precipitation.

The rate of run-off is also determined in large part by topography, the steeper slopes discharging the water more rapidly. This applies not only to the topography of the general surface which is drained, but also to the gradient of the streams which finally carry the water away from the area of precipitation.

The plant cover is also of distinct value in controlling run-off. Much of the rain is dashed to spray against the leaves and stems, and this spray is more readily absorbed by the soil, or remains suspended in the air, in either case diminishing the volume of running water. A film of water also remains on the plant surfaces, soon to be evaporated without reaching the soil.

It has been estimated** that the water (rain or snow) thus evaporated from plant surfaces may be as much as one-third of the total precipitation. This, of course, does not include the amount discharged by transpiration (Shepard 131).

* Citation not located. — Ed.

** Daly and Miller — 1923. Citation not located. — ED.

Plants, moreover, diminish the rate of run-off by mechanically checking surface currents, especially on steeper slopes.

Experiments at the Missouri Agricultural Experiment Station showed that nearly one-half the rainfall ran directly into an adjacent stream from bare uncultivated ground, while only a little more than one-tenth ran off from a similar surface covered with blue-grass sod.

Shepard (131, p. 10) also reports that there was a remarkable difference in the run-off from denuded and wooded canyons at Pueblo, Colorado, during local cloudbursts. The floods which came from the denuded canyons reached their crest quickly in about six hours, while those which came from the forested canyons were reported as reaching their crest in 18 to 48 hours, and also doing less damage.

The porosity of the soil may also have some effect. Porous soils absorb the precipitated water more quickly to their capacity, thus somewhat diminishing the run-off. It is estimated (131, p. 6) that 20 to 50 percent of light or moderate rains is ordinarily absorbed by the soil. The amount and rate of absorption are also influenced by the plant covering which produces a soft, light leaf-mould or humus layer which absorbs water readily. Moreover, plants are constantly absorbing water from the soil by their roots, thus making room for more. The surplus water is then thrown off by transpiration and does not return to the soil except by being condensed into dew or rain. Since the average plant throws off several times its own weight of water during the growing season, it is evident that the aggregate of the water thus removed from the soil is very great.

Evaporation: — The rate of evaporation is also important in determining the continuity of the water supply. This is influenced by topography, which may either expose the plant-covered surfaces to drying winds and the sun, thus increasing both evaporation and transpiration, or it may shelter and protect them from excessive loss of water, thus conserving the water-supply.

The rate of evaporation is also determined in large part by the plant covering which protects the surface from excessive loss of water.

Evaporation as an ecological factor will be taken up more fully in connection with the discussion of prairie problems.

Our fluctuating climate is evidently due to the position of the state in the great central continental trough, which is open both to the north and the south, and the distribution of moisture is especially influenced by this position. The mountain barriers, to the east and west, condense the moisture from the great oceans on the outer sides, greatly increasing their rainfall, but cutting off the supply which otherwise would come to the inland areas.

The great central basin, therefore, must depend for its initial supply of moisture chiefly on the Gulf of Mexico, no matter what changes may result from the shiftings of barometric low pressure centers.

The Great Lakes evidently form a minor source of moisture for Iowa, and their influence is felt chiefly in the eastern part of the state, where it is often conspicuous. The drizzly rains which are brought to us from the east, often continuing two or three days in succession, evidently come largely from this source.

It may appear that relatively too much space has been here given to the subject of moisture, but in view of the widely prevalent use of total and average rainfall in estimating the possibilities of plant growth, it seemed necessary to point out that, at least within our territory, its seasonal and monthly distribution forms a far better index.

It will also be shown later that we must consider not only the amount received and the distribution thereof, but that the subsequent disposal of the amount precipitated before it is used by the plant is often a factor of great importance.

Water also serves to carry pollen for the pollination of numerous aquatic plants, and the flowers are well adapted to this end by usually having the naked stigmas at the surface where the floating pollen will readily come in contact with them. Our northern lakes and ponds are often covered in summer with distinct films of the whitish pollen of *Vallisneria*, *Potomogeton*, *Elodea*, and other submerged or floating aquatic plants.

Water also aids in seed-dispersal, if the seeds or fruits are light enough to float, or if they are too heavy, rounded and smooth so that they may be rolled along the bottom by currents. During heavy rains and floods many seeds and fruits which are adapted to transportation by other agencies, may also be carried by water.

4. Winds

Like all other ecological factors winds are extremely variable. They may vary in velocity from zero to that of a destructive tornado, and they may come from any quarter of the compass, though their prevailing direction may vary with the seasons.

If not too strong, winds may stimulate green plants to greater activity by gently swaying them, thus exposing all parts of the foliage to light more successfully; but, if strong, they may whip them into a wilted condition, or even mutilate or destroy them. Winds, especially tornadoes or strong winds following sleet-storms, may do much mechanical injury to plants, especially trees, but their chief effect on the distribution of our floras is produced by seed-dispersal and by their stimulation of evaporation and transpiration. They may also serve as carriers of moisture if passing over moist areas or bodies of water. Whether they are drying winds or bring additional moisture depends on their temperature and direction. If they come from the west, southwest, or even south they are likely to be dry; if from the southeast or east they are quite moist as a rule. Changes in direction may be caused by topography, by shiftings of the centers of low barometric pressure, or by cyclonic movements of wide radius.

In any event the direction is of much importance because it usually determines whether the wind is dry and dessicating, or moisture-laden.

In this connection the following table showing the prevailing direction of winds at a few Iowa stations will be of interest. The table is compiled from the U. S. Weather Bureau reports and includes the record for the four summer months, June to September, with the number of years covered by it.

Direction of prevailing winds.

	Years	June	July	Aug.	Sept.
Keokuk, Lee Co.	59	S.	S.	S.	S.
Oskaloosa, Mahaska Co.	36	S.W.	S.W.	S.W.	S. E.
Des Moines, Polk Co.	52	S.W.	S.W.	S.W.	S.W.
Mt. Ayr, Ringgold Co.	37	S.	S.W.	S.	S.
Clarinda, Page Co.	41	S.	S.	S.	S.
Audubon, Audubon Co.	40	S.	S.W.	S.W.	S.W.
Thurman, Fremont Co.	33	S.W.	S.W.	S. E.	N.W.
Logan, Harrison Co.	41	S.W.	S.W.	S.W.	S.W.
Sioux City, Woodbury Co.	41	S.	S.	S.	N.W.
Le Mars, Plymouth Co.	34	S.	S.	S. E.	S.
Sibley, Osceola Co.	25	S.	S.	S. E.	S.
Inwood, Lyon Co.	27	S.	S.	S.	S.

It will be noted that 42 of these local monthly records show the prevailing summer winds to be from the south and southwest, while but 6 are from the southeast and northwest. It follows, then, that plants growing in places exposed to the south and southwest will be affected more directly by the prevailing winds, and will be exposed to greater evaporation and transpiration. This will be shown more clearly in connection with the discussion of the prairies.

The direction of the prevailing winds is often determined by topography, for they are likely to follow river valleys, especially if rather straight, and they are frequently deflected by elevations.

The velocity of the wind is also an important ecological factor. Like all other factors of this kind it is extremely variable, ranging from 0 to 60 or more miles per hour. The usual daily currents, however, seldom exceed 15 miles per hour.

This variation in velocity produces a marked effect on both evaporation and transpiration, for while winds are not the cause of either, they facilitate both by the removal of the films of vapor from the surface of the soil and the plants. These variations in velocity may be due to cyclonic storms, to shiftings of the centers of low barometric pressure, or to changes in temperature. They may also be produced locally by mechanical obstructions, such as topography and vegetation.

There is also a well-known marked difference in wind velocity at different altitudes above the ground surface. The air-currents are retarded by contact with the surface, and their velocity gradually increases upward.

The following table will serve to illustrate this. It is compiled from Giddings' report (66, p. 312) on observations made under Shimek's direction in connection with an ecological study of *Silphium laciniatum*, the compass plant of the prairies. The altitudes were taken at the elevation of the lowest, intermediate and uppermost leaves of a plant of this species, and are, respectively, 10 cm. (4 in.), 114 cm. (3.7 ft.) and 237 cm. (7.7 ft.).

The hour of the day at which the readings were taken is given in the first column, and the velocities in miles per hour for the altitude appear in the succeeding columns.

Table of wind velocities at different altitudes.

Hour	*Alt. 10cm.*	*Alt. 114cm.*	*Alt. 237cm.*
7.30 A.M.	1.74	4.73	7.48
9.30 A.M.	1.66	6.04	8.00

11.30 A.M.	1.46	7.47	9.68
1.30 P.M.	2.91	11.27	17.42
3.30 P.M.	3.29	9.70	14.29
5.30 P.M.	2.09	6.85	9.91

It will be observed that there was the usual rise in wind velocity to the middle of the afternoon followed by a lesser drop. There was also a consistent increase in velocity from the lowest to the highest level for each hour of observation.

The effect of these increases in wind velocity is shown in the corresponding rise in evaporation as measured in cubic inches by Piche evaporimeters suspended at the several altitudes indicated above.* The evaporation for the day at the lowest altitude was .445 cu. in., for the intermediate altitude .600 cu. in., and for the uppermost altitude .760 cu. in. — a uniform increase with altitude not only for the totals, but for each hour, as shown in the complete table cited.

It is evident from the foregoing figures (and many others like them) that wind velocity influences the rate of evaporation, and that both are distinctly related to the altitude above the surface. It is therefore evident that plants of different heights are exposed to different conditions, those which are taller being in greater danger from excessive loss of water. In extreme cases this might lead to the elimination of the taller plants, thus modifying the local flora.

Wind also assists plants in pollination and seed dispersal.

Most wind-pollinated flowers appear in two groups; the amentaceous trees and shrubs in early spring while the plants are still leafless, and the grasses, with their exposed flower-clusters, in midsummer. It is also significant that these are usually periods of strong, persistent winds. Our few evergreen conifers are also wind-pollinated in early spring, but their flowers are mostly terminal on the branchlets and the foliage does not interfere with the free transfer of pollen.

Wind is one of the very effective agencies which assist in the distribution of seeds and fruits, many of which are well adapted to transportation in this manner because they develop wings, or hairs, for floating in the air; or are otherwise buoyant because they are

* In Giddings' paper (66), there is a confusing error in Table 2 on p. 312. For the hour 7:30 A. M. at each altitude the reading should be 0, and all the amounts of evaporation should be moved down one line, leaving out the larger numbers which appear in each case opposite the 5:30 P. M. hour. The latter are the totals for the days at each altitude.

inflated or minute; or may be blown over the surface of snow in the winter.

Of all agencies concerned with seed-dispersal wind is the most widespread because of its changing direction and velocity, because it acts over all surfaces, and because so many seeds and fruits are adapted to transportation by it. It plays a large part in the accident of distribution which so often determines modifications and relative adjustments of our local floras, especially on the prairies.

B. Biotic or Living Factors.

It is difficult to measure or estimate the value of biotic factors because of their complicated inter-relationships. In the endless circle of contacts, organisms not only encounter enemies as well as friends, but the friend of an enemy and the enemy of a friend may be equally destructive, while the enemy of an enemy may be quite as helpful as the friend of a friend.

In the plant world, as indeed in the living world at large, there is a constant, and usually many-sided contest, not only between different species, but between individuals of the same species.

Under the influence of light, plants reach upward and often overtop their neighbors, cut off their share of the light, and not infrequently destroy them, and this is just as likely to occur with individuals of the same species as with different species. Some years ago the writer followed a thicket of soft maple (*Acer saccharinum*) for seven years from the first year seedling stage. During the first season the seedlings practically covered an area of several square rods, to the almost complete exclusion of other plants. During this first season the average distance between the plants was less than 6 inches, but as the growth continued the stronger plants crowded out their weaker companions and at the end of the seventh season the average distance between them was nearer six feet, and the thinning out would have continued still farther but for the destruction of the thicket by a road improvement. Similar contests are also going on among individuals of different species.

This may seem a very destructive process, but in the end the species involved in the struggle, whether one or several, are distinctly benefited because only their strongest individuals remain to perpetuate them. Such elimination is destructive to the weaker individuals, but beneficial to the species in the end. Many other instances of partial good and partial evil might be cited, for it is just as difficult to place the various biotic factors into groups which are definitely either good or bad, as it was to classify climatic factors on a like basis. It is convenient, however, to consider the good and evil results separately, even though in many cases the same individual or species may bring them about. They are presented here briefly under the respective heads of the three principal factors, namely, plants, animals, and man.

Plants. — Every plant comes in more or less direct contact with other plants which may affect it favorably or unfavorably. Among the beneficial results the following may be enumerated: protection against excessive heat, light, or wind action; the addition of moisture to the atmosphere by transpiration, thus making possible the existence of plants which cannot resist drouth; conserving the soil in place, to the advantage of weaker plants with lesser holding power; formation of leaf-mould or humus, either by supplying the organic material, such as leaves, sticks etc., or by causing its decomposition, as by fungi and bacteria; the loosening of soil by the roots of other plants, and the supplying of humus at lower soil levels by their decay; and supplying nitrates and other useful products and conditions as by the nitrifying bacteria of root-tubercles, other soil bacteria, fungi and algae.

The most obvious evil results of these contacts are, the cutting off of necessary light by larger plants; and the destruction of plants, or parts of plants by parasites, such as bacteria, fungi and a few flowering plants.

In most cases it is difficult to determine how far these plant agencies affect the distribution of our floras, though there are some obvious cases, such as protection by larger plants against excessive heat, light, and wind-action; the preparation of the soil for the several stages in plant succession by the anchorage of finer material or by its enrichment by cast-off leaves, etc.; the providing of nitrates by root-tubercle bacteria.

[Evidently unfinished. Ed.]

Phenological record. — The author has accumulated a great mass of phenological records covering, more or less irregularly, the entire period of his observations, but they present so much variation that no effort is here made to present specific records, the seasonal distribution being indicated in more general terms.

The variations in flowering periods is due chiefly to the following causes:

1 — The time of spring-opening. The records show certain species appearing as early as the third week of February (very exceptional) and as late as the last week of April. The occasional long delay in the opening of the spring season usually brings about a crowding together of prevernal and early vernal (or even late vernal) aspects of the flora, causing unusual combinations in its conspicuous floristic composition.

2 — The exposure of particular species in different locations. Usually plants in places exposed to the early spring sun will flower earlier than those on northern slopes.

3 — The nature of the soil. Species growing both on the prairies and on exposed sandy areas will usually flower earlier on the latter.

4 — The occurrence of long drouth periods. This affects the late summer flora particularly, the appearance of the flowers often being delayed by protracted mid-summer drouth.

5 — Latitude. The 200 miles between the southern and northern boundaries of the state often produce a difference of more than three weeks in time of flowering, — the northern representatives of the same species appearing later in the spring and earlier in late summer than those of the south.

6 — The cropping or injuring of plants by grazing animals, etc., often delays the appearance of the first flowers and prolongs the flowering period, — often very late into the season. This is likely to affect individual plants chiefly.

For these reasons, and especially because of the extremely variable nature of our seasons, the specific phenological record for any one season, (or limited number of seasons) is of comparatively little value, excepting as, in general, it presents the phenological sequence, — which, however, may be materially disarranged during an extreme season.

For these reasons it is deemed best merely to present a rather loose outline of seasonal floristic progression, which will give some concept of the diverse phases of the prairie flora which appear as each open season advances.

1 — The prevernal aspect. The earliest plants to appear in flower (or spore-stage among the vascular cryptogams) are the following:

Androsace occidentalis
Anemone caroliniana
Anemone patens var. *Wolfgangiana*
Antennaria campestris
Antennaria neglecta
Carex pennsylvanica
Corylus americana
Draba caroliniana
Equisetum arvense
Lomatium orientale
Ranunculus fascicularis
Ranunculus rhomboidea
Salix humilis

2 — The early vernal aspect.

[Evidently unfinished. Ed.]

CHAPTER III

PLANT SUCCESSION

Under the conditions herein described, operating in various degrees and combinations upon plants exposed to them, and with their own equipment to meet the extremes in these conditions, the several floras of the state have developed through long periods of time. The characteristic flora of any distinctive area, such as a prairie, a grove or a swamp, was in no case the product of a single season, or a short cycle of seasons, but resulted from the balancing of the relations between the plants and their ecological environment through many centuries. There were no doubt many changes, such as fluctuations in the relative ratio of species, and the introduction or local extinction of individual forms, but after earlier major adjusting stages (which will be discussed under plant succession) are passed, each plant formation will retain its ecological characteristics even though there be some variation in species, so long as all the conditions which produce or modify climatic factors are reasonably constant. Minor changes are constantly occurring even today, but transformations or substitutions of ecological types can take place only with radical changes (often quite local) in the immediate surroundings of the plants.

The sifting out of certain species, and the segregation of the major plant groups, or formations, is not a matter of chance, but depends upon the fitness of the plants to meet the conditions of a particular habitat. These groupings of ecological types may be characteristic of large areas, such as prairie or forest, or they may be very local, as where a small pond or swamp, with its characteristic flora, appears in the midst of a dry prairie, or where a limited prairie opening caps a ridge in a great forest area. In these cases a local modification of climatic factors brings about a striking difference in the flora.

In practically all portions of our state our larger floristic areas were started at some period of its history on surfaces left bare by the retreat of glacial ice-sheets. The smaller modified portion of the larger areas likewise made their beginnings on surfaces which had been subsequently wholly or in part denuded by various agencies.

Plant Succession. The processes by which floras are introduced to, and developed upon, bare areas are of interest not only in their relation to the successive restorations of floras on our glaciated areas, but because on a smaller scale they are going on all about us at the present time. Areas of greater or lesser extent are constantly being disturbed and their flora partly or wholly destroyed.

This disturbance or denudation may be caused by water, ice, wind, fires, burrowing and scratching animals, man, etc., and it may bring about the exposure of new surfaces by removing soil material from one place and depositing it in another, thus creating two new surfaces. As soon as favorable conditions are restored after the disturbance has taken place, the surrounding flora begins to advance upon the new surfaces, the initial introduction of seed being not infrequently accomplished by the same agency which caused the disturbance.

With the establishment of this first flora further erosion or disturbance is checked or prevented, and the process of repopulation, change and readjustment continues until the plants unsuited to the permanent occupation of the habitat are eliminated, and a balance is established among the adapted plants such that they continue in more or less definite associations when a climax has been reached, without further change in ecological type, unless a radical change in environment takes place.

Our most common illustrations of such succession are furnished where artificial excavations have been made, or where water has exposed fresh surfaces by erosion, or by piling up new bars, etc. In none of these cases, however, is the beginning of restoration made from an absolutely clear new surface, for the very process of disturbance is sure to leave some remnants of the old flora, and to introduce other plants from the vicinity.

The initial introduction of plants on the new surface, as well as the subsequent development of the flora, will be determined by the ecological fitness of the new surface and the character of the flora of nearby areas. This may be illustrated by a few concrete cases.

For several years the writer studied the problem of the restoration of the prairie along the old Wilton-Muscatine branch of the Chicago Rock Island and Pacific R. R.*

* For a partial report see Shimek, 136.

Here there had been a complete return of a pure prairie flora to the surfaces of the old cuts, and to the sides of the fills which had remained undisturbed, but that part of the roadbed between the drainage ditches on either side, excepting for most of the slopes of the fills, continue to be disturbed by repairs of the road, attempts to destroy the weeds etc. Upon this disturbed area the following mixture of plants was observed on two (of many) occasions, namely, July 11, 1923 and June 21, 1924. The area covered by these observations extends for about three miles north of Summit, Muscatine Co.

The species are checked in separate columns for the 2 yrs.

Plants on the R. R. roadbed

Forest plants (seedlings)	1923	1924		1923	1924
Acer Negundo		+	*Psedera quinquefolia*		+
Fraxinus pennsylvanica var. *lanceolata*		+	*Pyrus ioensis*		+
Populus deltoides		+	*Salix longifolia*		+
Prunus americana		+	*Sambucus canadensis*		+
Swamp plants					
Carex vulpinoidea		+	*Scirpus fluviatilis*		+
Carex xanthocarpa		+	*Stachys palustris*	+	
Sand plants					
Ambrosia psilostachya	+	+	*Cyperus filiculmis*	+	
Asclepias amplexicaulis		+	*Cyperus Schweinitzii*	+	+
Astragalus lotiflorus		+	*Mollugo verticillata*	+	
Cassia chamaecrista		+	*Oenothera rhombipetala*	+	
Cenchrus carolinianus	+		*Strophostyles helvola*	+	+
Croton glandulosus var. *septentrionalis*	+		*Strophostyles pauciflora*	+	+
			Tephrosia virginiana	+	

The species marked with an asterisk have escaped from cultivation. All others are introduced weeds.

Introduced plants.	1923	1924		1923	1924
Anthemis Cotula	+	+	*Pastinaca sativa*	+	+
Arctium minus	+	+	**Phleum pratense*	+	+
Brassica arvensis	+		**Poa pratensis*	+	+
Bromus secalinus		+	*Polygonum aviculare*		+
Bromus tectorum	+	+	*Polygonum Convolvulus*	+	+
Capsella Bursa-pastoris	+	+	*Radicula Armoracia*		+
Chenopodium album	+	+	*Robinia pseudoacacia*		+
**Medicago sativa*	+		*Rumex Acetosella*	+	+
Melilotus alba	+	+	*Rumex crispus*	+	+
Melilotus officinalis	+		*Setaria glauca*	+	
Nepeta Cataria	+		*Setaria viridis*	+	

	1923	1924		1923	1924
Sisymbrium altissimum	+	+	**Triticum sativum*	+	+
Taraxacum officinale	+	+	*Verbascum Thapsus*	+	+
**Trifolium hybridum*	+		*Veronica peregrina*		+
**Trifolium pratense*		+	**Zea Mays*	+	+
Trifolium procumbens	+	+			

Native weeds. These are practically all prairie plants.

	1923	1924		1923	1924
Achillea Millefolium			*Oenothera muricata*	+	+
Agropyron Smithii			*Oxalis corniculata*	+	+
Amaranthus blitoides			*Oxybaphus nyctagineus*	+	+
Ambrosia artenisiifolia			*Physalis pruinosa*	+	+
Ambrosia trifida			*Plantago aristata*	+	+
Asclepias syriaca			*Plantago Rugelii*	+	+
Cassia chamaecrista			*Poa compressa*	+	+
Convolvulus sepium			*Potentilla monspeliensis*	+	+
Erigeron canadense			*Silene antirrhina*	+	+
Erigeron ramosus			*Sisymbrium canescens*		+
Equisetum arvense	+	+	*Solidago rigida*	+	+
Euphorbia corollata	+		*Specularia perfoliata*		+
Euphorbia maculata	+		*Teucrium canadense*	+	
Euphorbia Preslii	+		*Trifolium repens*		+
Hordeum jubatum	+	+	*Verbena bracteosa*	+	+
Hypericum cistifolium	+		*Verbena stricta*	+	+
Lepidium apetalum	+	+			

Prairie Plants.

	1923	1924		1923	1924
Acerates viridiflora	+	+	*Fragaria virginiana*	+	+
Amorpha canescens	+		*Helianthus grosseserratus*	+	+
Andropogon scoparius		+	*Koeleria cristata*	+	+
Anemone cylindrica		+	*Lactuca canadensis*		+
Antennaria neglecta		+	*Lepachys pinnata*	+	+
Apocynum cannabinum	+	+	*Lespedeza capitata*	+	+
Artemisia ludoviciana		+	*Liatris scariosa*		+
Asclepias tuberosa	+	+	*Lithospermum canescens*		+
Asclepias verticillata	+	+	*Lobelia spicata*		+
Aster multiflorus		+	*Oxalis violacea*		+
Aster novae-angliae		+	*Panicum Scribnerianum*	+	+
Brauneria pallida	+	+	*Panicum virgatum*		+
Carex festucacea		+	*Parthenium integrifolium*	+	+
Cirsium discolor	+	+	*Petalostemum candidum*		+
Ceanothus americanus		+	*Petalostemum purpureum*	+	
Desmodium canadense	+	+	*Physalis virginiana*		+
Desmodium illinoense	+	+	*Polygala sanguinea*	+	
Elymus canadensis		+	*Polygala Senega*		+
Eryngium yuccifolium		+	*Potentilla arguta*		+

	1923	1924		1923	1924
Potentilla canadensis		+	*Solidago canadensis*		+
Rosa pratincola	+	+	*Solidago graminifolia*		+
Rudbeckia hirta		+	*Solidago speciosa*		
Ruellia ciliosa	+		var. *angustata*		+
Rumex altissimus		+	*Spiraea salicifolia*	+	
Salix humilis		+	*Stipa spartea*		+
Scutellaria parvula	+	+	*Veronica virginica*		+
Silphium integrifolium		+	*Viola cucullata*	+	+
Silphium laciniatum	+	+	*Viola fimbriatula*	+	
Sisyrinchium campestre		+			

From either woods or prairie.

	1923	1924		1923	1924
Rhus glabra	+	+	*Vitis vulpina*	+	+

The forest plants in this list are all bottomland species and were probably derived from the creek bottom to the north.

The few swamp plants (few both as to species and individuals) were evidently derived from the small wet depression nearby. Neither this nor the preceding group would survive.

While there are old sand-dunes not far away, the species in the sand plants list were evidently introduced with sand used for road-ballast. This ballast was derived from the sandy flats below Muscatine.

The species of the native weed list were mingled with the introduced weeds and both in the main occupied the more open (and more disturbed) parts near the roadbed proper.

The native prairie plants occurred either in colonies or as scattered individuals, and they were much more abundant on the outer and less disturbed part of the roadbed. They were derived from the strips of native prairie which still persist along the outer part of the railway right of way, and would ultimately undoubtedly crowd out all the other groups if there was a complete cessation of disturbances. This evidently occurred along the sides of the older cuts and fills and their flora is now distinctly that of the prairie, without admixtures of any kind.

A similar case (reported in part with the preceding) is that of a formerly cultivated area near Mason City, Iowa. Here a prairie tract had been cultivated for a number of years, and was then permitted to lie fallow for ten years. 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, namely:

Solidago rigida	*Aster multiflorus*
Aster azureus	*Aster laevis*

Aster laevis was least abundant.

With these typical prairie plants (derived from the adjoining tract of undisturbed prairie), there were mingled the remnants of the weed flora which had at first taken possession of the tract. This weed flora consisted of both native and introduced weeds, and included the following species:

Native weeds.

Achillea Millefolium	*Helianthus grosseserratus*
Agropyron Smithii	*Hordeum jubatum*
Ambrosia artemisiifolia	*Lepidium apetalum*
Asclepias syriaca	*Potentilla monspeliensis*
Erigeron ramosus	*Rosa pratincola*
Hedeoma hispida	*Trifolium repens*

Introduced weeds.

Melilotus alba	*Taraxacum erythrospermum*
Phleum pratense	*Trifolium pratense*
Poa compressa (native?)	*Trifolium procumbens*
Poa pratensis	

The small number of introduced weeds was probably due to the absence of other cultivated tracts nearby, the area being bounded on the north by the low wooded bluffs of an old swampy bed of Lime Creek (or Winnebago River), on the east by an upland grove, and on the south and west by unbroken native prairie and one small grove.

The dominating asters and *Solidago*, and the native weeds were evidently derived from the adjoining prairie to the west.

At the end of another five-year period the native prairie weeds as well as the pioneer asters and *Solidago* were distinctly reduced in numbers, though all of the species were still present; and the physiognomy of the area was changed to resemble very closely that of the adjoining prairie by the addition of a generous mixture of the following typical prairie plants:

Typical prairie plants:	*Ceanothus americanus*
Amorpha canescens	*Cirsium discolor*
Andropogon scoparius	*Coreopsis palmata*
Anemone cylindrica	*Desmodium canadense*
Artemisia ludoviciana	*Elymus canadensis*
Asclepias tuberosa	*Fragaria virginiana*
Bouteloua curtipendula	*Helianthus scaberrimus*

Heliopsis scabra
Lepachys pinnata
Lespedeza capitata
Liatris scariosa
Linum sulcatum
Lobelia spicata
Monarda mollis
Muhlenbergia racemosa
Petalostemum candidum
Petalostemum purpureum
Phlox pilosa
Pycnanthemum flexuosum
Rudbeckia hirta
Salix humilis
Senecio plattensis
Solidago canadensis
Solidago nemoralis
Solidago speciosa angustata
Sorghastrum nutans
Viola pedatifida

The grasses, *Andropogon*, *Bouteloua*, *Elymus*, *Muhlenbergia* and *Sorghastrum*, were scattered, like the other plants, and they dominated neither the restored area, nor the adjoining older native prairie.

It is also interesting to note that at the end of the ten year period the adjoining native prairie had not completed the repopulation of the restored area, for though 37 species, exclusive of the prairie weeds, had found their way to the latter tract, there still remained the following 48 species upon the native prairie which had not yet migrated to the newer surface:

Acerates viridiflora
Amphicarpa Pitcheri
Andropogen furcatus
Antennaria neglecta
Asclepias verticillata
Aster novae-angliae
Aster sericeus
Baptisia bracteata
Brauneria pallida
Carex festucacea
Cirsium Hilli
Cirsium iowense
Comandra umbellata
Equisetum hyemale intermedium
Eryngium yuccifolium
Gentiana puberula
Gerardia aspera
Helianthemum majus
Helianthus occidentalis
Heuchera hispida
Hypoxis hirsuta
Koeleria cristata
Kuhnia eupatorioides corymbulosa
Lactuca canadensis
Liatris cylindracea
Lilium philadelphicum
Lithospermum canescens
Oxalis violacea
Panicum Scribnerianum
Pedicularis canadensis
Physalis virginiana
Polygala Senega
Polygala verticillata
Potentilla arguta
Prenanthes racemosa
Scrophularia leporella
Silene stellata
Silphium integrifolium
Sisyrinchium campestre
Smilacina stellata
Solidago graminifolia
Solidago missouriensis
Sporobolus heterolepis
Stipa spartea
Thalictrum dasycarpum
Tradescantia reflexa
Veronica virginica
Zizia aurea

Most of the species in this list could have their seeds transported just as readily as those in the preceding list, yet they had not become established on surfaces manifestly favorable to them even by the end of the ten-year period. The unsuccessful competition on their part must, therefore, be ascribed to some other cause than differences in seed dispersal. From incomplete tests the writer has reason to believe that a more thorough study of the viability of the seeds of these species will throw much light on this subject.

Unfortunately, soon after the foregoing observations on this tract were made, the area became a part of a golf course, and both native and restored prairie were destroyed.

In both the foregoing examples succession started upon new surfaces created by man for his own uses. Many fine illustrations of succession are also furnished by many of our streams which are constantly tearing down and building up sand and mud bars. The following examples will illustrate the process.

Several years ago observations were made by the writer on sand and mud bars located near the present aviation field at Iowa City and formed during a flooded condition of the Iowa River in late spring.

During the first season a heterogeneous mixture of plants appeared upon 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. longifolia* was left.

In the Muscatine County and Mason City cases the very direct development of a prairie flora on the newer surfaces could be predicted with certainty because of location, and of the nature of the surrounding flora, but in the instance of the river bar portions of the bar might have remained swampy or sandy for a long time, though ultimately either prairie or alluvial woods would have been formed. Which of the two latter, however, would result could not have been foretold definitely, because in the vicinity both alluvial woods and alluvial prairie had persisted for a long time, the latter being the result of exposure on the broadly expanded river flat, which is really the head of glacial Lake Calvin.

Another illustration covers a much longer period of time. Forty-one years ago the writer studied plants on the long bar on the west side of the Iowa River at Iowa City, chiefly on the part below the present City Park bridge. 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 *Stenophyllus capillaris*. During the first summer the river flooded the bar for short periods 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 quite 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 plant flotsam carried by our streams, weeds, prairie, swamp and forest plants being indiscriminately mixed. As the years passed the forest vegetation took possession, and, despite some inroads by wood choppers, 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. Not only has the bar been covered with a dense vegetation such as characterizes our alluvial woods, but each succeeding freshet brought in silt until a fine soil now covers the undisturbed part of the bar to a depth of three feet, or more.

During one winter a strip close to and parallel with the old shore was cleared by cutting, and the floods of the following season cut a narrow channel almost the length of the bar, leaving a lagoon which still sustains a hydrophytic vegetation, but which will probably be filled in time, as before.

The bars of our larger border streams, the Mississippi and Missouri, furnish innumerable examples of a similar nature. The fall of each year finds the higher parts of the bars, then well-exposed, covered with seedling trees, particularly of soft maple, cottonwood, and the low-ground willows, with an admixture of other plants, chiefly weeds and swamp plants. If subsequent floods do not sweep the bars away, there is a rapid and very direct development of alluvial thickets and groves in which *Salix longifolia*, *S. nigra*, *S. amygdaloides*, *Populus deltoides*, *Acer saccharinum* and *Betula nigra* at first predominate, to be followed later by a more varied lot of alluvial trees, such as *Fraxinus nigra*, *F. pennsylvanica* var.

lanceolata, *Platanus occidentalis*, *Celtis occidentalis*, *Juglans nigra*, etc.

A similar evolution of bottomland floras may be observed upon the bars of the Missouri River along our western border, though the number of shrubs and trees is usually smaller, and the more xeric condition of the region often results in the direct development of a sand and prairie flora. One of these was studied by the writer.

This bar is located on the east side of the Missouri River, due west of Modale, Harrison County, at the intersection of two old channels, that of Lewis and Clark survey, 1804, and that of the U. S. survey of 1853. Observations were made in August, 1908, after a heavy flood. It was practically bare of vegetation. A year later, August, 1909 observations were again made. At this time it was covered with seedlings of *Salix longifolia* and *Populus deltoides* with various smaller covering. If subsequent floods had not disturbed this area it would have developed a cottonwood grove, similar to that in the far background. The latter grove is located over one of the old channels of the river.

A later development, quite characteristic of this part of the Missouri border, is next described. This area is also similarly located on the east side of the river at the intersection of the two old channels, and lies due west of California Junction, four miles south of the bar described above. Here the river has not cut eastward for many years, and dunes have been built up from the old sandbars. Portions of the surface are still made up of loose, shifting sands; some parts are covered with a low, xerophytic flora, while areas of considerable extent are covered with cottonwood groves. Portions of this area have, therefore, been stable for many years, and both prairie and forest plants have invaded it, though constant shifting of the sand and occasional floods have disturbed the surface sufficiently to invite a large number of weeds to the open spaces. The following plants were found on these areas:

Foreign weeds:

Cannabis sativa
Chenopodium album
Digitaria humifusa
Eragrostis megastachya
Lactuca scariola
Melilotus alba
Salsola kali tenuifolia
Setaria glauca
Setaria viridis
Solanum rostratum (from S.W.)
Taraxacum erythrospermum
Taraxacum officinale

Native Weeds:

Acalypha virginica
Achillea Millefolium
Amaranthus blitoides
Ambrosia artemisiifolia
Ambrosia psilostachya
Ambrosia trifida
Apocynum cannabinum
Aristida oligantha
Cassia chamaecrista
Convolvulus sepium
Crotalaria sagittalis
Dyssodia papposa
Erigeron canadensis
Erigeron ramosus
Euphorbia marginata
Euphorbia Preslii
Euphorbia serpens
Hedeoma hispida
Helianthus annuus
Hordeum jubatum
Lactuca canadensis
Lepidium apetalum
Muhlenbergia racemosa
Panicum capillare
Plantago aristata
Polygonum pennsylvanicum
Sisymbrium canescens
Solanum nigrum
Teucrium canadense
Verbena bracteosa
Verbena stricta

Several of the species in this list might, with all propriety, be included with the prairie list proper, such as the *Achillea*, *Apocynum*, *Erigeron ramosus*, *Lactuca*, *Lepidium*, *Muhlenbergia* and *Verbena stricta*. The remaining species also appear upon the prairie, especially in disturbed places, and a few, like *Ambrosia psilostachya*, the *Cassia* and *Crotalaria*, are more common on sandy areas.

Prairie plants:

Andropogon furcatus
Andropogon scoparius
Anemone cylindrica
Aristida basiramea
Artemisia dracunculoides
Asclepias verticillata
Aster multiflorus
Aster sericeus
Astragalus canadensis
Chenopodium leptophyllum
Cirsium iowense
Dalea alopecuroides
Dalea enneandra
Elymus canadensis
Equisetum hyemale intermedium
Fragaria virginiana
Gerardia aspera
Glycyrrhiza lepidota
Kuhnia eupatorioides
Lespedeza capitata
Linum sulcatum
Lithospermum canescens
Lygodesmia juncea
Panicum huachuchae silvicola
Panicum Scribnerianum
Panicum virgatum
Petalostemum candidum
Petalostemum purpureum
Rhus Toxicodendron (low form)
Rosa pratincola
Rudbeckia hirta
Rumex altissimus
Salvia lanceaefolia
Silphium integrifolium
Solidago canadensis
Solidago missouriensis
Solidago serotina
Sorghastrum nutans
Sphenopholis obtusata
Vernonia missurica
Vicia americana
Viola cucullata

None of the species of this list appeared in large or dominant numbers, but all were mingled in varying proportions in different parts of the field. Some, like the two species of *Dalea*, the *Gerardia*, *Linum*, both species of *Petalostemum*, the *Salvia* and *Silphium*, were represented only by a few scattered individuals.

Sand Species:

Cenchrus carolinianus
Cycloloma atriplicifolium
Cyperus Schweinitzii
Desmanthus illinoensis
Desmodium canescens
Eragrostis pilosa
Euphorbia dentata
Lygodesmia rostrata
Paspalum ciliatifolium
Strophostyles helvola
Strophostyles pauciflora
Xanthium commune

Practically all the species of this list might be included in the native weeds list, for all become weeds, especially in sandy soil.

Border shrubs and vines:

Rhus glabra
Rubus occidentalis
Vitis vulpina
Zanthoxylum americanum

Forest plants:

Amorpha fruticosa (low ground)
Cornus paniculata
Crataegus mollis
Desmodium Dillenii
Desmodium paniculatum
Rosa blanda
Populus deltoides
Psedera quinquefolia
Ranunculus abortivus
Ulmus americana (small)

Despite the fact that cottonwood groves of considerable extent have been developed on this area, there are practically no other trees, and the ordinary forest undergrowth is almost entirely lacking. Unlike its near relatives *Populus grandidentata* and *P. tremuloides*, the cottonwood, *P. deltoides*, is not a nurse tree, and when this short lived tree dies out there will be no forest to take its place. 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.

In the sandy depressions between the dunes limited ponds and swamps produce a characteristic vegetation. In addition to the submersed *Potamogeton illinoense* found in a small pond, the following swamp or low ground species were observed.

Ammania coccinea
Asclepias incarnata
Bidens sp.
Carex vulpinoidea
Cyperus acuminatus
Cyperus aristatus
Cyperus rivularis
Cyperus strigosus

Echinodorus cordifolius
Ilysanthes dubia
Lobelia siphilitica
Lycopus americanus
Ranunculus Cymbalaria
Rumex brittanica
Salix amygdaloides
Salix longifolia
Salix nigra
Scirpus americanus
Scirpus validus
Spartina Michauxiana
Spiranthes cernua
Stachys palustris
Typha latifolia

Because of the shifting sands these swamp species have a very uncertain tenure of occupancy and for this reason, and because of occasional flooding by the river, a systematic study of the flora of these small swampy areas would no doubt reveal great variation in its composition from year to year.

The first plants to take possession of the new dune-surfaces are mostly members of the Pea Family, the Leguminosae, which are sustained on the comparatively sterile sand by the nitrifying bacteria which are abundantly developed in the numerous root-tubercles of these plants. The Leguminosae are soon followed by other plants, chiefly of prairie species, and a sand-retaining mat is developed. The following pioneer plants were observed on these dunes, all being Leguminosae:

Astragalus canadensis
Cassia chamaecrista
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

The *Astragalus*, both species of *Dalea*, the *Glycyrrhiza*, *Lespedeza*, both species of *Petalostemum* and the *Vicia* are prairie species; *Melilotus* is an introduced weed, and the remaining species are more or less characteristic of sandy areas.

The shifting bars of our streams, and their possible attendant dunes, now offer the best and most varied opportunities for the study of plant succession. It must be observed, however, that such succession does not always result in the formation of a forest climax, for in broad, exposed alluvial valleys, or where the stream flows through a prairie area (and is without abrupt sheltering bluffs), the climax is more likely to be a prairie.

It seems to be assumed by some writers that plant succession proceeds along rather definite and uniform lines, though interruptions and fluctuations in the process are generally recognized. As a matter of fact, in our territory it involves at least two distinct lines of procedure (and even these may vary greatly) which may bring about very different results. In the one, the changes which take place in the course of the development of the floral climax may consist chiefly of a readjustment and rearrangment of species belonging to the same ecological type, but always with some individuals of most of the pioneers persisting, and forming a part of the climax. Such might occur on sheltered excavations (made by water, man, etc.) when forest plants sometimes constitute the major part of the pioneers on the new surfaces; or in the case of the railway cut in Muscatine County, where prairie xerophytes were among the pioneers; or where a prairie flora has been completely destroyed by cultivation, and then returns when the latter is stopped; or where a prairie flora advances quite directly upon a newly formed sand-dune, the latter being ultimately covered by a typical prairie flora; or where the river bars are not too hydric at first, and have a goodly number of forest mesophytes among the pioneers. In all these cases at least a considerable part of the pioneers, that part which is of the same ecological type as the climax flora, will persist, to form a part of the latter.

But even in these cases succession proceeds along different lines despite certain points of similarity, and the results may be quite different. In the cases of the railway cuts and the cultivated tract there was being staged a direct return of the prairie, with the final result readily discernible; in the case of the sand dunes the outcome is usually less certain, as either prairie or forest may develop, and either may finally yield to the other, according to environment, but the greatest uncertainty exists in the case of the river-bars, for they may develop an alluvial forest if the valley is sheltered, but may result in an alluvial prairie if the valley is broad and exposed.

In the second type there is not only a change in kinds and relative numbers of species as the flora advances towards a climax, but there is a complete change in ecological types, sometimes due to the reaction of the flora itself upon its environment, and sometimes to external causes such as erosion.

Thus, the hydrophytic flora of a pond gradually tends to fill it up by its seasonal growth and decay, and this filling is hastened by additions resulting from erosion by both water and wind. As the water becomes shallow, the true hydrophytic flora is gradually displaced by a swamp, or helophytic flora, and as the filling goes on and the new surfaces emerge, this is followed by either a xerophytic prairie flora or a mesophytic forest flora, the final result depending on environment.

In this type of succession the flora presents at least three distinct stages which differ not only in physiognomy and floristic composition, but also in structural ecological type. There is, therefore, a gradual but complete replacement of one flora by another as environmental changes are produced.

The process may become even more complicated if the original pond is located in a sand-dune area. The flora then progresses through the hydrophytic and helophytic stages, but may also pass through a mesophytic stage where trees and shrubs develop, which in turn may be followed by a xerophytic stage as the sand accumulates and the tops of the dunes become more exposed. Should the diminished vegetation on the dry dunes make a "blow-out" of sufficient depth possible, a pond might be formed, and the whole successional series could be repeated.

A similar result may be anticipated over all the prairie area in which erosion is going on. At first, as previously noted, this erosion results in the creation of shelters in which a mesophytic forest flora can develop, but when the base-leveling process finally nears completion there will again be an exposure of the general surface, and in our part of the country only xerophytes will be able to exist, excepting where blocked channels will again create hydrophytic conditions, with a return to the most primitive circumstances under which our flora started.

This may not be "retrogression," but it certainly is progression in a circle.

Reaction. In the process of succession the flora itself produces changes which affect (react upon) its environment to such an extent that it may, at any stage in the succession, hasten the coming of its successors. Thus, the first established colonists on the sand-bar retain a little silt in floodtime, and prepare the way for a different floristic type, and the accumulation goes on until a deep and rich alluvial soil is produced, which is capable of sustaining a vigorous and varied flora. The forest may (and usually does) develop on poor soil, but its cast-off foliage and branches, as well as its eliminated individual members, enrich the soil until it becomes suitable for the most fastidious of smaller plants, which also find shelter from dangerous loss of water and excessive brilliancy of light, under its protecting cover. The improved soil conditions are, however, more essential to the smaller subordinate flora of the forest than they are to the dominant trees, for the latter are not the products of the rich forest soil, but the producers of it.

The reaction of a flora on its environment usually results in the hastening of the various steps in plant succession by preparing the way for newcomers, but not always. Thus, the shade of an established forest in its earlier stages of succession may prevent or retard the introduction of other trees which are just as competent to grow in the modified forest environment, but which cannot make a start because of the successful competition of established species. Similarly the formation of a prairie turf may check the entrance of additional species, even when they are well adapted to the prairie habitat.

A similar retardation may take place when one plant formation gradually replaces another because of local changes in topography which bring about a modification of the general climatic factors. Thus, the forest flora encroaches upon the general flora of the prairies along river valleys which are gradually being scoured out by erosion. The forest flora covers the slopes in the shelter of the valleys. Its advance into the prairie territory would usually be greatly facilitated by deeper and more extensive erosion of the main valley and its tributary ravines. Yet the very flora which would be expanded by this erosion, checks or prevents it, and thus retards its own advance.

The environmental changes which result from the reaction of the flora and from modifications of the topography either by erosion or by sand-dune and loess formation, are purely local, yet they bring about changes in climatic factors which result in the production of a flora entirely different from that which appeared on the original surfaces, and which responds to wholly different climatic conditions. All this may take place without any change in the amount or rate of rainfall, and without unusual variations in temperature. It is due primarily to the effect of both plants and topography upon evaporation and run-off, the run-off being strongly influenced by both topography and plant-covering and the amount and rate of evaporation being governed by the extent of exposure to wind and sun.

All this shows clearly that climate can be employed only in a very general way as a measure of greater plant provinces, and that in all regional studies of plant formations both climatic and local factors must be taken into consideration because they are inextricably bound together in their effect upon plants.

CHAPTER IV

POST-GLACIAL PLANT SUCCESSION

Interglacial and post-glacial conditions in Iowa. — In view of the fact that Iowa was twice entirely, or almost entirely, covered by glacial ice-sheets (Nebraskan and Kansan) and suffered three additional invasions, (Illinoian, Iowan and Wisconsin)* each of which covered large sections of the state, the question of the re-establishment of our floras after each invasion becomes one of deep interest, especially in view of its real or frequently assumed relation to changes which are taking place in our flora today. The part which the glaciers played in this process was simply the destruction (or at greater distances the partial destruction) of existing floras and the preparation of the surface for new invasions of adjacent floras.

Many of our writers have perhaps too freely ascribed many of our floral conditions and pecularities to glacial influences. Of course there can be little doubt that the advances of our great Pleistocene glaciers destroyed or strongly modified the existing native floras over large areas, including Iowa. The recession of the glaciers, which probably took place very slowly, left successive areas exposed to the advance of new vegetation from contiguous plant centers. The advance of the vegetations as a whole was also probably rather slow, though some species, especially such as are distributed by wind and by aquatic birds, were probably very early forerunners of the general advance.

These changes took place over all of Iowa after the retreat of the Nebraskan and Kansan ice-sheets, as both covered practically the entire state, and also over the parts of the state covered by the Illinoian, Iowan and Wisconsin ice-sheets, the last being most directly connected with the development of our modern flora. How far the influence of the Arctic climate was felt beyond the border of the latter ice-sheets is problematic. In all probability a belt of tundra

* According to Kay and Graham: The Illinoian and Post-Illinoian Pleistocene Geology of Iowa, Iowa Geol. Surv. 38: 1-262, p. 90, the Wisconsin Age (stage) includes the Iowan, Peorian (interglacial) and Mankato Subages (substages). The drift that is called Wisconsin by Shimek is now known as Mankato. — Ed.

developed southward as the ice moved slowly forward. How wide this was cannot be determined, but it was probably much narrower than that which now borders the perpetual cap of ice around the North Pole, and it was probably not the boggy type. Adams (1, p. 56) assumed that three belts, similar to those now found in portions of the Arctic regions, occurred beyond the margin of the ice: a narrow belt of tundra; a transcontinental belt of stunted coniferous trees and shrubs; and a miscellaneous belt consisting of deciduous forests in the southeast and of plains and desert types in the southwest.

Adams questions his own second groups, however, for on p. 60 (1) he says that the division into eastern and western groups, and the marked differences in climate, "do not favor the idea of transcontinental unity of the coniferous forests but show that the direction of geographic origin, the adaptations of the biota to mountain conditions, and proximity, are factors which must be reckoned with in understanding the Post-glacial repopulation of the Northwest."

It should be added that the final repopulation of the glaciated or near-glaciated areas by plants was likewise dependent on these and other ecological factors, especially those related to seed-dispersal and moisture rather than upon anything which the glaciers left behind in their retreat.

There is, however, no convincing evidence of any such transcontinental coniferous belt. It is true that in the wooded portions of northeastern Iowa, and in a few outlying "islands," there are small groups of *Pinus Strobus*, *Abies balsamea*, *Juniperus communis* and *Taxus canadensis*, but, while it may seem remotely possible that they were left behind after the retreat of the Wisconsin glaciers, it is much more likely, judging from their deciduous-leaved associates, that they entered the state, with other forest floras, from the mixed border to the east and northeast which joins the northern coniferous forests with the more southerly deciduous forest, and they persisted because they found congenial habitats.

Certainly on that large area of Kansan which was not covered by the subsequent drifts as well as on the corresponding lesser part of the Illinoian, vegetation existed continuously, or with interruptions in composition which resulted from the advance of a cold climate with subsequent ice-sheets, and of which there is some evidence in our loess deposits consisting of the presence of the shells of forest or thicket-loving species of fossil land snails. Some of the earlier flora was pushed, or more correctly, left to the southward with each advance of the ice, only to return with its subsequent retreat, leaving the region in which Iowa is included practically the same in the end. Thus, during each of the interglacial periods, Iowa was covered with essentially the same kind of flora after the readjustments which were necessary at its beginning.

Not only does this seem extremely probable and natural, since no ecological groups were destroyed, but merely reduced, but we have direct evidence of it in the practical identity of the land-snail faunas (so closely related to definite plant associations) in the several interglacial loesses in Iowa.

When the ice-sheet receded, the vacated areas were occupied by the nearest suitable flora. The greater part of the prairie flora came from the south (see subsequent more detailed discussion of the more striking members of these several invading floras); a smaller part, particularly that of the prairie-steppe, from the west and southwest; somewhat later, because the forest flora would naturally advance more slowly, a smaller forest contingent from the south, the main deciduous forest from the southeast, and the characteristic mixed coniferous and deciduous northeastern forest of the "driftless" and adjoining rough areas, from the east and northeast.

Despite the fact that the modern forest flora of the "driftless" area is developed on the oldest exposed surfaces in the state, it is in reality one of the newest, or latest, for it is a part of the mixed coniferous and deciduous forest belt which extends to the northeast over the latest, or Wisconsin, drift area across Wisconsin, Michigan, southern Ontario, and eastward. It contains the conifers *Pinus Strobus*, *Abies balsamea*, *Taxus canadensis* and *Juniperus communis*, besides northeasterly and easterly angiosperms, such as *Aconitum noveboracense*, *Dicentra canadensis*, *Liparis liliifolia*, *Vitis bicolor*, etc., mingled with the ordinary forest flora of the Great Lakes region, which includes common trees of the genera *Acer*, *Betula*, *Carpinus*, *Carya*, *Celtis*, *Crataegus*, *Fraxinus*, *Juglans*, *Ostrya*, *Populus*, *Prunus*, *Pyrus*, *Quercus*, *Tilia* and *Ulmus*, and their accompanying shrubs and herbs which will receive later attention. The few northerly forms which it contains are also found in the northeastern belt, and the floristic relationships of our area are distinctly with that belt.

At least portions of this flora are sometimes regarded as the survival of a pre-Wisconsin flora, but no such flora could persist, or at least does not now exist, so near a general ice-covered area.

The existence of plants near (or even on) the borders of the Alaskan glaciers is sometimes cited as proof that plants could have existed at the edge of the Wisconsin ice, but the cases are not comparable. There is a great difference in the cold resisting power of plants, as is illustrated by the great northward extension of some of our apparently delicate species such as *Cystopteris fragilis*; and the flora of Alaska is, in the main, different from the dominant flora of the area under discussion.

Cooper's report on the recent ecological history of Glacier Bay, in southern Alaska (35) shows that on surfaces only recently vacated by retreating glaciers, there were found but two species which are also members of the Iowa northeastern flora, namely, *Equisetum arvense* and *Pyrola secunda* in the pioneer community, and two others, *Aspidium spinulosum* and *Asplenium filix-femina*, in the Willow-Alder community.

Moreover, the proximity of the sea, with its warm Japanese current, tempers the climate of the seaward side of Alaska, despite the glaciers which crowd down from the mountains, — a condition very different from that of our wide-open areas, which, during glacial times, were more nearly comparable with the Arctic coast. Single species, or small groups of species do not form a safe measure of past conditions, especially where they are very restricted in distribution, as is the case with most of our northerly species in this area, for there are too many possibilities of later accidental local introduction.

Larger floristic groups, taken collectively, form a much safer criterion.

An examination of the lists of Arctic plants* shows that of the species belonging to this northeastern Iowa flora, 8 prairie species and 6 swamp species extend to the far north, — neither group representing the major floristic conditions existing in the area, and all their members widely distributed, also extending eastward and northeastward.

There are 4 rock species as follows:

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* For Greenland, Durand (48), Gray (69) and Meehan (104): for the northern Arctic coast, Holm (76) and Johanson (82); and for northern Alaska, Rothrock (123), Gray (70) and Eastwood (49).

(In the lists which immediately follow the species preceded by A are known in the far north only from northern Alaska, those marked G, only from Greenland, and those unmarked have a wider northern distribution.)

A. — Arctostaphylos Uva-ursi
G. — Campanula rotundifolia
G. — Potentilla tridentata
G. — Woodsia ilvensis

Of the forest flora, which constitutes the most characteristic feature of the northeastern area, 16 species extend to the far north. They are:

A. — Adoxa Moschatellina
A. — Alnus incana
Aspidium spinulosum
A. — Arenaria lateriflora
G. — Bromus Kalmii (?)
Chrysosplenium tetrandrum
A. — Claytonia virginica
Cystopteris fragilis
Epilobium angustifolium
G. — Habenaria hyperborea
Linnaea borealis
G. — Phegopteris Dryopteris
A. — Phegopteris polypodioides
A. — Populus balsamifera
A. — Prunella vulgaris
A. — Pyrola secunda

Three species of this group, namely, *Bromus Kalmii*, *Epilobium angustifolium* and *Prunella vulgaris*, are often found in open places, but usually near the borders of thickets.

Most of the species named above have a wide distribution, extending far to the east and northeast of Iowa. Two of them, *Potentilla tridentata* and *Woodsia ilvensis*, are chiefly northeasterly in distribution, while one, the debatable *Chrysosplenium tetrandrum* seems to be chiefly northerly and northwesterly. Britton (17, p. 483) and Rydberg (124, p. 391) regard the Iowa form as distinct, and call it *C. iowense* Rydb.

In these northern lists there is a striking absence of the woody plants, and many of the easterly herbs, which predominate in our Iowa area. Only three woody plants appear, namely, *Alnus incana*, *Arctostaphylos Uva-ursi* and *Populus balsamifera*, and these are very rare and local, and constitute no striking part of our own flora. The same may be said of most of the plants in the northern list. The northerly species are here associated with the predominating forms of the area in the same manner as in the region to the northeast, and there is no valid foundation for the assumption that a part of this flora survived the Wisconsin ice on this area.

That this area was occupied quite early in the period of forest-invasion not only appears extremely probable because the deeply cut valleys offered immediate shelter to the advancing forest, but it is attested by the fact that this area, with its adjoining rough Kansan, contains the best developed climax groves with *Acer saccharum*, mixed with oaks as the dominant species, since *Fagus grandifolia*, the other dominating member of the climax *Fagus-Acer saccharum* association, eastward, is not native to Iowa. Only a few cultivated specimens have succeeded where well sheltered. The rough Kansan surfaces in the southern part of the state were also ready for the early advance of the southeastern and southern forests, but the somewhat lesser development of *Acer* groves suggests that the advance was later, or perhaps slower because of the less rugged character of most of the surface.

The prairie flora is spread irregularly over the entire state, and before man's invasion, covered the nearly level or exposed surfaces of the several drifts indiscriminately. This flora also suffered from the several advances of the ice, but its return was probably rather prompt after each withdrawal of the ice, and unaccompanied by any radical change in character. The promptness of the return would naturally result from the readiness with which the seed of most prairie plants is dispersed by the wind and migrating birds, and the re-establishment of the flora would be facilitated by the fact that the plants are herbs or small shrubs, and require less time for maturing.

Adams (3, pp. 63 and 65, and also 1) regarded the arid southwest as the center from which our prairie and plains floras were derived. This is evidently an error so far as the prairie flora is concerned, for, while in the prairie region there are a few species clearly of the west and southwest, such as *Yucca glauca* and *Mentzelia decapetala*, the bulk of the characteristic prairie flora connects directly with the region due south. Thus, in the list of Oklahoma plants recently published by Jeffs and Little (81), the writer finds more than 250 species of prairie plants which occur also in Iowa. This does not include western species, such as those mentioned above, nor does it include the species of the ecologically closely related open sandy grounds, of which there is a goodly number. The Iowa species of the latter group are, however, practically all included in the Oklahoma list. The writer travelled through Oklahoma, from what is now Ponca City to Oklahoma City, in 1891, prior to the opening of the Cherokee Strip to settlement, and there were then enormous areas covered with typical prairie. There were some species of plants not represented on our northern prairies, but the bulk of the vegetation consisted of species which make up our northern prairie flora. Subsequent visits have demonstrated that the destruction of native prairie has been quite as general in Oklahoma as in Iowa, and many species which were collected as common in 1891, are now quite rare or are distinctly local.

It is evident that when the ice retreated the prairie flora followed it northward from the region due south of us, and that the relative distribution of the plains and prairie floras has not been determined by the movements of the glacial sheets, but rather by climatic conditions in which relative drouth played the most important part.

The advance of the flora over the newly exposed glaciated surfaces could not have been uniform. Several floristic groups, requiring entirely different environment, spread out from centers which differed in marked degree in their floras, and finally met on the glaciated surfaces, but in unlike contiguous habitats.

It must not be assumed, however, that this advance was uniform for each floristic type, or that all progressed at the same rate. Undrained areas, forming lakes, ponds, and swamps, were soon ready for the reception of a hydrophytic flora, which was readily brought in by migrating aquatic birds, and even aquatic insects; the prairie and sand floras found the level denuded surfaces ready for their introduction by wind, and to some extent by other agencies; but the forest plants at first found no topographic shelter, excepting to a limited extent on some of the moraines, and, if present, were limited to the immediate borders of streams and lakes where the air was sufficiently moist for their maintenance.

The Wisconsin drift lobe, our most recently glaciated area, serves as a good illustration of the probable sequence of the advance of the several formational groups. The rounded and mostly low moraines offered indifferent shelter to forest plants, and as there were no larger adjacent forests, the advance over them was at first slow, and never resulted in really extensive forests.

The main Wisconsin plain had an abundance of lakes and kettleholes, especially in the northern part, where the aquatic flora was probably early established, and persisted to the present day where artificial drainage has not destroyed the suitable habitats.

The prairie flora also advanced freely over the open spaces, its vanguard in all probability consisting of those native lovers of disturbed or new surfaces, which the writer has previously designated as *native prairie weeds.*

This group includes such species as *Ambrosia artemisiifolia*, *Asclepias syriaca*, *Convolvulus sepium*, *Erigeron canadensis*, *E. ramosus*, etc. It will be discussed more fully later in the chapter.

This vanguard was probably followed quite rapidly by the main body of the prairie flora, no doubt passing through diverse degrees of adjustment before the prairie climax was reached. The wide open spaces were particularly well adapted to the development of this flora, as will be shown in the chapter on the prairie, and it probably took early possession of the drier areas to the exclusion at first of other formations.

The forest had no place upon this area until the streams had cut valleys of sufficient depth to give the needed protection to its distinctly mesophytic flora. As the valley deepened, and as lateral tributary valleys were formed, the forested areas spread until they covered considerable areas, as near Boone and Fort Dodge along the Des Moines River.

These forests, however, were not established in direct succession from the prairie, nor do they represent a final adjustment to prevailing general climatic conditions, for they developed primarily where these conditions had been overcome in part by topographic changes due to erosion. They did not gain a foothold until the prairie flora had been destroyed or weakened by erosion, and until new conditions, permitting the retention of a moister atmosphere in the valleys, had been created. Nor would they spread laterally to any appreciable extent in this general area until the surface had been cut by numerous protected valleys and ravines, in which the forest would find its beginning, and from which they could sometimes spread to a limited extent under conditions which the trees themselves had created by the lateral extension of their own crowns.

The period required for the erosion of sufficiently deep valleys for the development and protection of even the limited forests which were found on the Wisconsin area must have been very extensive. It is noteworthy that the upper courses of the larger streams of this area are not wooded even now, though in some cases they have cut valleys well below the general surface of the prairie. These shallow valleys, usually with rather gently sloping bluffs, did not offer sufficient protection to forest plants. But where more abrupt slopes were produced by the cutting stream, especially on its southern or western side, even though the bluffs were rather low, more or less restricted groves were developed. Note the scattered small groves along the upper courses of many of the streams in the prairie region, as represented on the map.

It is very evident that the prairie flora was quite well established before extensive erosion had taken place; that the invasion by the forest flora was made possible only as the cutting of the valleys provided protection from those climatic conditions which periodically dessicated the prairie plains; that no such invasion would have taken place had the original glacial plain remained unbroken; and that such invasion could not have started until long after the ice had retreated.

There is direct evidence of this later forest invasion in the vertical distribution of the fossil land snails of the loess. All the species exist today, and their habits are well known. Most of them are living in the state today, with few exceptions, inhabitants of groves and brush land. Their shells are rarely found in the lowermost parts of this dust deposit, and if so, are few, scattered, and of the kinds found in open places. As the groves developed and the deposit thickened, the snails increased, but they again taper out upward as the greatly increased accumulations brought about greater exposure to more xeric conditions, as in the western part of the state where the loess has attained great depth, and its ridges greater altitudes.

Incidentally, this same plant and snail evidence also shows that the loess on the older deposits, and most emphatically fossiliferous loess, was deposited after the flora was well established, serving as an anchorage for the loess dust, and that its formation was in no way related to near-glacial conditions.*

This is also confirmed by the present condition of the surface of the Wisconsin drift area. Erosion has been so recent that broad valleys with numerous sand-drift bars, forming the chief source of the loess dust, have not yet been formed; invasion by the forest flora has been comparatively recent; and the loess-like deposits are therefore quite thin and fossiliferous loess would rarely, if ever be found.

Surface conditions on the Iowan area are not radically different from those on the Wisconsin plain, and it is evident that these drifts are relatively not far apart in age. There are fewer kettleholes, and shallow drainage channels have been formed, which are usually

* See Shimek, B. 138.

more or less swampy near their heads, the latter probably representing remnants of earlier kettleholes. The comparatively slight erosion of the Iowan indicates that the Wisconsin followed it rather closely, and the surface conditions are very much the same, excepting that the stream valleys are frequently broader, and with numerous sandbars. The Iowan has also developed a little more loess, though most of it is on the morainic border.

The remnants of the Kansan drift plain indicate how persistent the prairie flora is on such exposed plains. The Kansan plain was covered with prairie, and groves developed only in the valleys carved out of it. Where no extensive erosion had taken place, the prairie persisted, and the remnants of the original plain were uniformly covered with prairie until cultivated. The process of erosion was probably delayed on these areas because they lack larger streams. Whatever the effect of subsequent ice-sheets which entered Iowa but did not cover these remnant plains, the prairie flora evidently continued to occupy them, or very quickly returned after each recession, and it held its own excepting where it was removed by erosion of the advancing valley. Here too, the prairie flora was not replaced by the forest flora in direct succession, but the latter appeared only where the former had been destroyed partly by erosion, and partly by new conditions created by erosion and not belonging to the prairie itself.

The climatic changes which resulted from (or caused) the advance and retreat of the ice-sheets have been the object of much study and speculation. It is difficult to avoid thinking of geological time in terms of current chronology, and thus failing to grasp its magnitude. Undoubtedly thousands of years are involved in these changes, and even the last retreat of the ice is now estimated by geologists as having occurred at least 25,000 years ago. That the period of the more radical adjustment of the flora had been passed long ago is suggested by the fact, cited by the writer (137), that the prairie flora of Manitoba, lying at least 8° north of central Iowa, is almost identical with that of this state. The climax in Iowa had evidently been reached long ago, and the prairie flora was subject only to the fluctuations which occur in every climax, and to the local climatic changes resulting from erosion.

Unfortunately, the fossil material which might throw light on the character and length of the interglacial and post-glacial periods is comparatively scant, and there has been a tendency to exaggerate or misinterpret its true value in the urgent attempt to reach definite conclusions.

The Toronto interglacial beds. An excellent illustration of such exaggeration of evidence offered by fossil material is furnished by the case of the interglacial Don and Scarboro' beds at Toronto, Canada. As this is assumed to furnish definite evidence of just such fluctuations in climate under glacial influences as are ascribed to our own territory, Toronto being located at about the latitude of middle Iowa and its drift-sheets being extensions of those found here, this case is worthy of more detailed notice in this connection.

The interglacial deposits which have been studied most fully are located on the north shore of Lake Ontario, and have become famous particularly through careful and detailed studies of Hinde, Penhallow and Coleman. Two series of sections have received special attention in geological literature, that along the valley of the Don at Toronto, and that at Scarboro' heights, a bluff extending northeastward along the shore of Lake Ontario for about 5 1/2 miles from a point about 9 1/2 miles northeast of Toronto, and ranging from 140 to 190 feet in height.

The first detailed description and figure of the Scarboro' section was published by Hinde (75), though it had received some attention much earlier.* Hinde showed two interglacial beds alternating with three drift-sheets. There has been some dispute among geologists as to the age of these drift-sheets, some regarding the underlying drift as Illinoian, and others as Iowan. Perhaps there is some reason for regarding the lowest drift in Hinde's section as Illinoian and the two later respectively as Iowan and Wisconsin, but the exact horizon is not a matter of serious consequence, the important point being that we have here interglacial deposits which contain abundant remains of still existing species of plants and animals which have been widely employed as evidence of climatic conditions existing during the interglacial interval.**

From the lower Scarboro' interglacial deposit Hinde reported

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* Memoirs by Sanford Fleming and H. Y. Hinde (58) and A. C. Ramsay, (116).

** Bensley (11) also suggested that the fossiliferous Toronto beds might be Aftonian, our oldest interglacial deposit. He based this opinion on a fragment of a *Cervalces* antler found at Toronto, but he also stated that it "had doubtless been transported from another region." It is also possible that it might have been washed out from some older deposit. It is because of the doubtful status of the few fragmentary mammalian fossils from these beds that they are disregarded in the following discussion.

three genera of diatoms, a *Chara*, three genera of mosses, and fragments of wood and leaves of several flowering plants, including a pine and a cedar, and the following animals; one crustacean, one beetle, and two snails, one freshwater and the other terrestrial.

A much more thorough study of the fossil plant material from both the upper interglacial bed at Scarboro' and the lower interglacial bed in the Don valley at Toronto, was made by Penhallow, (109, 110, 112, 113) and also by Dawson (46).

These studies, coupled with those made on the fauna by Coleman (31, 33) have formed the basis of definite conclusions concerning the climatic conditions which existed during the interval represented by these fossiliferous deposits. Hinde (75, p. 28) was of the opinion that the climate during the formation of the fossiliferous deposits at Scarboro' was "temperate, similar to the present," but the authors who followed him uniformly concluded that within the total period there had been marked changes in climate, the lower bed in the Don Valley representing a period warmer than the present, while the fossiliferous bed at Scarboro', stratigraphically above the Don bed, was formed in a colder climate.

Penhallow presented this conclusion most definitely (110, p. 334) in the following statement "— it may be repeated at this time that the definite and abundant occurrence of *Maclura aurantiaca*, *Juniperus virginiana*, *Quercus obtusiloba*, *Quercus oblongifolia*, *Asimina triloba*, *Chamaecyparis sphaeroidea*, and *Fraxinus quadrangulata* points without question to the prevalence of a much warmer climate than now prevails, while, on the other hand, the equally abundant occurrence of boreal types at Scarborough points to the existence of a colder climate at the time these deposits were laid down."

This conclusion has been widely accepted, though Dawson previously (44, p. 92) had more cautiously expressed the opinion that "judging by the flora and fauna the climate was by no means subarctic, but on the contrary fully as mild as at present, if not a little milder." Penhallow's conclusion, however, has been adopted without question by many geologists and botanists.

Thus, Chamberlain and Salisbury (26, p. 491), referring to the fossil plants of the Don beds, state that "many of these species indicate a climate appreciably warmer than that of Toronto at present," and that the "cold-climate fauna and flora in the Scarboro' beds — implies a cold-temperate climate of about the type which now prevails in the region just north of Lake Superior, or that of southern Labrador.''

Penhallow, himself, restated (112) his conclusions in similar terms, representing the Don climate as equivalent to that of Virginia.

Scott (127) accepted the same view and declared that the fossils of the Scarboro' formation ''indicate a cold temperate climate and herald the approach of a renewed glaciation.''

Some botanists have been quite as willing to accept the conclusion without closer analysis. Thus, Harshberger (73, pp. 185-187) repeats Penhallow's statement concerning the significance of the southerly plants in the Don beds, concurs in the view that the Scarboro' climate was like that of Quebec and Labrador and reprints his comparative table for the fossil plants of the Don, Scarboro' and Green's Creek beds.

Even a more emphatic endorsement is given by Clements (29, p. 400) who asserts that ''Penhallow (110) has made by far the most important contribution to the study of the Pleistocene clisere of America,'' and also reprints his comparative table of fossil plants from these beds.

Despite the concurrence of these distinguished students, an analysis of these fossil floras and faunas does not bear out the accepted conclusions. Before this analysis is attempted, it is necessary to recall that Toronto is located near the head of a floristic and faunistic lobe which projects much of the southerly biota into the region of the Great Lakes, and particularly into southern Michigan and southern Ontario. The writer has briefly previously called attention to this lobe (138, p. 676) but its relation to the Toronto problem is so important that it is worthy of additional attention.

It is a well-established fact that the Great Lakes temper the severity of both summer and winter extremes of temperature and that they increase the relative humidity in their vicinity much above that of other parts of the Mississippi basin at the same latitude. This equalizing tendency has resulted in the development of an extension of a more southerly flora and fauna in a lobe which includes southern Michigan and southern Ontario, as noted. The result is that southern Ontario has a hardwood flora which in many respects resembles that of the Ohio valley, as was noted by Howe and Dymond (1926, p. 288),* who stated that this hardwood flora extends

* Citation not located. — Ed.

to "a line drawn from the most western point of Lake Ontario to the southernmost point of Lake Huron," but that outliers of this type may be found as far north as Toronto.

In this territory the ordinary hardwoods of the north-central region prevail, such as the following:

Acer saccharinum	*Populus deltoides*
Acer saccharum	*Populus grandidentata*
Acer Negundo	*Quercus alba*
Carya cordiformis	*Quercus macrocarpa*
Carya ovata	*Quercus Muhlenbergii*
Crataegus punctata, etc.	*Quercus rubra*
Fraxinus americana	*Quercus velutina*
Fraxinus nigra	*Salix amygdaloides*
Juglans cinerea	*Salix nigra*
Juglans nigra	*Tilia americana*
Ostrya virginiana	*Ulmus americana*
Platanus occidentalis	*Ulmus racemosa*, etc.

Most of these species extend well southward, but they form the common hardwood groves in the region including southern Ontario.

In addition to these species there is a group of southerly forms which extend into southern Ontario. Some of the more striking are the following woody plants:

Asimina triloba	*Magnolia acuminata*
Castanea dentata	*Nyssa sylvatica*
Cercis canadensis	*Quercus bicolor*
Cornus florida	*Quercus palustris*
Fagus grandifolia	*Quercus Prinus*
Fraxinus quadrangulata	*Sassafras variifolium*
Liriodendron Tulipifera	*Tecoma radicans*

Aesculus glabra, a native of southern Iowa, which would naturally be associated with some of the members of this group, is not native in Ontario, but grows freely in cultivation.

Of the species in this list the *Castanea, Cornus, Fagus, Liriodendron, Magnolia, Nyssa, Sassafras* and *Quercus Prinus*, are not natives of Iowa. The remaining species occur only in the southern or southeastern part of the state with the exception of *Quercus bicolor*, which extends along the Mississippi nearly to McGregor. Four southerly herbs may also be added:

Frasera carolinensis	*Mikania scandens*
Gillenia trifoliata	*Rhexia virginica*

Of these only the *Rhexia* occurs in southeastern Iowa. This list distinctly emphasizes the fact that Iowa receives merely the western rim of this southern lobe, or its lesser off-shoot which follows the Mississippi river valley into the southeastern part.

It is a significant fact that these southerly species are accompanied in their northerly venture by a group of land-snails, mostly of larger forms. The following species known to occur in southeastern Michigan are of this type:

Anguispira solitaria
Gastrodonta ligera
Gastrodonta multidentata
Omphalina fuliginosa
Polygyra elevata
Polygyra fallax
Polygyra inflecta
Polygyra palliata
Polygyra Sayi
Polygyra thyoides
Polygyra thyoides bucculenta
Polygyra tridentata
Polygyra zaleta

Of these species only *Polygyra thyoides* reaches the eastern part of Iowa, these colonies of snails evidently following only the denser forests.

The complete list of plants reported from the interglacial beds of the Toronto region will be of value in comparison with the preceding lists of modern forms, and a similar comparison of the fossil mollusks from the Don beds, here nearly all freshwater species, with those of today. Attention is given chiefly to the flora and fauna of the lower, or Don beds, which are generally assumed to represent a warmer climate. Comparative notes on the lesser flora of the upper, or Scarborough beds, usually regarded as of colder-climate origin, are also included. (Some writers use this form of the name, while others adopt the abbreviated form Scarboro'.)

The plant lists are compiled from the lists of Penhallow (109, 110, 112, 113), while the lists of mollusks are taken from Coleman's papers (31, 32, 33, 34), who also includes Penhallow's plant lists.

Fossil plants. The doubtful, presumably extinct, forms named by Penhallow as *Acer pleistocenicum*, *A. torontoniensis* and *Gleditschia donensis*, are not included in the general discussion but receive special attention, for if they are extinct species they cannot serve as a reliable basis for climatic determinations or comparisons. For the same reason the plants designated only by generic names are also omitted, since each one of these genera includes species differing in habitat, or at least in geographic distribution. Such are the forms listed from the Don beds as follows:

Chara	*Hypnum* (moss)
Cyperus	*Picea* (unnamed species)
*Eriocaulon**	*Prunus*
Fontinalis (moss)	*Salix*

The species from the Don beds are arranged in three groups, — those which are now inhabitants of the general region; those which belong in the main to a more southerly flora, but reach Ontario in the projected tongue or lobe from the south; and those which belong to a more northerly flora. A small group of doubtful or non-distinctive forms is also noted.**

1. Inhabitants of the general region:

Carya ovata (alba)	*Quercus alba*
Crataegus punctata	*Quercus macrocarpa*
Fraxinus americana	*Quercus Muhlenbergii (acuminata)*
Fraxinus nigra (sambucifolia)	*Quercus rubra*
Festuca ovina	*Quercus velutina (tinctoria)*
Ostrya virginiana	*Tilia americana*
Populus grandidentata	*Typha latifolia*
Potamogeton natans	*Ulmus americana*
	Ulmus racemosa

2. Southerly species:

Asimina triloba	*Juniperus virginiana*
Cercis canadensis	*Maclura pomifera (aurantiaca)*
Chamaecyparis thyoides (sphaeroidea)	*Platanus occidentalis*
Fraxinus quandrangulata	*Quercus stellata (obtusiloba)*

3. Northerly species:

Acer spicatum	*Pinus Strobus*
Hippuris vulgaris	*Populus balsamifera*
Larix laricina (americana)	*Taxus canadensis*
Picea mariana (nigra)	*Thuja occidentalis*

It will be observed that all but two of the species in the first, or general list, are also found in the list of species characteristic of southern Ontario hardwood groves. The first of the two exceptions is *Festuca ovina*, a grass which is a native of the Great Lakes re-

* In 1898 Penhallow (113) reported this as *E. septangulare* (?), now called *E. reticulatum*, but it does not appear in subsequent lists. If this determination of the species should prove to be correct, it would only add one more species to those of the Don list which now inhabit Ontario.

** The nomenclature of Gray's Manual, 7th ed., (71) is followed for the vascular plants. Where the species was reported under a name now regarded as a synonym, the latter is given in parenthesis.

gion; and the second is the widely distributed *Typha latifolia*, or common cat-tail. All the species of this first list are well represented in the modern flora of southern Ontario. All these species also reach Iowa.

The second list includes a group of southerly species the northern limit of whose distribution is found in most cases not far from Toronto, some of them occurring in the outliers to which reference has been made. This is the group upon which Penhallow and those who accept his views, placed their chief reliance in the effort to prove that the climate of the Don period was milder than that of the present. Penhallow was very positive in his conclusions. Thus, he declared (Dawson et al. 46, pp. 337-338) that "it may be repeated at this time that the definite and abundant occurrence of *Maclura aurantiaca, Juniperus virginiana, Quercus obtusiloba, Quercus oblongifolia, Asimina triloba, Chamaecyparis sphaeroidea,* and *Fraxinus quadrangulata* points without question to the prevalence of a much warmer climate than now prevails, while, on the other hand, the equally abundant occurrence of boreal types at Scarborough points to the existence of a colder climate at the time these deposits were laid down." This statement was quoted in full, without dissent, by both Harshberger (73, p. 184) and Clements (29, pp. 400-401), and it received the approval of Chamberlain and Salisbury (26, p. 491) and others.

Later, Penhallow (112, p. 451) made this still more emphatic in the following declaration: "The present studies serve to give renewed emphasis to the idea which has now passed beyond the limits of a working hypothesis, that successive northerly and southerly movements of the continental ice sheet, involving corresponding movements in vegetation, were productive not merely of plant migration from north to south and vice versa, but that they established conditions which permanently eliminated those species which, we may suppose, occupied a somewhat unstable position in the flora and were therefore susceptible to a relatively slight change of surroundings." In this paper Penhallow also reported two additional trees from the Don beds, namely, *Cercis canadensis* and *Ostrya virginiana*. He regarded the *Ostrya* as "essentially a southern type," despite its wide northerly range to Nova Scotia and Manitoba, because the largest trees are found in the south. In an earlier paper (109, p. 76) he had also regarded *Ulmus americana, U. racemosa* and *Platanus occidentalis* as southerly because of their greatest development in the south, and considered it proper to even include *Picea mariana* (*nigra*) and *Taxus canadensis* because they extend well to the south of Toronto. These were not included, however, in his well-known list of southern species noted above (110).

Analysis of this group of the Toronto fossils does not sustain the positive declarations that the climate during the formation of the Don beds was warmer than it is at present.

One species of this group, *Quercus oblongifolia*, appears in the 1900 list, but this must be an error in identification or transcription, for this species is confined to the far, dry southwest, and it does not again appear in any of Penhallow's later lists. Manifestly this species cannot be included as an index of climatic conditions in the Don area.

Quercus stellata (called *obtusiloba*) was first reported from the Don beds by Coleman (31, pp. 87 and 95) on the authority of Penhallow. Later Penhallow (109, p. 68) published it himself, but stated that the identity was uncertain because the wood, constituting the fossil material, had been altered. Both reported the species as living in southern Ontario. Penhallow did not include it in his report of 1898 (113), but referred to it as one of the southern species in 1900 (110, p. 338), without additional information as to the certainty of its identification. He, however, again omitted it from his report of 1907 (112, pp. 443-452). Macoun (99, p. 440) had not found this species living in Canada, but reported it on the authority of others. Britton and Brown (18, vol. I, p. 520) report it from Michigan. In view of the fact that there is some doubt as to the correctness of the identification, and that *Q. stellata* does extend into Michigan and southern Ontario, the presence of these wood-fragments in the Don beds offers no evidence of climatic changes in the region under discussion. It should also be noted that oak outliers, far removed from larger forests of their own kind, are not uncommon, notable examples in Iowa being the small "islands" of *Quercus alba* and *Q. rubra* in the northwest; *Q. velutina* in the west; and *Q. lyrata*, *Q. marilandica*, *Q. imbricaria* and *Q. stellata* in the south. Similar outliers of *Q. stellata* may have appeared at Toronto during the Don period without any marked change in climate.

The same statement applies to *Fraxinus quadrangulata*. This was similarly first reported in Coleman's paper (31, pp. 87 and 94). Here, too, Penhallow (109, p. 68) questioned the correctness of the identification of the wood which had been found, saying that "the species was a matter of considerable doubt'' as ''the structure of the wood was found to be greatly altered.'' He later stated (113, p. 527) that this may be *F. nigra* (called *sambucifolia*), a species which extends northward to Newfoundland and Manitoba, and is included in the list of more generally distributed species. A single fruit in rather imperfect condition, collected by the writer in the lower part of the Don beds at Toronto in 1916, resembles *F. nigra* rather than *F. quadrangulata*, but the fruits of the two species are quite similar. In his last report (112, pp. 443-452) Penhallow omits this species. Sargent (125, p. 762) and Gray's Manual (71, p. 651) credit the latter species to Michigan, while Britton's Manual (17) reports it from Ontario, and Macoun (98, p. 317), from the north shore of Lake Erie. Whether correctly identified or not, the species does not indicate any marked change in the climate of Toronto.

Two of the species, presumed to be indicative of a warmer climate, namely, *Juniperus virginiana* and *Platanus occidentalis*, are now living in the vicinity of Toronto (Macoun, 99, pp. 462 and 432, etc.), the former extending much farther north, and for this reason may be dismissed as climate indicators, though, like all the species of this group, they do extend far to the south.

Two additional species in this list are reported from southern Ontario. *Asimina triloba*, first reported from the Don beds by Penhallow in 1900 (110, pp. 337-338), according to Macoun (97, p. 28), extends along the north shore of Lake Erie. *Cercis canadensis*, reported from the Don beds by Penhallow (112, pp. 446 and 450), is not included in the flora of Canada by Macoun, but both Gray's (71, p. 505) and Britton's (17, p. 529) Manuals report it from southern Ontario. While both are southern species, they reach so near to the Toronto region in the northward extension of the southerly ecological lobe that their disappearance from the immediate Toronto region may well have been merely a result of the fluctuations which everywhere occur in border areas. Certainly no marked change in climate would be necessary to account for their retreat of a few miles, especially since equally southern species, such as *Magnolia acuminata*, *Nyssa sylvatica* and *Sassafras variifolium*, persist farther to the north.

This leaves but two species, *Chamaecyparis thyoides* and *Maclura pomifera*, which do not approach the region under discussion, though the former, now seemingly occurring only far to the south and east, is said by Gray's Manual (71, p. 66), to be ''doubtfully indigenous in Nova Scotia, and said to have been originally collected in Canada by Kalm." Macoun (99, p. 461) also credits it to Nova Scotia under the name *Thuya sphaeroidea*, but adds: "Whether planted or indigenous — we have no means of determining, but one beautiful tree is growing at Windsor, Ontario, where it was planted many years ago."

Maclura pomifera is a distinctly southern species, which has not been reported from Ontario. Otis (107, p. 133) however, states that it is extensively planted for hedges, and is "hardy throughout Michigan."

Both cases suggest that, assuming the identification to be correct, these species are absent from Ontario for other than climatic reasons. In view of the more general northward extension of southern plants into this region, and their persistence today, the failure of one or two species would seem to offer wholly insufficient evidence of general climatic changes.

While this presence of southern species in the Don beds is striking, it is equally notable that this flora contains a number of northerly species which would ordinarily be regarded as pointing to a cooler climate. The more striking are:

Acer spicatum
Festuca ovina
Hippuris vulgaris
Larix laricina (americana)
Picea mariana (nigra)
Pinus Strobus
Populus balsamifera
Taxus canadensis
Thuya occidentalis

All these species are northern in their main occurrence, though several extend southward (particularly in the mountains). They belong quite as distinctly to the north as the "warm-climate" species of the same list belong to the south, and it would be just as logical to use them as evidence that the Don period climate was colder than that of the present.

The Scarborough flora is no more convincing as proof of a colder climate for that period. Penhallow's comparative list (110, pp. 338-339) contains the following plants in the Scarborough column:

Abies balsamea
Alnus sp.
Carex aquatilis
Carex rostrata var. *utriculata* (called *C. reticulata*)*
Equisetum sp.
Fontinalis sp.
Hypnum commutatum
Hypnum revolvens

* This was reported as *C. reticulata* by Penhallow, and the name was thus

Larix laricina (as *L. americana*)
Lycopodium sp.
Picea canadensis (as *P. alba*)
Salix sp.
Vaccinium Oxycoccos (as *Oxycoccus palustris*)
Vaccinium uliginosum

The *Alnus*, *Equisetum*, *Fontinalis*, *Lycopodium* and *Salix* may be northern species but in the absence of definite identification they throw little light on differences in climate, especially since all these genera are represented by living species in the Toronto region. The mosses, *Hypnum commutatum* Hedw. and *H. revolvens* Schw. are northerly species, and Macoun (100) reports *H. commutatum* (p. 232) from New Brunswick and North Hastings, Ontario, and *H. revolvens* (p. 227) from Lake Superior, etc.

But Lesquereux and James (88, p. 387) report *H. commutatum* from Watkin's Glen, New York, and *H. revolvens* (p. 384) from northern Ohio, and a variety from Niagara Falls. These species also fail to establish a colder climate for the Scarborough beds since they exist today in regions lying south of the latitude of Toronto.

The remaining species are all northerly, but most of them extend well south of the latitude of Toronto. This is true of *Abies balsamea*, both species of *Carex*, *Larix laricina*, and *Vaccinium Oxycoccos*. This leaves only *Picea canadensis* and *Vaccinium uliginosum*.

Howe and Dymond (1926, p. 289)* list the following conifers in the mixed hardwood-coniferous association, outliers of which extend to Toronto:

Abies balsamea
Picea canadensis
Picea mariana
Pinus Strobus
Thuya occidentalis

It will be observed that this list contains *Abies balsamea* and *Picea canadensis* (both included in the "colder-climate" Scarborough flora) and that the remaining species are all included in the Don list which is presumed to belong to a warmer climate.

Vaccinium uliginosum, the sole remaining species, is reported by Britton (17, p. 709) from the Adirondacks to Lake Superior and north and west, and Gray (71, p. 640) gives the range as from Arctic America south to northern Michigan and the mountains of north-

copied by both Harshberger (73, pp. 185-187) and Clements (29, p. 400). This should have been *C. utriculata*, a variety of *C. rostrata*. Penhallow also listed *Carya alba*, which Clements interpreted as *Chara alba*, but Penhallow later (111) gave it as *Carya alba* (now *C. ovata*), which was also recognized by Harshberger.

* Citation not located. — Ed.

ern New York. This brings the southern limit sufficiently near to the Toronto region to make possible the development and disappearance of outliers of this species in that vicinity.

There is also another possibility in the case of this as well as other species recognized in the Toronto flora. From the very nature of the fragmentary material the accurate determination of species in many cases is extremely difficult, if not impossible. Penhallow himself recognized this fact, for he called attention (113, p. 527) to the difficulty of recognizing "such genera as *Ulmus, Fagus, Carpinus, Ostrya,* etc." and surely the difficulty would be no less with the genus *Vaccinium*, the species of which are often difficult enough to distinguish even when in a full-fledged living condition.

Whether the species are correctly identified or not, there is nothing in the aggregations of plants to warrant the conclusion that the climate of that period differed from that of today, or that the two divisions, represented respectively by the Don and the Scarborough beds, were distinctly different in climate. The simple fact is that the general deciduous forest list of the Don beds, the "southerly" and "northerly" lists from the same beds, and the "northerly" list from the Scarborough beds, point, by their close association in the same region, to just such mixed or intermediate coniferous-hardwood floristic combinations as occupy the general Toronto region today. Differences similar to those between the Don and Scarborough flora could no doubt be duplicated today in many places in the same region by a careful selection and comparison of the different local floristic groups which appear more or less abundantly in such border areas.

Extinct (?) species. — The three forms from the Don beds, described as new (extinct) species by Penhallow, are deserving of an additional note because they are a type of the flimsy paleobotanical "evidence" which was so often accepted in the past. These forms are: *Acer pleistocenicum, A. torontoniensis* and *Gleditsia donensis.*

Acer pleistocenicum was first described and figured from a single leaf in 1890 (108, pp. 327-328) and later (112, p. 445) another from a later collection in which "one or two (leaves) are nearly perfect." A comparison of these figures with a large series of leaves of *Acer saccharum* (a common species of the Toronto region) shows that the former deviates but little from common forms of the latter, and that this deviation is no greater than that which will be shown in any large series of leaves of the modern species. Penhallow, however, compared it (108, p. 329) with *A. rubrum* and *A. platanoides*, — the latter an introduced species, — in the following words: "The venation is most nearly comparable with that of *Acer rubrum*, where, as in the fossil, only two veins are arranged palmately with the midrib." *Acer rubrum*, however, often has five distinct palmate ribs, while some forms of *A. saccharum* have only three prominent ribs. He also stated that the fossil form "approaches *A. platanoides*, from which it differs in its much broader terminal lobe and in the broader and more shallow sinuses." In both these characters the fossils agree much better with *A. saccharum*.

Acer torontoniensis was described (112, pp. 444-446) from leaves collected from the Don beds. Two leaves are shown in Fig. 2 (p. 447). Both are somewhat imperfect, and show only the larger veins. Penhallow (112, pp. 444-445) compared it with its "nearest representative," *A. saccharum* and stated that the chief difference is "in the forms of the sinuses and in the character of the larger teeth or smaller lobes." The variation in these two characters in *Acer saccharum* is so great, however, that it would easily include those of the fossil. The basal sinuses of the fossil leaves in the figures, however, are much wider than those of any *A. saccharum* which has come to the writer's notice. It is evident, however, that the fossils are not far removed from *A. saccharum*. Penhallow regarded the former as the ancestral type of the latter.

Gleditsia donensis was also named as a new species by Penhallow (112, p. 446), but without description. He stated that "one or two leaflets are clearly comparable with those of the Genus *Gledits(ch)ia*—." In the absence of both a figure and description, it can only be said that this is probably *G. triacanthos*, a species now living in Ontario, the range of variation in the form, size and venation of the leaflets of which probably includes these characters of the fossils.

These fossil forms, if distinct, throw no light on climatic conditions, and if they belong to the species named they merely confirm the modern character of the Don flora, developed under conditions not unlike those of today.

The fauna of the Don and Scarborough beds. — Much emphasis has also been placed on the fauna of these beds as confirming the differences in climate which seemed to be shown by the somewhat diverse floras. By far the greater part of the animal remains consists of fragments of beetles in the Scarborough beds, and shells of mollusks in the Don beds.

The list of beetles from the Scarborough beds was first published by Coleman in 1900 (32, p. 332) and republished in 1901 (33), and again in 1906 (34, pp. 17-18). The beetles were identified by Dr. S. H. Scudder, and Coleman noted (34, p. 18) that 70 of the 72 species are extinct, but that Dr. Scudder thought that relationship to living species shows that "the coleoptera— indicate a climate closely resembling that of Ontario today." This fauna evidently gives scant support to the view that the Scarborough climate was colder than that of the present time!

Greater stress has been placed on the evidence of a warmer climate for the Don beds as found in their molluscan fauna. A list of mollusks (identified by Dr. Wm. Dall and C. T. Simpson) was first published by Coleman (31, p. 87) and repeated with some additions in 1900 (pp. 32, 331), 1901 (pp. 33, 291-292), and 1906 (34, p. 16), including even three misspelled names. Simpson (140, pp. 591-595) also published the same list of mollusks, and discussed the distribution of the species. These several lists include the following species of larger lamellibranchs (bivalves), all but the first one of which were placed in the genus *Unio*, since subdivided into several genera. The names in parenthesis are those under which the species appeared in Coleman's lists:

Anodonta grandis Say.
Lampsilis luteola (Lam.) Bak. (*U. luteolus*)
Lampsilis recta (Lam.) Smith. (*U. rectus*)
Lampsilis ventricosa (Barnes) Stim. (*U. occidens*)
Pleurobema clava (Lam.) Ag. (*U. clavis*)
Ptychobranchus phaseolus (Hild.) Simp. (*U. phaseolus*)
Quadrula pustulosa (Lea) Bak. (*U. pustulosus*)
Quadrula pustulosa var. *Schoolcraftensis* (Lea) Simp.
Quadrula pyramidata (Lea.) Simp. (*U. pyramididatus*)
Quadrula solida (Lea.) Simp. (*U. solidus*)
Quadrula undata (Barnes) Walk (*U. trigonus*)
Quadrula undulata (Barnes) Bak. (*U. undulatus*)

To this list the writer added the following species from the lowest part of the Don beds, in 1915:

Obovaria ellipsis (Lea) Simp. (*U. ellipsis*)

In addition to this, the following smaller mollusks were included in the lists:

Bivalves.
Sphaerium 5 sp.
Pisidium 3 sp.

Gill-bearing water snails.
Pleurocera 3 sp., 1 doubtful
Goniobasis 2 sp.
Campeloma 1 sp.
Somatogyrus 1 sp.
Amnicola 3 sp.
Bythinella 1 sp.
Valvata 2 sp.

Freshwater pulmonate snails.
Lymnaea 2 sp.
Physa 2 sp.
Planorbis 2 sp.

Terrestrial pulmonate snails.
Bifidaria 1 sp.
Succinea 1 sp.

To this list the writer added the following species in 1915, — also from the lowest part of the Don beds:

Physa gyrina, a pond pulmonate.
Zonitoides arboreus, a terrestrial pulmonate.

Of the larger bivalves, upon which special stress has been placed in this connection, only two species, *Quadrula pyramidata* and *Q. solida,* are not known from the St. Lawrence River drainage (See Simpson, 1914).* One of the species, *Ptychobranchus phaseolus* reaches only the southern peninsula of Michigan, but it is well within our drainage area.

Of the two species which do not reach this drainage area, *Quadrula pyramidata* extends north to Prairie du Chien, Wisconsin, and is restricted to the Mississippi basin; and *Quadrula solida* extends north to Minnesota and Wisconsin, and also seems to be found only in the Mississippi River drainage area. The latter species is difficult to define, for as Simpson observes (1914, p. 886)* "it is almost impossible to draw up a description that will characterize all the variations of this protean species and separate it from the other closely allied forms." Among these closely allied forms are *Q. pyramidata, Q. obliqua* and *Q. coccinea.* It should also be added that competent authorities (see Simpson, 1914, pp. 882-884, and 889)* regard *Q. pyramidata* and *Q. obliqua* as forms of *Q. coccinea,* which occurs in the St. Lawrence drainage area.

Even if these species are distinct, however, their absence from the St. Lawrence area cannot be ascribed to climate, as both extend north of the latitude of Toronto in the Mississippi valley. Neither is it necessary to assume (see Simpson, 140, p. 593) that ice

* Citation not located. — Ed.

dammed the waters of the St. Lawrence and the Great Lakes until they overflowed into the Mississippi, to account for the presence of the two Mississippi River mussels in the Don beds. Mollusks, and especially bivalves, are no doubt frequently carried by migrating birds.

Many years ago the writer shot a solitary sandpiper which was flying, in rather erratic fashion, over a ridge in the bend of the Iowa River opposite Coralville. It was found that the bird had a living specimen of a rather large *Calyculina transversa* (one of our smaller bivalves) clinging to one of the toes.

Dr. Paul Bartsch of the U. S. National Museum recently submitted a photograph showing a duck which had finally been killed by a specimen of *Unio complanatus* still adhering to a toe which had been disjointed and hung by a tendon which had been drawn out by the weight of the mussel.

Smaller water snails are also carried by water-beetles and water-birds, and since all these forms may live for hours and even days after being removed from water, it would be possible to transfer them not only from one* body of water to another, but from one drainage system to another. It would certainly be possible to have the two species transferred from the Mississippi to the Great Lakes basin without assuming the violent conditions quoted by Simpson (140, p. 593), namely, that the surface of Canada was 1000 feet higher than at present, and that it was covered with ice to a depth of 3000 to 6000 feet, a condition deemed necessary to the assumed connection between the waters of the Great Lakes and the Mississippi River.

It is evident that the fauna fails quite as completely as the flora to sustain the widespread belief that the climate of the Don period was distinctly milder than that of the present in the same region.

Detailed attention is here given to the Toronto beds because they contain the richest interglacial deposits of plant remains known on this continent; because they throw light on conditions which existed during an interglacial period which extended into Iowa; and

* Prof. F. M. Witter, for example, reported (157) that 12 specimens of *Unio camptodon*, collected by him at Emporia, Kansas, "were found to be alive after remaining out of water, in a very dry place, from July 22nd till Aug. 29th 1886. They were kept alive at Muscatine in a tub of water till about the 1st of Jan. 1887.

The writer has repeatedly found mussels (especially those with heavier shells) alive after being kept out of water for several days.

because the history of the cases illustrates the ease with which sweeping conclusions may be (and often are) drawn on the basis of insufficient evidence, especially where glacial and interglacial conditions are involved.

We naturally rightly assume that as the several ice-sheets advanced there was both gradual destruction and emigration of plant and animal life, and that as the ice receded there followed a restoration of the fauna and flora. This would involve gradual change in climate and consequent biotic adjustment at both extremities of the interglacial periods.

The evidence of the Toronto beds, with their thickness and fossil content, shows that the period of moderate climate, similar to that of the present, was extensive, resulting in the development of a biota also similar to that of the present, and it suggests that the periods of more drastic climatic changes at both extremities of at least the later interglacial periods, were comparatively short, leaving but little (if any) evidence of the changes in biota. The reinvasion of the flora at the beginning was evidently quite rapid, leaving a long intermediate period for those minor changes marked by the introduction and elimination of individual species, and its going out was probably again comparatively abrupt. The character of the Toronto fossil biota suggests that we are now experiencing another stage (now post-glacial but later probably to become interglacial) which is similar in its climate, as it is in its flora, to the period during which the Don and Scarborough beds were being deposited.

Interglacial and post-glacial fossils in Iowa. — Evidence of interglacial or immediate post-glacial floras in Iowa is very scant. Occasional fragments of wood are reported from wells, but specific references to identified material are few, and they apply chiefly to a few mosses, diatoms and to coniferous wood mostly of doubtful identity. These are of little direct interest in connection with the problem of our present floras, because they belong to older interglacial periods and are perhaps, of little importance in connection with the development of our modern floras,* though they point to the probable repetition of similar conditions during the several interglacial intervals.

* Bibliographic references to this subject will be found in the Reports of the Iowa Geol. Sur., Vol. XIX, 1909, pp. 731-733; and Vol. XXII, 1912, pp. 707-709 and 715-717.

Peat beds. — Of much more importance are the post-glacial peat-beds within the Wisconsin drift lobe. They have received some attention in Iowa (see Beyer, 13), but they have not been studied sufficiently with a view to the determination of biotic succession. A direct step in this direction was taken by Lane (85) in his preliminary analysis of fossil pollen from the East McCulloch peat-bed in Hancock County. Similar pollen studies have been carried on in Europe, particularly in Sweden, for nearly a quarter of a century, and in this country they have been taken up more recently, especially by Sears and his associates. The general conclusion based on the study of bogs within the Wisconsin area (after all quite limited in scope in America) has been that fossil pollen, taken from different depths, shows that there has been a fairly uniform advance from early coniferous forests to deciduous forest and prairie.

While these studies are of great interest and give promise of results, there seems to be little doubt that these conclusions concerning climatic conditions, as exemplified by the successive floras represented by fossil pollen have been altogether too sweeping and too positive. This definite assertion of conclusions on insufficient studies of pollen alone is likely to result in the subconscious bending of evidence to find support for the conclusions, and to the neglect of evidence lying in other fields.

Sears (128, p. 95) and Erdtman (52) have called attention to the difficulties which attend this work. Sears' statement, given in numbered sections, is here presented with additional comments under each number:

1. — "There are no comprehensive manuals of pollen structure." This is still true, though such a key was attempted as early as 1835 by Hugo von Mohl (105) for European plants (see also, Wodehouse, 158). In this country Pope (115) attempted it for northern Colorado flowers, and Sears (128, pp. 98-101) prepared a more comprehensive key, but unfortunately the identifications are limited mostly to genera and families.

2. — "Pollen grains in bogs act as centers for flocculation of organic and inorganic materials, and are not always easily loosened from the matrix."

The violent methods used to free the pollen grains probably cause the destruction of more delicate forms.

3. — "It is not always possible even for an expert to distinguish related genera by their pollen, much less species of the same genus."

Wodehouse (158, p. 148) pointed out that in the large Grass Family there are no characters "that can be used at all adequately to distinguish the different species, genera or even tribes from each other." This is also true of some other families, and especially of some genera. The species in these families and genera often differ widely in habit, and so long as they cannot be distinguished definitely they have no value in determining the conditions under which the species grew.

4. — "There are a number of cases of accidental resemblance between pollen of widely separated families."

This, of course, makes definite identification still more uncertain, and further reduces the value of the pollen as a criterion for measuring conditions.

5. — "Not all pollen is equally well-preserved, for example it is well-known that the pollen of *Juniperus* quickly breaks down." The same is true of *Populus*. The effect of this is merely to reduce the amount of evidence and diminish its value.

6. — "Some species of trees might contribute pollen quite out of proportion to nearness and abundance of species. The phenomenon known as 'sulphur showers' consists of heavy wind deposits of pine pollen, often at considerable distance from pine forests."

This seems to be one of the most potent of all the objections to extensive dependence upon fossil pollen as an index to climatic conditions. It must be remembered that cool and warm, and dry and moist areas, with their corresponding floras, may exist in close contiguity under the same general climatic conditions. Thus, at the "Grottoes" in Illinois, opposite Fairport, Iowa, the white pine, a northern species, grows on a bluff, while at its foot the papaw, and on the nearby alluvial flat the pecan, both southern species, have flourished equally well. Countless examples of swamp and dry prairie floras living but a few feet apart could be given, while prairie and forest have existed side by side in all parts of the state. In such cases pollen from one type of area could easily be carried to another, — especially where it is light and dry, and hence carried readily by wind. It is, moreover, a notable fact that the principal families and genera represented by fossil pollen in our bogs, particularly the Pinaceae, Gramineae, Cyperaceae, Juglandaceae, Betulaceae, Fagaceae, Amaranthaceae and Chenopodiaceae, all contain species of very diverse habits and wide distribution, and all are pollinated by wind.

"Sulphur showers" were quite frequent before our coniferous forests were depleted. Gray (68, p. 217, and earlier) referred to them as "familiar" and stated that they occurred "several or many miles from the nearest source." Numerous records have been made of various materials, including pollen, carried in dust-storms, but most of them are limited to mineral content, either because the storms occurred in the fall, winter, or very early spring, when no pollen was available for transportation, or because the observers were interested chiefly in the inorganic load.

Ehrenberg's work (51), of which an extended review was given by Dana (43), contains a record of 340 dust-showers, 249 of them during the Christian era, which carried diatoms, sponge-spicules, pollen-grains, etc., the latter, as a rule, not abundant. In most of the dust-showers diatoms greatly predominated. In one, that of Lyons, France, organic forms made up one-eighth of the mass. Among them were two species of South American diatoms! The two extensive tables, (pp. 383-389 in the review) contain lists of organic materials precipitated in dust-showers during the first half of the 19th century. Pollen-grains are recorded for but six of these showers, but the number would no doubt have been much larger had more of the storms occurred during the later spring and summer, for it is evident that these storms had the power to carry objects even larger than pollen grains.

The extent of some of these dust showers may be illustrated by two additional examples.

Herrmann (1903)* reported on the dust-showers of February 19 to 23, 1903, extending across the north Atlantic Ocean, Great Britain and middle Europe. At Buckfastleigh, Great Britain, 36.4% of the material was unidentified organic material; at Uecle, Belgium, among the organic materials occurred a diatom, spores of *Mucor*, and a little pollen of *Corylus*, and in one case of *Alnus*; at Delft, Holland, bacteria, spores of fungi and fragments of leaves were abundant; and at Travers and elsewhere in Switzerland, the organic materials contained spores of fungi and pollen of *Corylus*. In some of these cases the materials may have been local, but in others they were evidently carried great distances.

Another case, of even more direct interest to us, is that of the dust-shower of March 9, 1918, reported by Winchell and Miller (156). The material was mostly inorganic, but contained some or-

* Citation not located. — Ed.

ganic substances, including a considerable number of diatoms. The dust particles ranged from .003 mm. in length to .1 mm., while the diatoms varied from .02 to .035 mm. in length. In addition to the diatoms there were fragments of leaves and of coniferous wood, and saprophytic fungi and their spores. The total amount of the organic and inorganic material which was precipitated at Madison, Wisconsin, during this storm was estimated at more than 13.5 tons per square mile. The storm continued across the continent from March 7 to March 10, and covered a total area of at least 100,000 square miles. The velocity of the wind was reported from several points and ranged from 44 to 48 miles per hour. Extraordinary dust-storms prevailed in the far west and south-west, and the composition of the mineral material precipitated at Madison led to the conclusion that the dust was brought from our arid southwest.

Mention should also be made of the work of Udden (145), who collected dust from the atmosphere at several localities (pp. 40-50), and also studied shower-dust from a number of points, one of them being Alta, Iowa. The wind-velocities when the first group was taken ranged from 12 to 33 miles per hour, and the particles of dust varied from 1/8 to 1/128 of a mm. in diameter. The particles of shower dust varied from 1 to 1/128 mm.

While Udden gave no attention to the organic materials of the dust-showers his work shows that the wind has ample power to carry pollen grains to great distances, though this power would vary with the velocity of the wind.

This evidence is sufficient to show that pollen of a certain type (light and dry) may be freely transported by winds. Since the latter shift to all points of the compass, and vary greatly in velocity from time to time, it is evident that pollen may be received from floras at different distances, some of them quite remote, and that this may be mingled with pollen from the immediate surroundings, thus producing a confusing mixture which is of little value in determining climatic or ecological conditions.

Before pollen can be accepted (or positively rejected) as an index to environmental conditions it will be necessary to conduct much wider investigations of the behavior of modern pollen, not only in northern bogs, in the midst of, or near, coniferous forests, as Erdtman has done (52), but also in the bogs which still remain on our prairies, at more remote distances from coniferous and other larger forests. Even such investigations, however, will always leave a strong element of doubt unless species can be identified.

To the difficulties enumerated by Sears, the writer would add another group which has to do with the application of the results of such studies:

7. — In drawing conclusions concerning climatic conditions indicated or suggested by the fossil pollen, the following circumstances should be carefully heeded:

a. — Unless (or until) species can be identified definitely it is impossible, as a rule, to judge of climatic or habitat conditions on the basis of family, or even generic relationships, for it is well known that in many cases species of the same genus differ widely in habitat and geographic distribution. Thus, in Iowa we have four species of the genus *Phlox*, of which one (*P. divaricata*) grows in woods, another (*P. maculata*) in swamps, a third (*P. pilosa*) is common on the prairies, and a fourth (*P. bifida*) is rare and local on sandy areas. Our flora furnishes many other illustrations of a similar nature.

Several genera, and the groups usually mentioned in our pollen-analysis lists by family name, only, such as the Gramineae, Cyperaceae, Amaranthaceae and Compositae, extend from the tropics to the Arctic regions, and vary in habitat from hydrophytes to extreme xerophytes. Unless specific identification is possible, they have little value as a measure of climatic or habitat conditions.

b. — A narrow or distorted view of the flora (and hence of the environmental conditions) of the entire region may be received from the fossil pollen, which represents only (or chiefly) the species which dwelt in or very near the more or less restricted bogs, or those with pollen which could be transported long distances by wind. Species with heavier, sticky pollen, which might have occupied much of the territory surrounding the bog, as they do today, would scarcely be represented in the peat.

c. — Even the pollen of wind-pollinated species is not carried in the same amounts and to the same distances because plants differ in the amount of pollen which they produce. This may be true of families, genera, or even species. Thus, *Populus deltoides* produces much more pollen, as a rule, than *P. tremuloides*, and very much more than *Salix humilis*, a member of the same family.

Even where the production of pollen is approximately the same, however, the amount transported to a bog would vary with the distance and the height of the plants producing it. Taller plants, especially trees, would have their pollen carried much farther than the lower herbs or shrubs because it would be caught up by the stronger currents above. It is well-known that the velocity of the wind increases as the altitude above the surface of the earth becomes greater, hence its velocity among the treetops would be distinctly greater than near the ground level, and more pollen would be taken up in larger amount and carried farther than from lower plants. Thus even a few trees, and at a considerable distance, might still contribute a larger percentage of pollen than other lower plants nearby could supply.

Percentages, therefore, may be very deceptive for the reasons here given. A larger percentage of tree-pollen, for example, does not necessarily show that a forest covered the surrounding region. It may have been derived from a distant forest, or from less remote scattered clumps of trees, such as our prairie swamp borders often produce.

d. — Even if verified, alternating layers of pollen representing dry and moist conditions would not necessarily be an index to greater climatic changes, but might represent alternating moist and dry cycles, or periodic changes in the direction of prevailing winds, similar to those which take place today; or they may represent in part the successional changes which are inevitable in any bog.

Sears has been the leader in this work in this country, and he has proceeded carefully, with a due appreciation of the uncertainties which lie in the way, but even he has found it necessary to revise conclusions which had been drawn from the study of a single bog. Thus, in 1930 (129, p. 217), on the basis of four borings made in a peat-bog near Bucyrus, Ohio, he expressed the opinion that the climate of Ohio is warmer today than it has ever been, but in the following year (130, p. 654) he stated that on the basis of a similar study of Mud Lake bog in Ohio "certain inferences, therefore, of the earlier paper must now be revised, notably the idea that deciduous forest time has been brief, and humid throughout. The conclusion that the Ohio climate is now warmer than it has ever been since Wisconsin glaciation is no longer tenable —." This experience suggests the necessity of studies of larger series of sections, as well as a careful correlation of existing floras with climatic conditions, before general conclusions concerning earlier climatic and other conditions are drawn.

The only Iowa study of fossil pollen thus far published is that of Lane (85). In this paper the author assumes (p. 169) climatic shifts from swamp, to coniferous forest climate, to deciduous forest climate, and finally to grassland climate. This assumption is based on the percentage list of fossil pollen grains from plants which are listed only by their generic or family names (p. 166), and in a second table (p. 169) these genera and families are listed under the kinds of conditions and climates, respectively, of coniferous forests, deciduous forests and grasslands.

As this case is of direct interest because of its relation to Iowa conditions, it is here discussed somewhat in detail, not in a spirit of criticism, but as a specific illustration of some of the difficulties which are encountered in efforts to draw definite conclusions from studies of this type. The paper contains two tables (pp. 166, 169) which are here reproduced in slightly modified form both because of their intrinsic interest, and because they, and the conclusions based upon them, serve as an excellent basis for the discussion of some of the difficulties to which reference has been made.

Table I contains the percentage of fossil pollen, for each foot of depth in the McCulloch peat-bed in Hancock County, Iowa. Lane's alphabetical list has been rearranged, without change of names or percentages, to bring more closely similar groups of plants together under the several heads inserted in the table.

The author's conclusions as to the climatic significance of the groups named in Table II, with the omission only of the blank "unknown" column.

Table I — Percentage of fossil pollen for each indicated foot of depth.

Feet from surface	Top	1'	2'	3'	4'	5'	6'	7'	8'	9'	10'	11'	13'	15'
Conifers														
Abies	1			3	2	1				1	5	16	24	11
Picea	1		2	1	1			1	1	1	1	8	20	69
Pinus	1	4	1	1	2	3	1	1	4	5	4	1	6	11
Deciduous trees, etc.														
Acer					1						1			
Betulaceae			1	1					1	1	11	28	16	1
Carya				1	3		4	2	5	5	5		1	
Fagus											1	1		
Juglans											1		1	
Quercus	3	5	4	2	6	4	3	4	20	27	28	14	11	3

Salix	1		3	1	2			2	2	1			7	
Tilia					1				1		1			
Ulmus											1	1	1	
Prairie or mixed														
Amaranthaceae and Chenopodiaceae	6		3	32	32	37	5	11	21	17	6			
Compositae	1	4	7	1	3		3	1	4	7	3	1	3	2
Cyperaceae	21	4		7	14	7	7	10	8	7	6	3	1	
Gramineae	39	74	70	33	24	35	69	60	23	17	13	14		
Swamp and water														
Potamogeton	1			1	1	1					1			
Sparganium	5	1		1	1	10		1	2		3	4		
Typha			1		1	1				1	1		1	
Unknown	20	8	9	16	7	2	8	8	9	11	9	9	4	1

able II. — Assumed Climatic Significance of Fossil Pollen.

ake Margin Plants	Coniferous Forest Climate			Deciduous Forest Climate				Grassland Climate
	Moist		Dry	Moist	Dry			Dry
yperaceae	*Abies*	*Picea*	*Pinus*	*Acer*	Betulaceae	*Carya*	Gramineae	Amaranthaceae
otamogeton				*Fagus*	*Quercus*		Compositae	
alix				*Juglans*				
parganium				*Tilia*				
ypha				*Ulmus*				

The conclusions embodied in Table II are based on the percentage of predominating pollen at various depths, and rest on the assumption that the pollen indicates approximately the relative predominance of the group of plants producing it, and that these groups represent definite climatic conditions which differed at the time of the deposition of the pollen at depths indicated in Table I. The assumed succession of these climatic conditions is shown from left to right in Table II.

An analysis of the grouping of the genera and families in Table II reveals some of the weaknesses of the assumptions on which the conclusions are based, due chiefly to the lack of specific identifications.

Thus, in the "lake margin" group are included 3 genera, *Potamogeton*, *Sparganium* and *Typha*, which are distinctly swamp or water plants, and which are common in and about the bogs and ponds of the region. But the same column included the Cyperaceae, or sedges, many of which are swamp or swamp-border plants, but among which are also found several species which prefer drier prairies, *Carex festucea* being the most common. The genus *Salix* likewise contains both swamp-border and dry prairie species. When the writer visited Twin Lakes (about a mile north of the McCulloch peat-bed) in 1882, the low shrubby prairie willow, *Salix humilis*, was very common, especially on the somewhat elevated points or low ridges which here and there ran out into the prairie swamps which everywhere abounded in the region.* Pollen from this, originally the most common willow of that region would certainly not indicate swampy conditions.

All the groups mentioned in this column are now represented by species existing in the vicinity, and two of them, *Salix* and Cyperaceae by both swamp prairie species.

The column containing the groups assumed to be indicative of a "deciduous forest climate" includes a family and several genera of deciduous trees and shrubs, all but one, *Fagus*, being represented in nearby groves.

Fagus, represented eastward by the beech, *F. grandifolia*, does not occur in Iowa, and, so far as the writer knows, no other trace of other than cultivated specimens has ever been found within its borders. Table I shows that only 1% of the pollen representing this genus was found at the 10 and 11 ft. levels, respectively. This suggests that the pollen may have been brought from a distance, probably from the northeast together with coniferous pollen. This conclusion seems especially reasonable in the light of the fact that *Fagus* is regarded as typical of the most highly developed hard-

* The writer camped on the southern shore of East Twin Lake, about a mile north of what is now the McCulloch place, for several days in May, 1882, with a fellow-student, Mr. J. W. Preston, who was helping himself through the State University by collecting the eggs of prairie and water birds for museums. Comparatively little of this part of the county was settled at that time, and there were large areas of unbroken prairie and undrained swamps. Countless prairie-chicken nests were observed, especially among the scattered clumps of the common low *Salix humilis*, nests of the wild goose were common on the muskrat houses in the swamps, and seven species of ducks were found nesting along the borders of the latter in that vicinity. All the species of plants noted in the subsequent deciduous forest list (and several others not represented in the McCulloch peat) were found in the grove on East Twin Lake, and were again checked in August, 1927, and found without material change. There were also specimens of *Salix longifolia* and *S. amygdaloides* along the swampy borders.

wood forest climax, and it is not likely that such a climax would have developed this early in the ecological history of the region, and then leave so little evidence of its existence as appears at that low level.

The Family Betulaceae is represented in the modern flora of the region by the genera *Corylus* and *Ostrya*. *Betula* does not occur here, but occurs in Iowa with the white pine. If some of the pollen should prove to be that of *Betula* it could probably be traced to the same source as that of *Pinus*.

The remaining genera of this group are all represented in the grove on the south shore of East Twin Lake, one mile away, and in the larger grove along the Iowa River about 5 miles east of the peat-bed. These are the two largest (and almost the only) native groves in the southern half of Hancock County. The following species (with several others not included in the Lane list) were observed in the East Twin Lake grove in 1882, and were still present at the time of the last visit, in 1927:

Acer saccharinum	*Quercus macrocarpa*
Carya cordiformis	*Ulmus americana*
Juglans cinerea	*Ulmus fulva*
Juglans nigra	*Tilia americana*

Acer saccharum occurred in the larger grove to the east, and *Salix*, also placed in the deciduous group in Table I, was represented on the prairie, and along the lake shore and swamp borders, as noted.

The grouping in the "moist" and "dry" columns is not satisfactory, since each of the genera *Acer* and *Ulmus* contains one upland and one low ground species. *Ostrya* and *Corylus*, representing the Betulaceae, should also be transferred to the "dry" column.

All these species occur in a narrow fringe of woods in the heart of the prairie region, and their presence, like that of their pollen in the peat-bed, is surely not indicative of a "forest climate" for the entire region.

The "grasslands climate" column in Table II contains two families, the Compositae and the Amaranthaceae, but in Table I the Chenopodiaceae are included jointly with the latter.

The Compositae are represented at nearly all the levels in the borings, but they reach a maximum of only 7 percent, which is reduced to 1 percent at the top. When we consider that the Compositae formed more than 20 percent of our prairie flora, including that of the McCulloch vicinity, and were dominant over large areas, the very small percentage of their pollen, especially towards the top, strengthens the suspicion that this peat pollen does not correctly represent the major floras of the vicinity of the peat-bed.

The Amaranthaceae and Chenopodiaceae are regarded as evidence of a drier climate. Sears (129, p. 216) specifically refers to this case, and states that "at the four-foot level, — there is a strong increase in Chenopodiaceae and Amaranthaceae at the expense of grass. This suggests a xerophytic climate marked by strong evaporation and possibly alkaline or saline conditions in Iowa during the period of maximum dessication in Ohio."

Unfortunately for this view, which evidently presumes more xerophytic conditions than now prevail on our prairies, both families are represented today in the region under discussion, and not all their representatives are xerophytic. Of the Amaranthaceae, *Amaranthus blitoides* was common on the drier prairie, and probably *A. graecizans*, another dry-ground species, occurred with it; but *Acnida* was very common on the swampy borders of the prairie swamps and ponds. The Iowa representatives of neither one of these genera would suggest a more xerophytic climate than we have at present. The same is true of the Chenopodiaceae. One species, *Chenopodium leptophyllum*, is quite common on the prairies, while *C. hybridum* and *C. Boscianum* are frequently found in prairie groves, especially near their margins or in more open parts. Both occur in the East Twin Lake grove.

Since all these groups, excepting *Fagus* (and that scantily) are present in the vicinity of the McCulloch peat-bed today, the presence of their pollen in the peat cannot at any stage indicate a marked deviation from the climate of today.

Great reliance in all similar estimates of climatic conditions is evidently placed on the coniferous pollen, and this seems to be true in the present case.

The "coniferous forest climate" column contains three genera of the Family Pinaceae, namely *Abies*, *Picea* and *Pinus*.

The genus *Abies* contains one species in this part of the country, namely *A. balsamea*, which is abundant in northern and northeastern Minnesota, and also occurs in scattered groves in the southeastern part of that state. In Iowa it is found in similar scattered groups (or singly) in Howard, Winneshiek and Allamakee Counties, in the northeastern part of the state, scarcely 100 miles from the peat-bed in question.

In the corresponding section of the country two species of *Picea* occur, but neither reaches Iowa. *P. mariana* is a swamp species which extends from northern Minnesota to New Jersey and northward. If this should prove to be the fossil Picea it should be transferred to the "moist" column in Table II. The other species, *P. canadensis*, prefers dry or sandy higher ground, and extends from northern Minnesota and Wisconsin to New York and far to the north. If the doubtful *Picea* is this species, it should be placed in the "dry" column.

The genus *Pinus* is represented in Iowa by one species, *P. Strobus*. It occurs in scattered groves in the northeastern part of the state, and detached colonies are found in Muscatine and Hardin Counties, the latter point being scarcely 50 miles from the McCulloch peat-bed.

The presence of the pollen of these genera, now mostly northerly in distribution, in a peat-bed quite remote even from their stray outliers, is noteworthy, and has been regarded with some justification as evidence of a colder climate during the period of its deposition. There are, however, two other possibilities which militate against the unreserved acceptance of this evidence.

The first is the possibility of transportation from a distance. The pollen of these conifers is light, dry, and very abundant. There were extensive forests, containing the genera named, within two or three hundred miles to the northeast of the McCulloch peat-bog in recent time, during climatic conditions essentially the same as those of the present.* When we consider the carrying power of winds, the transportation of such pollen to points a few hundred miles away does not seem improbable. That the pollen came from more remote points is also suggested by the fact that the three genera are represented in the peat at all levels, even to the top, yet there is absolutely no evidence, in the immediate region of the continuance of these trees to the present time.

The other possible source of the coniferous pollen may have been in less remote outliers containing the conifers named. Outliers of *Pinus* are still near enough to have furnished this part of the fossil

* Many years ago pollen of this type was reported to be so abundant in the Lake Superior region that it was washed up in windrows along the lake shore in such quantities that it could have been scooped up with a shovel.

pollen, — which it will be noted in Table I, extends throughout the entire section. *Abies balsamea* is not far away, but this, like *Picea mariana*, is partial to low grounds, and it is possible that other outliers, much less remote from the prairie bogs, may have been present during the earlier period of peat formation, only to disappear as the swampy areas diminished in size and frequency. There is abundant evidence that such swamps did diminish in size, and in some cases were completely dried, through the normal successional changes of which every bog gives evidence, and which is not dependent on any major climatic changes but is the result of edaphic reaction. Specific evidence of such outliers nearby is lacking, however.

The appearance of a larger percentage of the coniferous pollen at lower levels may be due to a coincidence in the occurrence of large crops of pollen with the prevalence of strong winds; or it may have been due to the presence of adjacent outliers; or the variation may have resulted from fluctuations in the direction of prevailing winds at the time the pollen was discharged. It is just as difficult, moreover, to account for the presence of the smaller percentage of the pollen of *Pinus*, *Picea* and even *Abies*, at the upper levels of the prairie bog as of the larger percentages in the lower portions. Both required a source of supply, and in both cases it was probably remote. The coniferous pollen at the top may have been derived from cultivated trees of these genera which are now commonly planted on the prairies.

Admitting the demonstrated possibility of the long-distance transportation of the pollen of conifers (and other species) there is surely no warrant for the assumption that the presence of the pollen-grains noted is indicative of any distinct variations in climate during the formation of the peat-bed in question; nor do any of the species indicate the existence of earlier forests of greater extent than the small groves which fringed many of the lakes, streams and swamps of the prairie region in recent time.

Four possible sources of error must be kept in mind in connection with the use of fossil pollen for measuring climatic and habitat conditions. The complete but varying capacity of the wind for carrying only certain types of pollen long distances; the existence of both wet and dry (and even cool and warm) habitats in more or less scattered but contiguous areas, — often with forest, for example, mainly in one direction and prairie in another, while the bog itself furnishes swamp conditions, thus providing sources of pollen of different habitat types; the diverse directions from which prevailing (especially stronger) winds blow, — varying with the season, and often with different years, — thus bringing different types of pollen to the same boggy area; and, finally, the possibility that some of the vertical changes and alterations are due in considerable part to reaction resulting from the successional changes which would take place normally in all bogs.

Despite the declaration of Sears (129, p. 205) that "no successful impeachment of the method (of pollen analysis) has appeared," the general practice of drawing wholesale conclusions from limited observations may well be questioned, even though the method appears "to give results which agree with those obtained otherwise." Unfortunately, those obtained otherwise are too often subject to serious doubt, like those based on the Toronto beds studies, and the case resolves itself into the attempted support of one weak prop by another weak prop without adding stability to the main structure. That some of the chief advocates of the method have their own doubts, and are making a real effort to meet them, is shown by Sears' doubts, previously noted, and by Erdtman's effort (52) to determine how accurately the pollen deposited today represents the existing forest.

Whatever the results of such observations as those of Erdtman, pollen alone will always remain a doubtful criterion for the reasons given above. The study should be combined with that of other organic remains in the peat and interstratified materials. Such sections as were made by Dachnowski (42), for example, should be studied in greater detail. A hint of other possibilities may be found in the writer's own rather recent (139) experience. In making a partial study of a Clay County peat-bog he found several seeds and fruits at different depths, suggesting a vertical ecological differentiation. The lower strata of peat and associated materials contained shells of gill-bearing snails, *Valvata* and *Amnicola*, indicating a deeper and more continuous body of water, while nearer the surface only freshwater pulmonate snails, such as *Lymnaea*, *Physa* and *Planorbis* appeared, indicating shallow water, or even merely moist surfaces.

The determination of organic materials which are too heavy to be carried readily by the wind would add materially to the value of the organic evidence. Much wider and more detailed studies of the distribution of modern pollen should also be made. It is furthermore necessary that the same meticulous care be practiced in drawing conclusions concerning climate and ecological conditions that is applied to the technique of pollen analysis.*

It is probable that ecological conditions in Iowa have been much as they are now for a long time, — perhaps for several thousand years, — a period not extravagant when we consider that the most widely accepted estimates fix the time which has elapsed since the withdrawal of the Wisconsin ice as at least 25,000 years, and that the Iowa marginal lobe was probably about the first to go. This is suggested not only by the evidence of the peat-bogs (imperfect as it is at present), but by the existence of a fairly uniform climax prairie flora extending from far below the southern limit of the ice, well into Manitoba, Saskatchewan and even Alberta, through approximately 15° of latitude.

Of course, the diminishing number of species northward may suggest that the movement northward has not been completed, for of 244 species of more common prairie plants of all types in Iowa, 191 species extend from Oklahoma to Iowa (and most of them enter Minnesota), while but 158 species reach from Iowa to Manitoba, — 123 of the species ranging from Oklahoma to Manitoba, while a considerable number of Oklahoma forms, especially in the families Gramineae, Leguminosae and Compositae, do not reach as far north as Iowa. These differences, however, are probably due chiefly to the moisture factor, and there is little probability that the entire southerly prairie flora will ever reach the more northern latitude, just as it is unlikely that the entire southern forest flora will ever extend far to the north.

This does not mean that there have been no changes in conditions, for, following the major changes in climate which must have followed the retreat of the ice, and when approximately present conditions had been established, there were probably fluctuations similar to those of recent time; nor does it mean that, even while climatic conditions remain substantially the same for a time, there will be no further change in the flora, for new combinations of both favorable and unfavorable factors, and the local modifications of

* These suggestions are not offered in criticism of the work which is being done, but in the hope that they may lead to more satisfactorily tenable conclusions.

surface which are gradually being produced by erosion, will continue to produce changes which may occur even within a climax.

It does, however, signify that approximately the same general conditions have been maintained for a long time, providing warm summers of sufficient length to have permitted (probably long ago) the development and establishment of a climax prairie flora in a region of great extent; and it also suggests that winter temperatures were not the determining factor in its development, since 123 of the species extend from the comparatively mild climate of Oklahoma to the more boreal environment of Manitoba. The character and adaptations of the flora point, rather, to moisture as filling this important role.

The same is probably true of the northern forests, because a more or less interrupted belt of coniferous forest extends somewhat diagonally across the northern part of the continent, beyond the margin of the glacial sheet. The distribution of these forests is so obviously related to the Great Lakes, Hudson Bay and the north Canadian lakes, and they are so completely absent from the great central plains region, that it seems much more probable that moisture is also the determining factor, and that when the ice occupied Iowa (and as it receded) the region adjoining its border had, at most, only such scattered clumps and small groves of conifers as may now be found in sheltered valleys near the Arctic coast. (See Holm, 76, pp. 86B-88B; and Johansen, 82, p. 49C).

It might appear possible that the spruce (*Picea*) pollen of the 13- and 15-ft. levels in the McCulloch bog (Lane, 85, p. 166) represents the product of a subarctic thicket or grove of this type, but the remaining species, associated with it, belong to a much more moderate climate, and the entire aggregation probably represents a mixture derived from various unassociated sources.

Post-Wisconsin climax floras. — It is evident that much time, as measured by years, was required for the development of the climax floras which have become reestablished over much of the Wisconsin drift area. Such floras do not spring up in a day. If (or as) they followed other floras, representing different climatic conditions, the change no doubt occurred very gradually, with the change in climate. But after these conditions had been stabilized in a measure, there was a long period of readjustment and further competition among the members of the same ecological group before the climax was established. That this required much time is shown by the fact that both the prairie and forest climax floras have advanced over the Wisconsin drift area far to the north. This would indicate that the period of radical climatic change following the retreat of the Wisconsin ice was rather short while the temperate period following has been very long.

Kay (83, pp. 460-461) estimated that the total time required for the advance and retreat of the Wisconsin ice-lobe in Iowa was about 3000 years, the ice finally retreating at the rate of about one mile in ten years. In the study of the restoration of a strip of cultivated prairie near Mason City the writer (136, pp. 15-24) found that about ten years were required to accomplish the partial restoration of a strip only a few rods wide, though the conditions were very favorable, and an adjoining strip of native prairie furnished an abundance of seed. Here the prairie flora encountered two difficulties in its advance, — first the struggle with the opportunist (mostly native) weed flora which had taken early possession, and then in the competition between the pioneer prairie plants and the later-comers, which continued until a climax equilibrium was established. The same struggle and delay no doubt occurred all along the border line as the prairie advanced, and since the climax prairie is now well-established far to the north (even though with a somewhat diminished membership) the time required for its development must have been very great.

Kay also estimated the length of time since the retreat of the Wisconsin ice from Iowa at 25,000 years, and it is probable that during the greater part of that period the climate has been quite moderate. It is probable that the period of climatic readjustment following the retreat of each ice-sheet was quite short, as is indicated by the vertical distribution of the fossil plants and mollusks in the Don beds, the land snails in the loess, and the molluscan and plant fossils in our peat-bogs. Changes which have taken place in our floras since the restoration of a moderate climate have evidently resulted largely from the filling up of bogs and low places, and from erosion.

It is not the writer's intention to give the impression that there have been no striking changes in post-glacial climate, but rather that, as shown by organic remains, present general climatic conditions have prevailed for a long time, probably several thousand years, and that our present floras and faunas have been developed and maintained under these conditions and have occupied substantially their present limits during this long period, subject only to such fluctuations, both climatic and edaphic, as are taking place today.

Interglacial and post-glacial climates. — The question of interglacial and post-glacial climates has received a vast amount of attention, both in Europe and on this continent. It was at first regarded as a problem for the geologists, but later the biogeographer entered the field, and too often the work of the two groups has not been correlated. On the other hand, too much credence has been placed by each group in the unsubstantiated or not definitely established conclusions of the other. The biologists have found great differences of opinion among geologists concerning both the age and the genesis of various deposits, making any effort at correlation in time of very doubtful value, while the geologists have sometimes been tempted to accept too implicitly the conclusions of biologists which were based on fragmentary material or incomplete information. An admirable review of some of the older contentions concerning European conditions was prepared by Novak (106) and modern scientific literature bristles with similar difficulties. Domin (1915, p. 2)* referred to the same difficulties and suggested that "plant geography loses ground under foot as soon as it attempts to solve in too great detail the problems from individual periods of the glacial epoch; it here falls into hypotheses which, though they read well and arouse interest by their consistency and learning, yet lack the reliable basis of unquestioned facts," — a warning which needs to be heeded in our own country. Clements (29, pp. 387-408) also set out some of the conflicting conclusions based on the study of peat-beds, etc., in Europe and America.

Our American literature on this subject is also quite extensive, and its history is much the same as that of Europe. In later years, geologists and biogeographers have also depended upon each other, and, as in Europe, often too implicitly, without analyzing the evidence. There has been much dispute, for example, concerning the true age of some of the loesses; of the Don and Scarborough beds; of the "forest-bed" in different regions; of various buried peat-beds, etc. On the other hand, geologists have been confused by the differences of opinion among biologists concerning the identity and significance of various organic remains.

The subject of climatic conditions is of particular interest be-

* Citation not located. — Ed.

cause of its relation to the distribution of our floras. The character of our Iowa flora, especially, has been determined by migration following each retreat of the several ice-sheets, for we have practically no endemic flora in Iowa.

Most of the work relating to this part of the subject has been done in the eastern part of the continent. There is a clear relationship between (or rather continuity in) the flora of the region embracing our eastern mountains, and that of southern Canada and the region about the Great Lakes and northwestward. The migration of this flora, and the corresponding fauna, from southerly centers after the withdrawal of the ice has been repeatedly pointed out. (See Transeau, 142; Adams, 1, 2, 3.) It is of special interest to students of Iowa plant-geography because this flora reaches into northeastern Iowa, occupying, in the main, the "driftless area."

This does not signify that this flora originated in the south, for there are many plants in our own flora which are distinctly northerly in phytogeographic relationships, and, indeed, Wieland (155, p. 430) held "that polar climate has been the major factor in the evolution of plants and animals." The gradual advance of each ice-sheet, however, evidently produced a corresponding gradual retreat of the flora to the south, whence it advanced again, equally gradually, after the ice had retreated.

There were no doubt irregularities in both advance and retreat. Some species, like *Cystopteris fragilis* and *Equisetum arvense*, were broadcasted without losing their rank in the more southerly floras; others, like *Polypodium vulgare, Asplenium filix-foemina* and *Onoclea Struthiopteris*, which are common, or at least locally frequent, in our flora, failed to return to our American Arctic regions, though they are circumpolar in distribution; still others, like *Arctostaphylos Uva-ursi* and *Potentilla tridentata*, advanced in the main, and left only straggling colonies behind, though some of the latter may have been reintroduced later; and there are probably many more that retreated entirely, though some of our present far-northern plants (as well as mollusks) may have been reintroduced from other continents.

Much effective work has been done by Fernald (54, 55, 56), particularly in the region of the Gulf of St. Lawrence, to demonstrate these northern relationships, and to show the persistence of many of the northern types on the non-glaciated, or slightly glaciated areas of that region. His efforts to correlate the conditions and his conclusions with northeastern Iowa and adjacent territory were, however, less fortunate. The facts that the Labrador region is nearly 10° farther north, and that it is strongly affected by oceanic climate, create conditions which are entirely different from those in Iowa.

The difference is shown strikingly in the flora. Fernald (54) gives four tables of plants, three of them Arctic or boreal, which enter his general region. Table I (pp. 266-269) contains a list of 93 Arctic species and varieties which are found in New England, only four occurring also in Iowa; Table II (pp. 269-272) contains 78 Arctic plants centering southeast of the Gulf of St. Lawrence, but one occurring in Iowa; Table III (pp. 272-274) contains 51 boreal or European species centering in the Gulf of St. Lawrence region, one of which also occurs in Iowa; and Table IV contains 296 western and endemic species centering about the Gulf of St. Lawrence, of which 13 occur in Iowa.

Thus only 6 "Arctic" species in Fernald's first three tables also occur in Iowa. They may be grouped according to habitats as follows (the Roman numeral in each case indicating the number of the Table in which it occurs):

In swamps and bogs:

Eriophorum angustifolium I. *Hierochloe odorata* I. *Ranunculus Cymbalaria* I.

On rocky ridges and ledges:

Arctostaphylos Uva-ursi II. *Potentilla tridentata* I.

On wooded ledges:

Phegopteris (Thelypteris) Robertiana III.

None of the members of the swamp group occur in the "driftless area," but are found chiefly on the Wisconsin and Iowan drifts in this state. All three species are widely distributed north, west and east, and there is no particular reason for viewing them as though they were exclusively Arctic plants.

The two species listed in the rock group are exceedingly rare and local in Iowa, the *Arctostaphylos* being represented by a few plants in one small area,* and the *Potentilla* by two small areas of a few square yards each. These three small colonies are located in the "driftless area" in Winneshiek County. Both species are widely distributed to the north and east, and the former also to the west.

* A similar restricted area is reported from across the Minnesota state line a few miles east (Wheeler, 153, p. 386, and Rosendahl, 122, p. 258).

The limited colonies in both cases, however, suggest the possibility of a more recent importation. The fleshy fruits of *Arctostaphylos* could have been carried by birds, and the small achenes of *Potentilla* by strong winds, or on the feet of birds.

The only representative of the third group in Iowa, *Phegopteris Robertiana*, is also rare and local in the "driftless area," being known in one very limited colony in each of three counties within the "driftless area," namely, Allamakee, Dubuque and Winneshiek. The species also occurs in Idaho, Alaska, Minnesota, Quebec and in Europe. It is here probably near its southern limit. Its wide and very locally limited distribution makes it a very unsafe species on which to base generalizations concerning origin and climatic conditions, for there are various ways in which the spores could have been carried, particularly on the feet of birds.

It will be observed that of the 222 species listed in Fernald's first three tables as belonging to boreal America (or Europe) only 6 occur in Iowa, a difference which strikingly brings out the inequality of conditions and the impossibility of correlating the far northeastern non-glaciated area with any part of Iowa. There is little in this record to show convincingly that a northern flora persisted on the least glaciated portions of Iowa, and it seems rather that if there are any laggards they appear among the marsh plants of the latest glaciated surfaces, the Wisconsin and the Iowan.

To show that the flora of the non-glaciated northeastern areas persisted during the invasion of the Wisconsin ice-sheet Fernald not only presented the three lists of Arctic and boreal plants in Tables I-III, but added a fourth list of 296 western or endemic species which occupy the same region, and which he regards (p. 303) as "relics of the pre-Wisconsin flora which must there have lived essentially undisturbed through the Wisconsin glaciation." Of this large number only 12 species are found in Iowa, and *not a single one of these species has thus far been found within our "driftless area,"* though Fernald expresses the opinion that western plants (like many of those in Table IV) which persist about Lake Superior, etc., retreated to these areas from the driftless area of Wisconsin and adjacent states, where they "apparently outlived the Wisconsin glaciation." The 12 species may be grouped as follows:

Swamp species:

Juncus Vaseyi *Ranunculus Purshii*

The writer has only one doubtful record of the *Juncus* from the Iowan drift in the western part of Winneshiek Co. The *Ranunculus* is known only from the east side of Spirit Lake (Cratty).

Species of rock-ledges:

Woodsia oregana

This occurs on Sioux Quartzite in the extreme northwest corner of the state more than 250 miles west of the "driftless area."

Species of the prairies and open places:

Agropyron tenerum
Artemisia canadensis
Comandra Richardsiana
Dracocephalum parviflorum
Gilia (Collomia) linearis
Juniperus horizontalis
Prenanthes racemosa
Zygadenus chloranthus

Of this list the *Agropyron*, *Dracocephalum* and *Gilia* are evidently native in northwestern Iowa, but they have spread somewhat (the two latter sparingly) towards the east and southeast, chiefly along railways. The *Artemisia* (somewhat doubtful), from northern Iowa, is very rare, as is the *Juniperus*, only a few specimens of which are known in the state in a very limited area on the Iowan in Floyd County. The remaining three species belong to the prairie flora, the more xerophytic *Comandra* and the *Zygadenus* extending across the northern part of the state, and the *Prenanthes* more widely distributed, but none of them occurring in the "driftless area," and all of them more abundant northwestward.

Fernald's explanation (p. 317) that these plants withdrew to the "hospitable areas" about Lake Superior, etc., because "the eastern margin of the region of pre-Wisconsin drift . . . is now, of course, too hot and dry," * [fails to take into account the fact that this area is relatively cool and moist] offering indeed the coolest retreats in the state, and of the further fact that most of the species of this list which are found in Iowa are xerophytes, the *Woodsia* now growing on the hot and dry Sioux Quartzite exposures; the *Juniperus* being found on a dry and barren knoll; and the remaining species being prairie xerophytes, only the *Prenanthes* and *Zygadenus* sometimes appearing on moist prairie.

Most of these species now live on surfaces which are, in fact, much drier than the greater part of the "driftless area."

It should also be noted that map 9 (p. 251) showing the distri-

* Phrase within brackets added by ed.

bution of *Woodsia oregana* omits the Iowa and Minnesota localities, and that map 42 (p. 319) greatly exaggerates the driftless area. The writer knows from personal observation that there are at least traces of drift on many of the highest ridges in Allamakee County, and Dr. A. C. Trowbridge, who has been studying this area for a number of years reports that there are only two or three sections in that county (and in this state) on which drift had not been found, and that the driftless area is limited to a few sections in Jo Davies County in Illinois, and a small area in southeastern Minnesota, the major part lying in Wisconsin. The whole area, however, is much smaller than was formerly reported, and than is represented in map 42.

Fernald also assumes that this non-glaciated area "is a definite center for plants of limited range, which there outlived the Wisconsin glaciation" and definitely names *Asclepias Meadii*, one of the rarest species, *Talinum rugospermum* Holz., and *Lespedeza leptostachya*, calling them "excessively local species," and adds *Quercus ellipsoidalis*, occupying a larger area outside.

Most of the localities for the *Asclepias*, indicated on map 43, (p. 319), are well south of the "driftless area," and occupy Kansan surfaces. The somewhat doubtful *Talinum* (ours is *T. parviflorum*) also extends well out on areas older than the Wisconsin drift, and could readily have survived on them. The *Lespedeza* is not most abundant in the driftless area, as indicated on map 45 (p. 319). It is very rare in Winneshiek County, just west of the "driftless area" and increases westward, appearing on both the Iowan and Wisconsin areas, and being most abundant near the western edge of the latter lobe. *Quercus ellipsoidalis* also extends far beyond the limits of the "driftless area," in Iowa extending much farther southwest than is indicated on map 46 (p. 319). It is now found in the "driftless area," on the Iowan and Kansan drift areas, and on the eastern moraine of the Wisconsin.

None of these species required the refuge of the driftless area, as they extended much beyond the Wisconsin border, and their history previous to that will probably remain a mere matter of conjecture.

It is evident that neither the character and distribution of the "western" species, nor of those which seem to be endemic, warrants the conclusion that they were perpetuated in or distributed from the driftless area, but suggests, rather, that they may have been preserved southward on the Kansan areas, and advanced northward, partly over the driftless area, and partly over the Iowan and Wisconsin drifts. In our "driftless area" there are several northern species, or species which have their main distribution northward, but they are associated with other species in essentially the same combinations as those which may be observed northeastward, in the Great Lakes region and eastward, and it is possible that they advanced northward with the Great Lakes flora, but more likely, viewed in the light of the distribution of the latter, spreading westward with its extension northwestward from the lower Great Lakes. At least there seems to be little reason for assuming that a part of this flora (in the main) came from one source, and a part of it from another when they are combined in essentially the same manner in the region noted.

Fernald places great stress (54, pp. 320-321) on the possibility of the existence of plants near glaciers, and uses this fact in partial support of his conclusion that much of the flora of his unglaciated or slightly glaciated area, survived the Wisconsin glaciation, and that our "driftless area" may have similarly harbored an older flora.

The fact that vascular plants exist in the far north has been known for a long time. In 1853 Durand (48, p. 184) prepared a table showing 76 species of flowering plants in N. Greenland, at 73° N. lat. He reported that at that time 264 species were known from Greenland, of which the greater part came from the southern extremity of Greenland, which was found to possess "nearly the same climate as Labrador, with an almost identical vegetation." He ascribed (p. 180) the possibility of the existence of this flora to "the uninterrupted action of light and heat, during the whole period between the rising and the setting of the sun, which marks the day or summer season of the poles —." The Howgate Polar Expedition (see Gray, 69, pp. 163-166) found 97 species of flowering plants at Cumberland Sound and Disco Island, 65°-70° N. lat.; the International Expedition to Point Barrow, Alaska (see Gray, 70, pp. 191-192), found 51 species at about 71° N. lat.; Wetherell (152) collected 82 species of vascular plants along the west coast of Greenland, 35 of which were found (by him) only at Cape York, north of 75° N. lat. (two of the latter, *Equisetum arvense* and *Eriopho-*

rum angustifolium also in Iowa); and Macoun and Holm (101) found 230 species on the Arctic shore between the 100th Meridian and Point Barrow.

The floras of these several regions are, however, quite distinct. At least 30 species of the last list have not been reported as far east as the Mackenzie River, and probably more than half the total list do not reach Greenland, which is credited with 416 species, which, however, are distributed over ecologically very diverse areas, — as are those of the comparatively rich flora of the Pacific coast of Alaska. The flora of Alaska is much richer than that of Greenland, especially if the coast of the Gulf of Alaska is included, and contains a larger number of forest trees, and also of plants which occur in Iowa. (See Rothrock, 123; Eastwood, 49; Coville, 38; etc.) Not only do the two extreme areas differ from each other, but they differ from that of the poorer intermediate Arctic coast in the number of species of plants. The composition of the floras of the three areas, moreover, is so different that the conditions under which they were developed could not have been the same, and it is evident that the mere presence of plants in the far north is less important as a measure of conditions than the character of the aggregations or associations in which they occur.

Neither Greenland, nor Labrador, nor Alaska, nor even the intermediate Arctic coast, should, however, be compared with our "driftless area," for all have been (and are) strongly influenced by oceanic climates. Even the coastal border of Greenland, which lies close to the margin of a continental ice-sheet but has a comparatively rich flora, owes this evidently to the proximity of the sea, the equalizing effect of which is also felt in Labrador and Alaska, and in somewhat lesser degree on the Arctic coast, but which had no counterpart in our "driftless area" during the Wisconsin, or any earlier glaciation.

The flora which might appear to approach most nearly to that which bordered the glacial ice as it began to retreat, is that of the Arctic coast, though even here the similarity is not striking. Of the 230 species reported by Macoun and Holm, only 10 are now found in Iowa.* These Iowa species may be grouped as follows:

* We have several additional species in Iowa which also extend far northward, but do not quite reach the Arctic shores. They are largely restricted to the Wisconsin drift lobe, and are mostly marsh plants.

Marsh plants:
- *Eriophorum angustifolium*
- *Potentilla fruticosa*
- *Potentilla palustris*
- *Ranunculus Purshii*
- *Senecio palustris*

Forest plants:
- *Chrysosplenium tetrandrum*
- *Cystopteris fragilis*
- *Populus tremuloides*

Plants of drier open grounds:
- *Equisetum arvense*
- *Hordeum jubatum*

Of these species the *Chrysosplenium* and *Ranunculus* are so rare and local that they may be new immigrants rather than old stragglers.

The *Populus* and *Hordeum* often appear at the edges of boggy places, and the *Chrysosplenium* and *Equisetum* are said often to occupy the wet grounds of the low tundra in the far north.

All of these species, with the exception of the *Chrysosplenium* and *Potentilla palustris*, extend well south beyond the glacial limits, and one species, *Cystopteris fragilis*, extends from Tropical America to 76° N. lat., in Greenland.

This Iowa group, while not large, is made up, with one exception, of species which at least sometimes favor low grounds, in that respect resembling the greater part of the flora of the Arctic coast, of which they also form a part. The great variation in the composition of these floras extending through the Arctic belt from Greenland to Alaska, and the diversity in habitats which they display, suggest that other than Arctic glacial conditions were responsible for their development and distribution, the most probable of these being moisture, exposure, and to some extent, soil conditions.

Judging from the flora, the climate of Labrador is much more like that of Greenland than of any other part of the Arctic belt, and is also no doubt greatly influenced by proximity to the sea. In all these northern regions there are no excessively hot days in summer, and relative humidity is high, — a condition which seems to favor the Arctic flora.

The Point Barrow Expedition (Ray, 120) kept an hourly record of temperatures (and relative humidity) from November 1, 1881 to August 27, 1883 inclusive. In the following condensed tables the record is given only for the months of June, July and August, 1882 and 1883. In each case only the mean maximum and the actual maximum for the month are given, and this is followed by the number of the page on which the detailed record appears in the Report. The figures (with decimals) indicate the degrees Fahrenheit.

	Mean max. temp.	*Act. max. temp.*	
June, 1882	34.53	53.5	(p. 235)
July, 1882	49.01	65.5	(p. 236)
August, 1882	43.75	58.9	(p. 237)
June, 1883	36.84	50.9	(p. 247)
July, 1883	40.76	53.2	(p. 248)
August, 1883	43.27	60.5	(p. 249)

Johansen (82, p. 18 C) reported a maximum of 70° F. for June, 1914, on the Arctic coast, while Chipman and Cox (28, p. 32 B) reported 76° F. as the maximum summer temperature at Coronation Gulf on the same coast.

The hourly determinations of relative humidity in the same period are similarly condensed in the following table. The first two columns give the daily average minima and maxima for the months designated; the third column contains the actual minimum for the month; the fourth column contains the number of hourly observations (out of a total of 4320 made during these three months in the two years) during which the relative humidity dropped below 70, and this is followed by the page of the report containing the detailed record.

	Av. Min.	*Av. Max.*	*Act. Min.*	*No. below 70.*	
June, 1882	74.1	88.3	65	126 hrs.	(p. 254)
July, 1882	66.3	95.9	58	185 hrs.	(p. 254)
August, 1882	78.7	94.0	57	80 hrs.	(p. 255)
June, 1883	81.8	94.0	74	36 hrs.	(p. 260)
July, 1883	77.7	94.2	70	35 hrs.	(p. 261)
August, 1883	81.0	93.7	67	20 hrs.	(p. 261)

That the Arctic coast eastward from Point Barrow likewise has a high relative humidity is indicated by Johansen's statement (82, p. 18 C) that during July, 1914, the "weather was often hazy, with rain or wet snow, to the breaking up of the sea ice. All the plants had green leaves and were mostly in bloom." (See also p. 35 C.) That the vegetation is also strongly influenced by protection from winds was also noted by the same observer. (See pp. 16 C, 26 C, 41 C, 42 C, 43 C, 48 C.)

It is evident that a high relative humidity and a moderately low temperature which varies comparatively little during the long Arctic summer day, are favorable to the flora of the far north.

On the other hand, the summer temperature in Iowa often reaches 90° F., and sometimes exceeds 100°, while the relative humidity commonly falls below 60°, and sometimes is even less than 30°. It is not likely that this was greatly increased (excepting by the lowering of the temperature) during the Wisconsin glaciation, for there were no seas nearby to furnish an abundance of moisture.

That habitat, with all its environmental factors, coupled with the accident of distribution, is chiefly responsible not only for the grouping of our floras but for their geographic distribution, is suggested also by the extension of northern floras southward along both our eastern and western mountains. In many cases these northern plants have been distributed far south of the borders of the glacial ice-sheets, and in many cases, no doubt, they were returned to repopulate the areas which had been devastated by the ice, where, of course, suitable habitats occurred.

These mountain extensions of northern floras consist chiefly of two floristic types: plants which require the shelter of deep forests or moist canons and glens; and those which prefer exposed and rather barren habitats. Both types of habitats are well represented in the mountains in question, and the northern floristic types probably entered them long before the advances of the ice-sheets because they found suitable habitats which have persisted and permitted these forms to remain in the far south after the retreat of the ice-sheets and the northward re-establishment of their own kinds.

The flora of the north central plains was much more directly affected by the ice-sheets. The destruction was complete on the ice-covered areas, and the retreat of the ice left fewer habitats suitable for the northern species, with the result that many of them entirely disappeared from southerly areas, while some may have left small colonies behind in the limited suitable places. In many cases, however, the latter probably returned to such suitable habitats as were created by subsequent erosion, or by the development of a protective flora. There has probably been a swinging back and forth of essentially the same flora and fauna with each advance and retreat of at least the later ice-sheets, for the best available evidence indicates that both the plants and land and freshwater mollusks have changed but little throughout the entire Pleistocene. Even the molluscan fauna of the Aftonian, the oldest interglacial interval, consists of modern species, though there was a marked difference in the mammals. (See Shimek, 132, pp. 328-347; Calvin, 21 and 22, pp. 207-216; Hay 74.)

The prairie and plains flora extended far to the south, beyond the limits of the glacial sheets, and readily advanced northward as favorable habitats were restored after each retreat of the ice. The swamp and aquatic floras persisted wherever favorable habitats remained, and were returned, perhaps most promptly, by migrating waterbirds to the numerous ponds and swamps which were formed on the ice-freed flats. It is doubtful, however, that boggy tundra conditions prevailed to any extent along the margin of the Wisconsin ice in Iowa. There are no evidences of such bordering bogs on either the Iowan or Kansan drift areas contiguous with the Wisconsin lobe, and if tundra developed along the margin, it was probably very narrow and of the dry type excepting within the Wisconsin lobe, for the climate of this region has continued quite as dry as it is at present (if not somewhat drier), as is shown by the vertical distribution of the fossil land snails in the loesses. (See Shimek, 138.)

The thousands of years which have elapsed since the disappearance of the last Wisconsin glacier from Iowa have given ample time for migration and adjustment of the major floras, as well as for the casual introduction of individual species or ecologically related small groups of species which form isolated colonies. In the case of such outlying colonies along our own border areas, consisting of one or few species which seem to be out of harmony with the surrounding major flora, there is always a possibility of later introduction, though it is customary to refer to such cases as remnants of older floras.

Some of these colonies, however, are now found on areas which were evidently completely covered by Wisconsin ice. Thus, in the heart of the Wisconsin lobe, near Fort Dodge, there are small colonies of such northern plants as *Campanula rotundifolia* and *Menyanthes trifoliata*; and of certain other northerly plants which, however, extend much farther south, such as *Diervilla Lonicera, Dirca palustris, Maianthemum canadense* and *Polypodium vulgare.* All these species are found in Iowa in scattered colonies, often very widely separated. All were evidently introduced into their present localities in Webster County after the withdrawal of the Wisconsin ice, which once covered the entire area of that region.

Eastward, at Iowa Falls, nearer the margin of the Wisconsin, but well within its border, is a small colony of *Juniperus communis* (here far removed from the nearest colony of its own kind) and a very small colony of the northern *Primula mistassinica*, which is not known anywhere else in the state. A few miles eastward, lying at least partly just outside the Wisconsin margin, are small outlying colonies of the northern *Pinus Strobus*, *Betula lutea* and *B. alba* var. *papyrifera*, and also the solitary Iowa colony of *Aspidium marginale*, which is also chiefly northerly in distribution.

It would seem to be quite as easy to account for the presence of these northerly colonies by more recent migration, as it is to account similarly for certain more southerly species which are likewise scattered in small colonies (in some cases over several of the drift areas without distinction), such as *Aspidium Goldianum*, *Asplenium platyneuron*, *Cheilanthes Feei*, *Myosurus minimus*, *Opuntia Rafinesquii*, *Quercus lyrata*, *Rhexia virginica*, etc.; or for species which have a wide distribution, but in Iowa are restricted to often widely scattered colonies, such as *Asplenium angustifolium*, *Camptosorus rhizophyllus*, *Carex eburnea*, *Selaginella rupestris*, *Ulmus racemosa*, etc.

In all such cases the plants of each species seem to find similar habitats, no matter how widely the colonies are separated. There may be some variation, it is true, as in the case of the *Selaginella* which grows on alluvial sand in Muscatine County, on limestone in Dubuque County, on St. Peter sandstone in Winneshiek County, and on Sioux quartzite in Lyon County, but even here the habitats are all about equally xerophytic.

Seeds and spores are scattered more or less promiscuously by the several agencies concerned, and no doubt many fall upon unsuitable areas and are lost, while those which find congenial surroundings, even though detached and limited in extent, survive. In such cases, for example, as that of the delicate *Woodsia mexicana*, which occurs in small colonies in crevices in the heart of the lava desert (Mal Pais) of New Mexico, many miles from the shelter of the mountains,* or of the marsh and aquatic plants which soon invade ponds formed on our Iowa upland prairies in recently excavated gravel pits far removed from other bodies of water, there can be no possibility of the survival of an older flora. These are clear cases

* Specimens of this delicate fern curled up visibly in a few moments when lifted into the dry atmosphere of the extremely xerophytic desert from their station 18 inches below the general surface of the comparatively recent lava.

of invasion such as has been repeated many times, no doubt, during the thousands of years which have elapsed since the Wisconsin glaciation, and as has taken place at some time over our entire glaciated areas.

A flora may have survived on the "driftless area" of Iowa and Wisconsin during each invasion of the ice, but it was not the flora of the present, or anything ecologically akin to it, and it would not survive in that area during each interglacial interval, being supplanted in each interval by a flora like that of today. If the surviving flora was moved into the Lake Superior region, as was suggested, it would have been returned just as easily from a temporary retreat beyond the ice-margin. Neither the presence of this "western flora" at Lake Superior, or of its few representatives in the "driftless area," offers satisfactory proof that the latter persisted in this area through all the ice invasions.

In his effort to show that that part of the northeastern flora which is included in Table IV did not reach that territory through the ordinary seed-dispersal agencies, Fernald did not give sufficient credit to these agencies though he was not unmindful of them. This is particularly true of wind and birds.

He recognizes (p. 286) the fact that most of the plants in Table IV are scattered by wind, but cites several with fleshy and a few with spinous fruits as examples of those which could not be carried by wind. Such windstorms as that of March 9, 1918, previously noted (Winchell and Miller, 156), when traveling eastward could carry even the larger seeds, especially if they were lifted to the upper strata with greater wind velocity by the not infrequent tornadoes, most of which in the upper Mississippi region also seem to travel eastward and northeastward. This method may not account for the presence of some of these plants in the far northeast, but it is worth noting that the carrying power of wind during more violent storms is often underestimated.

It is also possible to have the fleshy-fruited and adhesive fruits carried by birds which have been swept out of their path of migration by similar powerful storms, or by birds whose paths of migration are erratic. Vegetative parts and fruits of *Potamogeton* could be carried similarly by water-birds. Some years ago the writer saw a duck which had been shot some distance from a small lake in Winnebago County in northern Iowa, and adhering to one of its legs was a strand of *Potamogeton pectinatus* with a few fruits adhering to it. Such mode of transportation may not be common, but it has probably occurred much more frequently than can ordinarily be observed, since wading and swimming birds may be easily entangled in such vegetation.

Though Fernald (p. 292) dismissed birds with a three-line statement, they have undoubtedly been one of the most potent agencies in seed-dispersal in our territory. The great flocks which migrate chiefly north and south during each season no doubt carry many seeds, either of the hard, indigestible type, or those which adhere by hooks or spines, or in small cakes of mud or fruit-pulp on the feet or beaks. Water birds also undoubtedly carry either vegetative fragments or fruiting strands of aquatic plants (see also Thompson, 141, p. 251, and Coulter and Thompson, 37, pp. 262-265), and in some cases probably undigested hard seeds.

The movements of birds, however, are not always north and south. The study of migration in recent years, particularly with the aid of bird-banding, has brought to light many interesting facts concerning the direction of migrations. Chapman (27, pp. 42-47) and others have published maps showing the migration of various species. In all cases the migrating stream is shown expanding in fan-shaped fashion until northward it spreads across the country east of the Rocky Mountains, or even across the continent in the far north. No doubt there are also many individual deviations from the general route, determined, to some extent at least, by food and safety, and to some extent by storms.

There are also remarkable cases, like that of the golden plover (Chapman, 27, p. 47), in which the paths of the northward and return migrations do not coincide. The golden plover travels northward up the Mississippi Valley and spreads along almost the entire Arctic coast, breeding from the coast of Bering Sea in Alaska to the west side of Baffin Bay. On the return, however, the birds migrate southeastward to Labrador and thence to Nova Scotia, before undertaking the long flight to the Lesser Antilles and South America. Such birds might carry seeds northward during the spring migration, but eastward and southeastward from Alaska to Labrador on the return.

The writer has before him newspaper maps showing the migration of ducks and geese which had been banded in Jack Miner's famous sanctuary in Ontario,* and many of which had been secured

* Since 1915 Miner has banded and released 10,000 wild geese and nearly 700 ducks.

later by hunters. They were taken in every possible direction from the sanctuary, many of them at very remote points, and it is very evident that they did not restrict their migration to northerly and southerly courses.

This great army of the air has certainly transported many seeds and other parts of plants, and that not only northward, but southward and laterally as well. In the main, the water-birds and waders carried the marsh and aquatic plants; the insectivorous species, which are also, as a rule, fond of fleshy fruits, transported many of the forest plants; and the seed-eating birds carried the seeds and fruits of the prairie. In all cases, of course, other agencies, especially wind, contributed to the dispersal of our native floras.

In addition to the regular migrants we also have wandering residents, or winter-residents, which feed on seeds and fruits, especially during the fall and winter. That handsome vagabond, the Bohemian waxwing, breeds in the far northwest, but later wanders far to the south and east; the purple finch is likewise an irregular winter visitor, and breeds chiefly from British Columbia to Ontario; the flocks of berry-eating waxwings and seed-eating goldfinches, flit about promiscuously not only during the fall and winter, but well on into the summer, before nesting, and both are widely distributed, especially northward.

These species, and others like them, follow no regular path of migration, but wander about at random, north or south, east or west, apparently without rule or restraint.

With so many active agencies at work, operating no doubt through at least several thousand years, it is small wonder that some plants are carried beyond their usual limits to lodge in locally favorable though often restricted habitats. There is certainly no better reason for calling these colonies remnants of older floras than there is for regarding them as re-introductions. If they are remnants here in Iowa, they represent some later stage in the advance of our floras, for, as at present constituted, they do not represent any far-northern, Arctic association.

Let it be repeated, that since these few northerly plants are also still associated with the Great Lakes flora which has invaded our "driftless area," there is no need of assuming unusual conditions for their preservation when it must have been just as easy to introduce them as it was their associates in the major flora.

The flora of Iowa as a whole has been introduced into the state, at various times, by the usual agencies which aid in seed-dispersal, and it has been established in its modern climax formations and has persisted in much the present condition for a long period of time. The greater changes in its composition occurred early in post-glacial time (especially over the older surfaces), but it has since been subjected to minor changes which are still going on.

Post-glacial plant succession in Iowa. — To return to the restoration of our flora after the retreat of the glacial ice-sheet, the lines of succession were no doubt also varied, but on the whole, throughout the climatic prairie formation, the progress was evidently quite direct. The original flora was destroyed by the ice. On the retreat of the latter, portions of the bared surfaces were no doubt dry enough to receive the land plants from the well-populated areas to the south. At first perhaps the tundra returned, to be closely followed by the prairie from the south. Judging from the nature of advances made today, the first colonies of the prairie flora probably consisted largely of mixtures of the native weeds, and of rather large numbers of individuals of a few species producing many easily transported and readily viable seeds, but *all* belonging to the prairie.

On the undrained parts, where kettleholes had been left, the habitat was suitable for hydrophytes. Portions of these areas were gradually drained and directly covered by the prairie flora.

Such direct transitions from hydrophytic to xerophytic floras were once abundantly illustrated by the beaches of our northern lakes (and may still be observed in a few places), where there were no currents of water to bring seeds from diverse, more distant areas. In the drier seasons, as the beaches became more exposed, the prairie flora advanced, replacing the swamp flora bordering the lake, which had been forced back by the retreat of the waters. This has been observed repeatedly by the writer, within the past forty or more years, during dry seasons along various lake shores, notably at Terrace Park at the south end of West Okoboji Lake, at Orleans on Spirit Lake and at the north end of East Okoboji Lake.

Occasionally, as at Terrace Park and at the north end of East Okoboji Lake, there was a perfect and direct transition from upland prairie to the swamp flora bordering the lake. The typical prairie flora of the uplands had also taken complete possession of the older, more elevated, still distinctly sandy beaches, and thence blended with the more recent mixed beach flora. The upland prairie and the older beaches were distinctly xeric, the immediate border of the lake was hydric, and between them was a belt of varying width which may have appeared to be mesic, but in reality produced no distinct mesophytic flora. The flora of this belt was, instead, a mixture of truly* xerophytic with truly hydrophytic (or rather, helophytic or swamp) plants, more or less blended in this transition belt, but there was no suggestion of a zone of truly mesophytic types.

Of course the advance of the prairie floras has been checked repeatedly by high water in the lakes, by violent wave-action during protracted storms, and by ice-thrust (or "ice-shove"), but always on the return of drier conditions, the advance was resumed. Where artificially drained kettle holes were left undisturbed they, too, were entered by the prairie flora.

On parts of the lake shore, however, where there are abrupt banks or slopes and the prairie does not come down to a flat beach by a very gradual slope, a grove or thicket was soon developed, always starting in the shelter of the bank. Where gullies or valleys were left by the retreating ice, thickets and groves also took early possession of their sheltered parts, and later, as erosion extended the valleys and formed new ones, the groves spread to the rougher lands, excepting where their surfaces were exposed towards the west, southwest or south. Thus the forest was, in most cases, probably the last of the principal formations to become established, and in Iowa its development was usually checked before it reached the stage which in more favored regions eastward is regarded as the climax.

Very often, between the prairie and the forest, especially where the border surfaces were less abrupt, a transition belt was developed, the physiognomy of which was determined by shrubs or scrubby trees, but which consisted of a mixture of xerophytic prairie plants and more mesophytic forest plants, the latter, however, usually by no means as mesophytic as those in the heart of the adjoining grove.

Other plant formations were developed in lesser degree on the smaller sandy and rocky areas, and these, like the major formations, will be discussed in subsequent separate chapters.

* It will be shown in the chapter on the Prairie that even these moist beaches are periodically very xeric.

CHAPTER V

CLIMAXES AND ECOLOGICAL CLASSIFICATION

The Climaxes. — If the successive changes in a flora continue until a definite, quite stable ecological type or group of plants is produced representing the ultimate floral possibilities of the area occupied by it, provided no material modification of its climatic factors occurs, the whole series (or sere) is said to culminate in a climax.

There has, however, been some diversity of opinion among plant ecologists as to the definition of a climax; and from the very nature of the case, there has been much uncertainty as to its exact nature.

Cowles (39, p. 161) did not at first use the term climax, but designated "the final vegetative aspect" as a "climatic formation," and stated that "in every case, the ultimate or climatic plant formation is the most mesophytic which the climate is able to support in the region taken as a whole."

Clements (29, p. 105) defined the climax as follows: "Every complete sere ends in a climax. This point is reached when the occupation and reaction of a dominant are such as to exclude the invasion of another dominant." He further stated (p. 109) that "when the change of climate favors mesophytic conditions, the existing seres are continued by the addition of one or more stages dominated by higher life-forms."

McDougall (92, p. 227) practically repeated Cowles' definition in the statement that "the fully mature plant associations of any climatic region represent the most mesic vegetation that can be supported by the climate of that region," and hence are "climax associations."

Robbins and Rickett (121, p. 463) stated that plant associations advance until "a type of association is reached which does not produce any further change in environment (provided no changes occur in climate or in soil) and which therefore perpetuates itself instead of yielding to new types," thus forming a climax association; and further (p. 464), that "in general, associations progress from extremely hydrophytic and xerophytic toward mesophytic conditions.''

All the foregoing references might seem to imply that the ultimate climax is mesophytic, and they have frequently been so interpreted, though these statements can be so interpreted only by implication.*

A broader and more specific concept of the multiple climax or climax formation was presented more recently by Weaver and Clements (150) in the following statements: (p. 44) ''The major divisions or units of the vegetation possible under a particular climate''; and further (p. 75): ''while the general sequence of a sere is the same nearly everywhere, . . . the climax community in which it ultimately terminates, is determined by climate.'' They then enumerate (p. 425) a Tundra Climax, three Scrub Climaxes and the indefinite (and evidently comprehensive) Tropical Climaxes.

The writer has no desire to enter upon any details of the classification of climaxes which might add to the existing confusion of terms and concepts, for a regional study of this kind should not be used as a basis for broad or complicated classifications. There are, however, some considerations which have a bearing on our state problems which should receive attention.

The evolutionary concept of floras and floral climaxes is now generally, and often too literally, accepted in this country. There can be no question that all floras pass through a series of changes before a stage of reasonable stability, or a climax, is reached, but the steps in these changes are by no means uniform, even in the development of floras of the same climax type. Thus, either prairie or forest may develop from a swamp or a sandy area, but the several steps in the evolution of each climax will not be the same.

It should also be emphasized that climax floras are not always the direct result of general climatic influences, but may owe their character to the modification of these influences by environmental factors, particularly topography, and to some extent by the vegetation itself. In a hot and dry climate an appropriate flora may find a cool and moist retreat in a ravine or canyon, while in a cold, moist climate a flora exposed to the wind and sun may be quite xerophytic.

* The oft-expressed belief that our Iowa prairies would ultimately have been covered with forest, and the designation of them as sub-climax or something unfinished, carry the same implication. These will be discussed in connection with the prairie.

The successional series leading to a climax usually involves a series of processes, such as the following:

1. — The introduction of a flora on denuded surfaces, its nature and abundance being determined chiefly by the proximity and variety of plants in the established floras which form the source of supply, and by their adaptability to the new area.

2. — The gradual introduction of other suitable species and the competition between them and the pioneers, which gradually results in a balanced condition.

3. — More or less coincident with the foregoing, the reaction of the flora itself, usually resulting in the modification of the soil, and in the creation of shelter for other available plants requiring protection, and often modified by atmospheric conditions, rainfall, epidemics of parasites, etc.

4. — Succeeding steps of a similar nature until a climax is reached which is best adapted to the more stable conditions of the environment.

In many cases the result is a complete change from a hydrophytic to a mesophytic or xerophytic flora, with the practical extermination of the pioneer and the earlier succeeding floras, and the substitution for them of one with entirely different ecological requirements. In the case of the prairie flora, however, the denuded area (whether bared by ice, water or other agencies) is entered directly by the more migrant prairie types (the "prairie weeds") which become the pioneers, and are quickly followed by the more stable part of the prairie flora, which is finally established as a climax, without, however, entirely displacing most of the pioneers. In that case the whole process consists simply of the competition and readjustment of the species which belong essentially to the same ecological type, but differ somewhat perhaps in promptness of dispersal, viability of seeds, and rate of growth.

The flora of any particular local habitat may represent a climax, or any of the earlier stages, and even the latter may continue for a long time under the influence of counteracting forces of a more or less local character. Thus, either alluvial forest or prairie may finally develop on river-bars, as often occurs along our streams, but it is usually impossible to foretell which it will be, though the direction of the valley and the position of protecting bluffs often suggest the final result.

Even the climax, however, is not stable, for constant changes are going on within it, due to its own reactions, or to the fluctuation of its environmental factors. Thus, in our early upland rather open groves large trees occasionally failed, and almost immediately a thicket of forest seedlings took possession of the opening thus formed, and they were accompanied by large numbers of *Geranium maculatum*, *Polygonatum commutatum*, *Smilacina racemosa*, and other forest plants which are often found at the borders, while *Cypripedium parviflorum* var. *pubescens*, *Orchis spectabilis*, several of our ferns, etc., were practically crowded out. The seedlings would soon form a thicket which in time would be thinned out by competition, until the earlier conditions were restored. Here there was not only a temporary change in the physiognomy of the area, but also to some extent in the composition of its flora, and such cycles of changes were being repeated continuously in our wooded areas, at times presenting distinct phases of maturity, and at others juvenile conditions of an early invasion.

In our prairie climax flora there are also constant changes from year to year as a result of sharp competition and fluctuations in meteorological conditions. Some species increase greatly for a time and then drop back into a secondary place, occasionally some are crowded out entirely, while a few additions may slip in, — and all this may take place without materially changing the aspect of the prairie. In Iowa, along the borders of the prairie and forest contacts, and in prairie openings, forest plants frequently invaded the prairie during cycles of favorable seasons, only to retreat again before the advancing prairie flora with the return of drier seasons, and there was absolutely no way of determining which climax (if any) would finally win. Indeed, the border areas were constantly fluctuating quantities, varying more or less in position, in width and in floristic composition.

As a matter of fact the whole concept of a climax seems to be very indefinite. Writers in the forested regions to the east speak freely of the Beech-Hard Maple association as *the* deciduous forest climax, while those to the west of us regard the dry-prairie and prairie-steppe flora as the grassland climax. The first does not exist in Iowa at all, there being no beeches, though the hard maple occurs, and the second occupies only comparatively limited areas, chiefly in the western part of the state. Yet much of the intermediate flora is much older than the Beech-Maple associations on the

Wisconsin drift, to the east of us, or the dry prairie on the comparatively recent loess of the Missouri River bluffs.

We will probably be told that these are sub-climax stages in arrested development due to environmental factors, but this only emphasizes the fact that environmental factors, coupled with available sources of seed, are more potent than any "law" of succession in determining the character of our floral "climaxes."

The concept of a climax as the culmination of a successional series is convenient and serviceable, but it cannot be reduced to a rigid, or even approximate, rule as to the character of the final (?) stage or the nature of the route by which it was reached. Nothing has so revealed the weakness of this concept as the waverings of those who have attempted to use, define, classify, or illustrate it by examples.

As a matter of fact, certain very characteristic aggregations of plants occupy very distinct habitats, and they display in each type not only a definite and consistent physiognomy, even though the specific floristic composition may vary, but they possess certain more or less definite structural (and also physiological) adaptations. These adaptations not only contribute directly to the possibility of their existence in their customary habitats, but they also serve for the (usually) ready recognition of the ecological groups to which the plants belong, even when the characteristic habitat is masked during a part of the season by a temporary suppression of its more manifest qualities.

So long as the habitat is reasonably maintained, and after the adjustment which follows earlier competition among members of the same ecological group, the flora remains reasonably constant until the physical environment is changed through the operation of any cause, and thus directly affects the chief climatic factors, light, temperature and moisture, the two latter particularly in their relation to evaporation and transpiration.

As long as a pond retains a more or less permanent supply of water its flora will continue to be hydrophytic; so long as its borders, or marshy areas resembling them, are maintained, their flora will continue to be helophytic; the climax prairie will remain such until its surface is broken by erosion, or by eolian accumulations, and even where the prairie is due merely to temporary exposure on areas otherwise fitted for mesophytic forest, it will continue until the advance of the slower forest vegetation brings about a distinct change in exposure to climatic factors; and the forest will persist as such until its physical environment is changed by erosion, the invasion of sand-dunes, etc.

In the majority of cases there is a very distinct adjustment of plants to certain definite habitats, the latter including not only soil conditions and drainage, but atmospheric exposure as well. Where the environmental conditions are transitional or intermediate, the flora is always more or less mixed, but in all cases the flora is the most accurate index of either stabilized or transitional conditions.

The great emphasis which has been placed by American plant ecologists on the evolutionary successional concept has led to the neglect of the more detailed study of plant adaptations. Even the more characteristic plants of our several type floras are not generally understood, and no doubt a wealth of ecological information can be developed as a result of painstaking experimental study not only of the distinctly characteristic plants of our various major formations, but also of those species which display more or less adaptability to different habitats. Such plants as *Prunella vulgaris, Populus deltoides, Quercus macrocarpa, Potentilla monspeliensis, Veronica virginica,* and several others, which seem to adjust themselves readily to different habitats, should be studied especially carefully in their various phases and relations.

Such studies should include the determination of the rate and percentage of the viability of seeds under different conditions; the more exact determination of pollination and seed-dispersal in the components of each ecological group; the physiological relation of various soil and atmospheric constituents to the characteristic species of each habitat; the relation of the soil and of the plants themselves, to the absorption and transportation of water, this involving porosity of the soil, colloidal properties, etc.; the determination of structural adaptations in the constituents of each group for protective and other ecological purposes, and the extent and character of variations in them under the different conditions to which they are adapted; the determination of all the physical factors which influence, particularly, photosynthesis, absorption and transpiration, and their seasonal and diurnal variations; the seasonal progression and adaptions of plants growing in each major habitat; the determination of comparative transpiration from different parts of the same plant, and from other plants of the same habitat, under different conditions; the more detailed study of the complicated biotic relationships and influences which affect the welfare of the plants; the more exact correlation of various parts of like floristic areas; the reaction of the flora itself, and other local factors, on its own immediate environment; the competition which continues even between members of a "climax" formation, and the fluctuations, or "ups and downs," from year to year, among the more dominant species which prevent any one of them from gaining exclusive and permanent control of any larger area; the source of any given flora and its course and mode of migration; the closer study of seasonal progression in each floristic area with special reference to seasonal changes in ecological factors, etc.

Many of these studies should be made simultaneously since in ecological work comparative rather than absolute determinations are most valuable. Because of the extent of the field, moreover, satisfactory results could be secured only by the cooperation of several observers working in the same field simultaneously. Such observations would also call for continuity as well as cooperation, for no single season is adequate to furnish that knowledge of the behavior of floras under different conditions which is necessary to an understanding of our major ecological problems.

The results of such studies would not only increase our knowledge of the various natural groupings of plants, but they would also throw much light on successional studies.

The various ecological groups of plants are distinct, on the whole, and they are very definitely related to environment, not only as floristic groups, but by various structural and other adaptations of the constituent species. Until a much more thorough study of the plants in their relation to their environment is made, to supplant the hypothetical concepts with which so much of our ecological work starts, and towards which it again converges, it will make little difference whether we consider any particular formation a climax, or something else. The fundamental fact remains that within each geographic and general climatic area like conditions will bring about like, or very similar, floristic responses.

Despite the fact that much additional information must be secured before a comprehensive and generally applicable classification of floristic groups and areas can be formulated, many such efforts have been made, and too often they have been based on observations in restricted fields. In the following pages the writer will endeavor to show the characteristics and composition of the principal floristic areas within our state, and their natural subdivisions, with special reference to environmental adaptations and to relative adjustment, together with some notice of source and ecological relationship. While most of the complicated ecological and phytogeographical classifications will be avoided, a brief review of some of them will show the unsettled state of this phase of the subject.

[Classification of Communities. Ed.]

No system can ever be devised which will sharply separate ecological groups, for in nature there are no sharp lines of division. Moreover, it is not possible to apply even approximately the same basis for comparison in different regions, for we must recognize the importance of the relation of plants to habitat and the latter term covers the combination of all the atmospheric, soil and biotic factors which surround a plant. This combination may show great diversity, even in regions which appear to be much alike; — indeed, it is a constantly varying quantity in any given spot, from hour to hour during the day, from day to day during the season, from season to season during the year and from year to year. To meet these various conditions plants present an equally varied series of adaptations which must be considered and coordinated. What shall constitute the basis of ecological classification has been, for this reason, a bone of contention, and the author of each system has been able to give valid reasons for objection to other systems, which in turn applied in equal degree to his own.

The common, rather obvious division of our land plants into forest, shrub-land and "grassland," emphasized by the recent recognition (by some botanists) of shrub-lands as climax areas, leaves us with the primitive system once employed in systematic botany when plants were divided primarily into trees, shrubs and herbs, and it is quite as unsatisfactory; the range of habit and ecological adjustment is quite as wide within each of these groups as that of structure which now forms the basis of taxonomic classification.

[Raunkiaer's Life Forms. Ed.]

Raunkiaer's system (117, 118, 119) is based on adaptations which tide plants over resting periods during winter or dry summer seasons. It involves primarily the nature of the resting bud protection, the falling of leaves, and a change in the size of the plant.

While this system presents an interesting and worth-while ecological view-point with a rather unfortunately ponderous terminology, it is practically worthless, and quite misleading for the phytogeographical or plant sociological picture of our flora which this report aims to present.

This is well illustrated in the interesting account of the phaenogamous flora of Connecticut by Dr. Ennis (50) which is based on the Raunkiaer system.

Thus, under the head of "hemicryptophytes,* semi-rosette plants without running branches" the following species, among others, are grouped together, though they are never associated in nature, but occur in the habitats indicated at the heads of the several columns:

Prairie or open sand	Swamps
Andropogon scoparius	*Caltha palustris*
Andropogon furcatus	*Carex stipata*
Senecio aureus	*Elymus virginicus*
Artemisia caudata	*Parnassia caroliniana*
Zizia aurea	*Rumex brittanica*
Forest	
Anemone virginiana	*Hystrix patula*
Carex laxiflora	*Osmorrhiza longistylis*
Geum canadense	*Ranunculus recurvatus*

Similarly, under "Protohemicryptophytes" ** the following species of unlike habitats are likewise brought together:

Prairie or sandy soil	Swamps
Aster linariifolius	*Ludvigia palustris*
Aster multiflorus	*Lysimachia quadrifolia*
Solidago graminifolia	*Mimulus ringens*
Solidago tenuifolia	*Scutellaria lateriflora*
Forest	
Agrimonia gryposepala	*Chimaphila umbellata*
Aralia racemosa	*Maianthemum canadense*

A third group, the "rhizome geophytes with buds below the soil surface" similarly contains the following:

Prairie or sandy soil	Swamps
Asclepias syriaca	*Eleocharis acicularis*
Carex cephalophora	*Eriophorum gracile*
Carex pennsylvanica	*Phalaris arundinacea*
Panicum virgatum	*Phragmites communis*
Physalis heterophylla	*Scirpus americanus*
Polygala Senega	*Symplocarpus foetidus*

* Perennial herbs with their resting buds buried in the surface soil-stratum.
** Hemicryptophytes with the leaves as well as the floral shoots on the stem.

Forest

Actaea alba	*Circaea lutetiana*
Actaea rubra	*Polygonatum commutatum*
Anemone quinquefolia	*Smilacina racemosa*
Carex rosea	*Trillium erectum*

Not only do not the plants of the several habitat subdivisions of each group mingle, but in many cases even the members of the same general habitat group are not closely associated. These examples are sufficient to show that the Raunkiaer system, whatever may be its ecological interest, has little value for plant sociological studies.

[The Plant Associations of the Zürich-Montpellier School. Ed.]

It is not the province of a treatise dealing with a comparatively limited regional flora to present a complete general classification of floristic areas with a full terminology (the attempt, with our present incomplete knowledge, would only add to the present confusion), but when such a classification is completed it must be based on the relations of plant-adaptations to environment. It should be based on types of adaptations to groups of environmental factors operating to the same end, rather than on definite species or combinations of species or on single adaptive or environmental characteristics. In other words, it must be founded not merely on the sociological composition of ecological groups, but rather upon the types of adjustment on the part of the plants to groups of environmental factors. The system, moreover, must be sufficiently flexible to admit of the same variation in combinations of characters that is permissible in the taxonomic field, — no single character, or group of characters can be used throughout. Furthermore, so far as possible, mere coincidences must be eliminated, and the emphasis must be placed on causative relations. For this purpose much more careful and well-balanced work must be done on coordinated comparative histological, experimental and continued general field observations in many places, at least one of which should be selected in each major region as a basic station for comparative and directive or suggestive purposes. This would be a great task which could be undertaken successfully only with the cooperation of educational centers and interested organizations, aided by sufficient endowments. Until that can be done, groupings and classifications based on individual local and regional observations must be accepted as tentative, and will inevitably be found more or less inapplicable in other regions.

No one who has followed even local floras for a series of years will doubt that floristic types are related to habitat, and that (with few exceptions not now fully understood) like plants may be expected in like habitats. It does not follow, however, that they will all always appear in like places, — on the contrary, comparisons of like areas in any locality will show that while the floristic type of vegetation for like habitats is quite constant, the specific composition of the flora differs, as is shown in the various comparative lists which follow. In such cases there seems little doubt that the difference is due largely to the accident of distribution.

In the case of rare or very local species there is always doubt as to whether they represent remnants of a retreating flora, or accidental reintroductions. There is not a single case, however, in which the habitat of these isolated colonies is not multiplied in several if not many localities and often in many parts of the general region. Thus *Juniperus horizontalis* is found near Rockford on a dry bank in a low ridge of drift soil, mingled more or less with the decomposed Rockford shales. Such spots occur along Lime Creek (Winnebago River) for many miles, yet the area in which the species occurs is very limited.

Potentilla tridentata and *Woodsia ilvensis* occur on but two limited exposures of St. Peter sandstone near Hesper, about half a mile apart. One of these exposures also contains *Pyrus melanocarpa* and *Polygonum Douglasii*,* while the other has a limited colony of *Arctostophylos Uva-ursi*. These species are known in no other part of Iowa, though similar exposures are not infrequent in the northeastern part.

Prunus pumila is known in small colonies on the two exposures of St. Peter sandstone at Hesper, on a sandy (old beach) area east of Spirit Lake, and from one of the two larger exposures of Sioux Quartzite in the northwest corner of the state. Like areas appear elsewhere, — in the two former cases many times, yet no other colonies of this species are known.

Osmunda cinnamomea and *O. regalis* are each known in but one small colony in the state, — the former in a bog, associated with *Symplocarpus foetidus*, and the latter near the edge of a woodland bog nearby, both in Muscatine County. Both locality types are

* This proves to be *Polygonella articulata*. — Ed.

multiplied many times in the same region, as well as in other parts of the state, yet no other colonies have been found, though *Osmunda cinnamomea* was found by the author in a small, now extinct colony in the southern part of Johnson County, more than fifty years ago.

Brasenia Schreberi has been found in but three localities in Iowa, namely in a pond among the sand dunes northwest of Muscatine, in Little Wall Lake in Hamilton County, and in Dead-man's Lake in Hancock County. In recurring favorable seasons, often widely separated, the species has appeared in abundance, especially in the two former localities, but none have been found elsewhere, though many favorable localities, both in the same and other parts of the state, were formerly found and some still exist. *Abies balsamea, Pinus Strobus, Cercis canadensis,* while naturally limited in distribution, have been planted successfully in various parts of the state, while *Nelumbo lutea* and *Zizania aquatica* have been transplanted into ponds and swamps where they grew readily, though none occurred in them naturally, — showing that habitat alone was not responsible for their failure to appear in these localities. The temporary success of trees on the prairies comes here.

A number of other rare and local species might be cited to show that they are very restricted in distribution, though their habitat types are widely scattered, such as, for example; *Pentstemon grandiflorus, Bouteloua hirsuta, Opuntia Rafinesquii, Amorpha microphylla, Aster linariifolius,* etc., in prairie and sandy places; *Abies balsamea, Pinus Strobus, Cypripedium hirsutum, Hydrangea arborescens, Corylus rostrata, Aconitum novaboracense,* etc., among the forest plants, and *Callitriche, Potamogeton, Pontederia cordata, Acorus calamus, Liparis Loesellii,* etc., among swamp and water plants.

While it is true that these species strikingly illustrate the fact that given species are not always to be found in suitable habitats, all the other species of our flora are equally effective as examples when carefully studied in the field, for no species is distributed uniformly in like situations. It is this circumstance which makes all groupings on the basis of prevalent species quite unsatisfactory, for a species may be quite abundant in one place one season and rare the next, or it may vary in the same place from season to season because of seasonal variation in habitat. Or, even in a cycle of seasons favorable to certain species, we may still find them lacking in many favorable places largely because of inequality of distribution, though no doubt unequal competition also plays an important part.

Part 2. The Flora of the State

(Part 2 was never written. The following outline, pieced together from two manuscript outlines, indicates what Professor Shimek had planned. Ed.)

1. Outline

1. Ecologic groups.
   - A. Xerophytic Groups.
     1. Halophytes.
     2. Rocks and ledges.
     3. Trees: Lichens, liverworts and mosses (Fungi are parasites or saprophytes).
     4. Sand and gravel.
        - a. Beaches and bars.
        - b. Dunes and drift ridges.
     5. Prairies.
        - a. True prairie.
        - b. Prairie-steppe.
        - c. Prairie-meadow.
        - d. Sandy prairie.
        - e. Prairie wastes.
        - f. Prairie openings.
        - g. Prairie weeds.
     6. Border Areas.
        - a. Xerophytic.
          - (1) Sand and prairie.
          - (2) Prairie and forest.
        - b. Less Xerophytic.
          - (1) Sand and swamp.
          - (2) Prairie and swamp.
          - (3) Forest and swamp.
   - B. Mesophytic Groups.
     1. Meadows.
     2. Forests.
        - a. Dry upland.
        - b. Moist, mostly alluvial.
   - C. Hydrophytic Groups.
     1. Helophytes.
     2. Hydrophytes.
2. Floral areas and regions.
   - A. Floral type areas.
     1. Prairie and steppe.

Causes of treelessness.
Diverse types.
Flora, — comparison with other prairie regions.
2. Sand and gravel areas, — comparison with prairie.
Dunes; beaches.
3. Bark and rock floras, — rather limited in Iowa.
4. Forest areas. Presenting the easterly forest flora.
5. Water flora.
6. Swamp flora.

B. Floral regions — Iowa, the meeting place of several floras.
1. The prairie, — furnishing the basic flora.
2. The forest, — mostly dotting the prairies with groves.
3. Border regions reaching Iowa.
Michigan and southern Canada flora in the northeastern part.
Southern and southeastern mesophytic flora in the southeastern part.
Southern and southwestern flora in southern part.
Prairie-steppe and western plains flora in the western part, — also in scattered areas over the state.
Northern bog plants in northern part, — also somewhat scattered.
Northern steppe remnants, — also somewhat scattered.
Streams, lakes and ponds.
Swamps.

3. The establishment of floras as illustrated in Iowa.
Migration and succession.
Climaxes.
Relation to geological conditions.
Country rock.
Glacial influences.

4. Economic Problems.
1. Cultivation — adaptation of crops.
2. Windbreaks and shelter-belts.
3. Roadside planting.
4. Conservation.
a. Economic.
(1) Drainage.
(2) Flood-control.
(3) Erosion.
b. Recreational.
(1) Fishing and hunting. { Economic phase: Commercial fishing. Pearl-button clams. Fur-bearers.
(2) Parks.
c. Scientific.
d. (Historical) Not natural areas.

2. The Present Status of the Prairie Problem

[Professor Shimek's last words on a major problem of his lifelong studies. — Ed.]

The problem of the treelessness of the prairies has received the attention of a variety of observers and investigators. More than one hundred years ago it was taken up by surveyors, and Atwater, Bourne and Wells, who had seen the primitive prairie in the course of their field work, discussed it in the first two volumes of the American Journal of Science and Art, 1818-1820. Lack of drainage or fires were regarded as determining causes.

From 1833 to 1839 a group of rather diverse writers discussed the subject, and the causes of treelessness were sought in fires, wind, recent drainage and soils.

From 1844 to 1892 the problem was attacked chiefly by geologists, Dawson, Dana, the Owens, Newberry, Whitney, the Winchells, Worthen, White, Broadhead, McGee, Todd, Swallow, Tarr, Shaler and others, participating. A few botanists also took part, notably Gray, Lesquereux, Engelmann and Fendler. They were joined by Allen and Christy among zoologists, and Hinrichs among meteorologists.

This period was divided more or less sharply into two divisions. During the first, between 1844 and 1866, the more generally accepted causes were poor drainage, rainfall and soil, though fire had a few advocates. During the second, inaugurated chiefly by the work of White in Iowa, fires were the most widely accepted cause, though soils, drying winds, drainage, the bison, etc., still retained some advocates.

In the period between 1892 and 1910 a larger number of botanists took up the problem, and various phases of it were discussed by Macbride, Pammel, Bush, Hitchcock, Gow, Pound and Clements, Schimper, Warming, Harvey, Gleason, the present author and others. A number of geologists, among them A. Winchell, Shaler, Tarr, Geikie, Davis, Gilbert and Brigham, and Condra, also gave more or less attention to it.

During this period little was added to specific fundamental information on which conclusions could be based, but the subject was discussed chiefly in rather general terms on the basis of older views. Hence, again, fires, dry seasons, winds, soil, geological formations, rainfall, over-grazing by the bison, etc., were presented as determining causes, sometimes in new garb and combinations, but on the whole without specific additional data which could lead to more than mere conjectures or general conclusions.

While during this period a number of plant ecologists participated in this problem (which properly and completely falls within their field), and emphasized, more or less, the influence of climatic (meteorological) factors, no quantitative determination of the value of these factors in relation to the prairie problem appeared previous to the year 1910.

In that year the writer (133) published the results of field observations and measurements in western Iowa, and followed it in 1911 (134) with a more complete discussion based in part on the same data. These papers brought out the importance of those factors which facilitate evaporation (and consequently transpiration) and thus make for xeric conditions. Special emphasis was placed on the importance of the westerly and southwesterly dry summer winds and the high temperature and low relative humidity of the early summer afternoons, and the effect upon the flora of surfaces exposed to the combined effect of these conditions, making it of the prairie type.

Similar observations on the relation of evaporation to floras were made somewhat earlier by Transeau in 1907 (143), Livingston in 1908 (89, 90, 91), Yapp in 1909 (159) and Dachnowski in 1910 (41), but none of them included the prairies.

Many subsequent observations made by the writer and his research students merely confirmed the conclusion that the treeless xerophytic flora of the prairies is a consequence of those factors (particularly atmospheric) which bring about excessive evaporation and transpiration. Some of the results of these additional observations were published by the writer in 1915 (135), but many were withheld for further extension.

Other field observations on evaporation and transpiration followed, and papers were published by Fuller in 1911 (59), and Gleason and Gates in 1912 (67), but neither of these touched upon the problems of the prairie. The latter paper well illustrates the danger of drawing general conclusions from limited observations. The conclusion that differences in evaporation are due chiefly to the nature of vegetation was based on observations made in one locality during the earlier part of one summer, June and July.

In 1912 an important paper by Briggs and Shantz (14, 15, 16) called attention to the significance of the relation of the wilting coefficient to plants, and in the same year Brown (19) discussed the relation of evaporation to the water content of the soil at the time of permanent wilting.

While these papers did not discuss the prairie problem they called attention to the behaviour of soil-moisture, and since that time most of the published papers emphasized soil-moisture even above evaporation. Among the papers dealing with the general problem may be mentioned those of M'Nutt and Fuller (96), Caldwell (20), Fuller (60, 61), and Ullrich.* Cannon (24) also emphasized root development and soil temperature, and both have received much attention in recent papers. The study of the relation of roots to soil-moisture has been especially stimulated by Weaver's paper (149), which has been followed by others from the same source.

Studies on soil-moisture and evaporation in relation to the prairies were made by Weaver and Thiel (151) and Pool, Weaver and Jean (114). In both papers evaporation and soil-moisture are regarded as responsible for the treelessness of the prairies, with greater emphasis on soil-moisture.

It is impossible to take up this feature of the subject in detail within the limits of this paper, but some reference should be made to the need of caution in drawing conclusions on the basis of such observations as have been made thus far.

There is little doubt that the wilting coefficient of soils varies with texture, colloidal content of both plants and soil and other conditions, including those of the atmosphere. It is also very certain that plants of the same species become adjusted to somewhat different conditions, and then respond to the same tests in different degree.

The abundance of moisture during even very dry periods in the sandy soils of dunes, and old river-terraces and lake beaches, which nevertheless produce xeric floras on the surfaces exposed to strong atmospheric evaporation, also suggests caution, and need of closer study in all the situations in which such floras exist.

The importance of the study of subsoils in connection with the deep-seated roots of prairie plants must not be overlooked. These subsoils are exceedingly diverse not only in different sections of the prairie region, but often in the same locality. Indeed, not infre-

* Citation not located. — Ed.

quently even the roots of the same individual plant penetrate several subsoil strata possessing very different qualities.

A more accurate geological knowledge of the subsoils than has been displayed thus far in this connection is necessary for the interpretation of the subsoils of any given locality, as well as for the selection of different localities for comparative studies.*

The very rapid changes in the evaporating power of the atmosphere, even within the day, are noteworthy. This is especially high in the afternoon, a fact which seems to account largely for the usual appearance of prairie on southwest slopes, even in partly wooded territory. The writer has found that during drier summer days this has been from two to six times as high in the afternoon, between one and seven o'clock, as in the earlier part of the day, between seven and one o'clock.

These rapid changes produce a visible effect on the flora the cause of which can scarcely be traced to the less responsive, and hence less rapidly fluctuating, subsoil conditions.

That the full effect of these changes may be determined, it is necessary that experimental observations be made at short intervals. Much of the evidence concerning the causes of changes and conditions may be lost in the neglected intervals between observations made only once or twice a day. Where self-recording apparatus cannot be used they should be made at least every hour of the day.

There is some danger in the general tendency towards detailed experimental work: [An outline never filled out. Ed.]

Observation in areas too limited — leads to generalizations that are too broad.

Starting with local detailed observations (concentrating on them) before a broader view of the field is taken is likely to lead to a prejudiced or set state of mind when attempts are made to apply the results.

Difficulties to be kept in mind.

- Problems very complex and we are not sure that we always take all factors into account.
  - This weakens value of comparative observations made at different places.
  - Indoor experimental work — Inevitable creation of artificial conditions.
  - Outdoors — many factors operating, — not in same direction and de-

* An illustration of such lack of geological knowledge is furnished in Clements and Weaver's "Experimental Vegetation" (30), where the statement is made that at Lincoln, Nebraska, the soil called loess is really glacial drift. This is erroneous, both as a general statement, and as applying to the loess at Lincoln.

gree in different localities at the same time, and in same locality at different times.

In both cases element of time may be overlooked. — *Rhus glabra.*

The recent dictum of Clements that "the touchstone of instrument, quadrat and experiment" shall be the test of truly ecological work is likely to lead younger observers to avoid those general observations which are necessary both as an introduction to more detailed study, and in the final analysis of larger problems.

A combination of the two methods is essential.

The influence of the great daily changes in evaporating power, and their direct effect in elimination of the less protected mesic plants, can be observed and measured quite readily.

In all observational and experimental work on the prairie a very important fact must be kept in mind, namely, that in such work there are really two possible objectives. The first is to determine why the normal prairie flora persists in its habitat; and the second to ascertain the factors which exclude the mesophytes of the forest from the prairie.

The first problem involves a careful study of the prairie plants with special reference to the provisions which sustain them against the inclemencies of the air and soil, and which make their continuity possible. Most of the more recent experimental work bears upon this phase of the broad question. In this connection it is necessary to emphasize the need of a more careful study of the prairie flora, not only on the systematic, but the ecological side as well. It is all too common to include among prairie plants those which belong to prairie bogs, and which are at most xero-hydrophytic (helophytes).

The second problem, which really points to an explanation of the treelessness of the prairies, calls for a study of the factors which prevent the forest flora from gaining a foothold on the prairie areas. In this case the evaporating power of the atmosphere plays a most important part, both because of its direct influence on transpiration and its effect on the moisture of the surface soil. Work in this field should be extended to all parts of the prairie region.

The treatment of the prairie problem in most of our college (and some secondary school) texts has been unfortunate.

Clements merely includes the prairie among xerophytic formations, but does not discuss it and Cowles (40) makes no reference to it whatever. Martin (103) limits himself to the erroneous statement that the prairies are mesophytic, and Densmore (47) does likewise, both evidently following the earlier opinions of Coulter (36), Warming (148), and Schimper (126). Holman and Robbins (78) and Gager (62) do not mention the prairie, and McDougall (92) merely refers to the "tall-grass prairie region."

The majority of the college texts on general botany and plant ecology which do refer to the prairie recognize climatic factors as the main cause of treelessness.

Atkinson (10) regarded high winds and very dry summers as chiefly responsible, aided by grazing bison and prairie fires.

Bergen and Davis (12) consider forest fires, scanty rainfall and dry winds in winter as the most important factors.

Ganong (64, 65) regards climatic factors as dominant, but notes that fires and the bison have been suggested as causes. It is of interest to note that the prairie flora is a climax stage.

Transeau (144) also recognizes the climatic factors, but is inclined to overemphasize soil-moisture.

Campbell's recent ecological text (23) treats the subject somewhat more extensively, but not altogether happily. The explanation of the treelessness of the prairies is presented in the following words: "It has been conjectured that the prairies owe their origin to the burning of the forests by the Indians to furnish feed for the herds of buffalo, but the latter themselves may well have played an important role in the destruction by close cropping of any young trees" [pp. 106-107].

In most cases these authors are inclined to accept, at least in part, the older explanations which have been handed down from one author to another without close scrutiny or personal investigation.

Perhaps no work has done more in recent years to perpetuate some of the old untenable "theories" than Harshberger's "Phytogeographic Survey of North America" (73). This work spans an enormous field, — too large for one man to cover satisfactorily. It was necessary for the author to rely largely upon published records. The work was prepared before any more detailed ecological work on the prairies had been published, and the author was forced to depend on the old unsatisfactory records.

The result is a more or less contradictory restatement of old views, with fire still occupying the foremost place, while wholly undue influence was ascribed to grazing bison. The unverified story that Indians deliberately set fire to the prairies to secure pasture for the bison is repeated in this book.

It is evident that a number of the authors of our college texts have followed Harshberger wholly or in part.

In several cases these texts also contain more or less serious misstatements concerning the flora of the prairies, but that subject must be discussed at some other time.

It is unfortunate that our college text-books do not offer more satisfactory information on the prairies, especially since the subject is of so much importance to crop-growers in the prairie-region, for we must not forget that the same factors which influenced and determined the native flora, operate today on cultivated crops.

Limited space forbids a more extended discussion of some of the outstanding features of the prairie problem, but a synopsis of some of its interesting features is here presented.

Synoptical view of the prairie problem.

1. — Exposure to periodic excessive evaporation as determined by temperature, relative humidity, wind and topography, is fundamentally responsible for the occurrence of a xeric treeless prairie flora.

This conclusion is based on extensive field observations on the distribution of our prairie areas, especially on rougher (hence contrasting) surfaces, and on detailed field measurements of the factors involved in evaporation in their relation to plant transpiration.

These factors make for xerophytism in areas of comparatively moderate rainfall, and they may be reinforced or modified by various edaphic factors, such as soils, variations in topography, etc. Available soil moisture is largely dependent upon the same factors, and in the final analysis is one of its effects.

2. — The flora constitutes the only universal earmark of the prairies, and it persists on the exposed surfaces because it is xeric.

3. — This flora represents a climax stage as is shown by its persistence even in strips of a few feet in width between cultivated areas, and its permanent reinvasion of formerly broken surfaces when left undisturbed. There is no substantial reason for indicating or suggesting that this is a transition stage by designating it as "subclimax."

4. — The term *prairie* should be retained for that part of the so-called "grassland association" which centers in Iowa. Grasses were

not the dominant vegetation upon all parts of this region, but were often overshadowed over considerable areas by other flowering plants.

5. — The prevention of the advance of trees cannot be ascribed to the persistence of the prairie turf. This was frequently broken by gophers and other burrowing animals, by ant hills, erosion by water, etc., but the plants which advanced to the new surfaces were not trees, but the "prairie-weeds," followed by the normal prairie flora.

6. — Seed dispersal has been held accountable for the character of the prairie flora. This may explain the grouping of prairie plant societies, but it does not account for the presence of the prairie as a whole.

The fantastic view that the seeds of prairie plants were preserved in the glacial ice, and hence were on the ground when the ice retreated, does not help, for in that case the seeds must have come from similar preglacial prairie, and we have not yet accounted for the origin of the flora. It is clear, moreover, that this view would not apply to the extensive loess-covered prairie areas, nor to the prairies lying beyond the limits of glaciation.

7. — Soils and geological formations are of value only in so far as they affect conservation of water, — composition (particularly its colloidal constituents) and porosity of the former determining its power of holding moisture, and the latter often determining topography and subdrainage. Prairie is found upon practically every type of soil within the prairie region, and over every type of geological formation.

8. — Fineness of soil is not responsible for the prairie, since the latter is found on every type of soil from the finest prairie loam to coarse sand and gravel.

9. — The character of the prairies cannot be explained on the basis of immediate post-glacial conditions, since over large areas loess and other distinctly post-glacial deposits intervene between the prairie surface and the underlying drifts. Extensive prairies, moreover, are found far beyond the limits of glaciation.

10. — Rainfall and drainage, while important in determining the available supply of water in both soil and air, cannot be general determining causes since both are frequently equal on contiguous forested and prairie areas.

11. — Lack of drainage (or slow drainage) cannot account for the prairies. We have prairie on areas recently drained, but we also

find them on high ridges and bluffs, like those along the Missouri River, where both drainage and drying have been rapid, and where the surfaces have been dry and exposed for a long time.

12. — Soil moisture is exceedingly diverse in amount on different types of prairies and cannot be a general determining factor. The amount of available water in the soil proper is evidently largely an effect rather than a cause of the type of vegetation in forest and prairie.

13. — Prairie fires were an effect rather than a cause of the treelessness of the prairies, and where acting as a cause, were local and limited in effect. The following facts and conditions cannot be explained under the fire theory: the sharp transition from forest to prairie on the abrupt ridges along the Missouri River and elsewhere; the presence of heavily wooded bluffs on the Nebraska side of the river, while those on the Iowa side are largely bare prairie excepting where the bluffs curve in such manner that they are not exposed to the southwest; the similar situation along the Mississippi River between Iowa and Wisconsin, and, on a smaller scale in many other places; the usual appearance of prairie on those portions of ridges which face to the southwest; the numerous prairie openings which appear throughout the upland groves of our prairie region; the persistence of prairie on many areas untouched by fires for years; and the restoration of the prairie flora on areas which were once broken but remained undisturbed for several years.

14. — According to the best evidence which the writer has been able to secure, the Indians did not set fire to the prairies periodically for both the bison and later their ponies needed the dry forage during late fall and winter. If fires were started it was by accident, or for the purpose of harrassing an enemy.

15. — Reports of the advance of the forest after prairie fires ceased are greatly exaggerated, at least within the prairie region proper. In most cases there have been mere fluctuations of the border with varying cycles of dry and wet seasons, and they represent retreats as well as advances. In the main prairie region these fluctuations have been comparatively insignificant.

16. — That trees grow on the prairies when planted does not signify that the forest would ultimately extend over the prairies. Care, cultivation and mass planting throw the balance in favor of the trees for the time being. In the heart of the prairie region such planted groves do not expand, — on the contrary thousands of acres

of them have perished, especially in dry seasons. If left to themselves most of them (if not all) would soon disappear.

17. — There is no evidence to show that forests formerly covered all the prairie region. If, as has been claimed, these forests were destroyed by fires, we should be able to find some of the charred remains of the wood, which should be well preserved. This claim is a pure assumption without any foundation in fact.

18. — The treelessness of the prairie could not have been due to extensive grazing by herds of bison, elk, etc. Large areas persisted as prairie long after these animals disappeared. Furthermore, prairie openings and prairies on very steep slopes could not be accounted for in this way.

The attempts to combine excessive grazing and prairie fires as a cause is especially unfortunate, for if there was excessive grazing there should have been no fuel for the fires!

19. — The recession of the sea might account for some of the low areas in the Gulf region (where they are known as "prairies") but it cannot account for the prairies of the upper Mississippi valley where five glacial sheets have swept the surface, and where several interglacial deposits have developed their successive surfaces since the recession of the ancient seas. It should be remembered that the so-called "prairies" of the Gulf region are in reality canebrakes which are wholly unlike our true prairies. This use of the name has led to confusion.

20. — Local intensive experimental studies on various phases of the prairie problem are essential, but in order that cause and effect may be properly weighed, it is necessary that they be based upon a broader knowledge of the prairie region as a whole, and that they be carried on with due regard to seasonal changes, and to the fact that the prairie flora is not the product of one season, or of average conditions, but represents the survival of the effects of the hardest conditions of many seasons. The unfavorable seasons furnish the best evidence because they bring out contrasts, and because their influence is most patent.

3. The Lists of Plants. — Comments by the Editor.

In his final summary Professor Shimek divided the vegetation of Iowa into six categories:

1. Plants of the prairie.
2. Plants of the woods.

3. Plants of the swamps (mostly marshes).
4. Weeds.
5. Plants of sandy ground.
6. Plants growing on rocks.

In the field he listed under these headings, all the plants which he met. These field notes are in 48 field notebooks, now in the Botany Laboratory of the State University of Iowa. He was so exact in his recognition of species that it is safe to take these lists at face value. A very large collection of plants in the University Herbarium makes verification possible.

Apparently "woods" meant areas completely dominated by trees. Openings in the woods are listed as prairie. Low treeless land is prairie unless very wet — true marsh. "Swamps" are all very wet areas with emersed stems and leaves. In prairie areas these are marshes and fens. In wooded bottomlands they are true swamps. These terms are therefore very inclusive. Here are sample headings from his notes. Under "prairie" in Allamakee County we have, for example,

"North of Postville, north of Yellow River on prairie banks."

"Bare hillside (prairie); on upper half."

"Native prairie (bottom) 2 miles south of New Albin."

"New Albin, prairie along railroad, higher bottom."

"Prairie opening on top of hill: Bluffs near mouth of Yellow River."

"Alluvial prairie along railroad south of New Albin."

"Juniper bluff northwest of Waukon."

"Prairie openings west of Balsam Fir grove northeast of Postville."

All of these lists were copied from the field notebooks by Professor Shimek and his helpers and assembled by counties into prairie lists, wood lists, etc., for each county. The names were then arranged alphabetically into lists for prairie, woods, etc. In compiling lists from his field notes Professor Shimek felt free to remove names from a field list of prairie plants and transfer them to woods, swamps, weeds, or sand. Thus the lists are chosen on a somewhat subjective basis, or rather the notes taken in the field are duly evaluated.

Finally all of the species of the county were arranged alphabetically, in a chart with parallel columns for the six categories. Each species then received a check mark in the column or columns for the categories in which it occurs. *e.g.*

	Prairie	Woods	Swamps	Weeds	Sand	Rock
Mollugo verticillata	+					
Monarda fistulosa		+				
mollis	+					
Muhlenbergia mexicana	+					
racemosa	+					

Many of these charts were made, but they were not completed sufficiently to warrant printing.

For the finished work, The Plant Geography of Iowa, Professor Shimek promised Appendix 1. Systematic List of Plants of Iowa, and Appendix 2. Alphabetical list of Latin names, followed by common names when in use. Thirteen plates are referred to in the manuscript. Only plates 1 and 2 can now be identified as the plates Professor Shimek had in mind.

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