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The Postglacial Phytogeography of the Iowan Lobe

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Abstract: The Iowan lobe of the Wisconsin glaciation is located in northeastern Iowa. Evidence is summarized which pertains to the migrations of the regional vegetation following the Wisconsin glaciations. The most recent climatic fluctuation to influence the distribution of the present flora was the Hypsithermal interval.

The present distributions of several species are discussed in relation to the postglacial history of the flora. Eleven distribution maps of representative species are included. Most of the distribution patterns can be attributed to factors other than continuing postglacial migration. It appears that these plant distributions are primarily a function of the distribution of available habitats. Most species appear to have had sufficient time since the Hypsithermal interval to complete their migration into the Iowan lobe and to become well established.

The need for additional paleobotanical and phytogeographic research in Iowa is stressed.

INTRODUCTION

The Iowan lobe (Figures 1-11) was glaciated in fairly recent times geologically and is adjacent to the Cary lobe, which was glaciated even later. The entire present flora must have migrated into the region subsequently and this migration may still be continuing. It would seem logical that, if plants are still migrating into the Iowan lobe, their distribution patterns would show discontinuities at the limits of their range. At the time of the investigation reported here, the floras of the areas adjacent to the Iowan lobe had recently been intensively studied and a floristic study of the Iowan lobe was under way (1). Thus it was possible to plot detailed species distribution maps of the floras of the Iowan lobe and the bordering areas. These local distribution patterns were analyzed, together with the over-all ranges of these species, for evidence of continuing postglacial migration.

Evidence of Pleistocene plant migrations has been studied in detail in Europe; the British work was summarized by Godwin (2). Some research has been undertaken in this field in the eastern and central United States, but very little in Iowa. Shimek (3) discussed the question of postglacial vegetational migration at some length, but his reasoning was primarily deductive because of the lack of detailed floristic information at that time. Just (4) reviewed the literature pertaining to the postglacial

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vegetation of the northcentral United States. He pointed out the incompleteness of the records and suggested:

> A detailed and carefully planned comparative study of the floras and faunas of glaciated and unglaciated soils would open broad vistas not now known. . .the great theoretical and practical results accruing from such a survey would be well worth the cost and effort put into it.

Historical and Ecological Factors

Before it is possible to state with any degree of certainty that a particular species distribution is traceable to glacial influences, it is necessary to evaluate the historical and ecological factors which also might have influenced, or might still influence, the distribution of that species.

Postglacial Migrations.

The lowest levels of the McCulloch peat bog in Hancock County, Iowa, indicate that Iowa was covered with a *Picea* forest in early postglacial time (5). Other pollen studies of peat deposits in the Driftless Area of Wisconsin by Hansen (6), in Michigan and Indiana by Potzger (7), and in Texas by Potzger and Tharp (8, 9) indicate that this spruce forest was widespread. The succeeding stage in the McCulloch bog was interpreted as a deciduous forest, which was followed by a period during which grasses predominated. This sequence has been interpreted to mean that in this region an early cool, moist period was followed by a gradual change to a warmer and drier climate (Hypsithermal interval), indicated by the predominance of grass pollen. The base of the spruce layer of the McCulloch peat bog has been dated, by the carbon^{14} procedure, at 11,600 to 11,790 YBP (years before present), the transition from coniferous to deciduous forest at 8,110 to 8,170 YBP, and the beginning of grass dominance at 6,570 to 6,580 YBP (10).

The indications are that the grasses migrated from the southwest during the Hypsithermal period and encroached on the deciduous forests of the Midwest. Eventually the prairies reached as far east as Indiana and Ohio (11). A cooling trend with increased rainfall then began, continuing to the present. This change permitted the deciduous forests to recapture lost ground from the prairies by migration along the streams and the adjacent highlands (12). The pattern of this later migration can be seen in the distribution of the present forests of Iowa, for they are mainly gallery forests associated with large rivers and streams.

Present Climate.

The average July temperature shows a gradient from 72°F. in the northern counties to 74°F. in the southern. The annual precipitation varies from an average of 32 inches in the center of the Iowan lobe to 34 inches in the east and southwest. The mean length of the growing season (killing frost to killing frost) decreases from 160 days in the south to 150 days in the north. The variations in these conditions may not be large enough to have a significant effect on the vegetation, but they must be kept in mind when interpreting the distribution of plants at the limit of their range.

Physical Features of the Iowan Lobe.

The Iowan lobe as delimited by Tuttle (13) has a total area of approximately 9,000 square miles and includes all or parts of 25 counties in northeastern Iowa. It is completely blanketed with one to eight feet of glacial drift, except where eroded away by stream action. This drift is in turn covered with two or three feet of loess.

The topography of this area has been described by Kay and Apfel (14) as "gently rolling" with a relief of less than 100 ft. Nearly all parts are well drained by the major rivers shown in Figures 1-11. Very few natural ponds and no major lakes exist in the Iowan lobe. The bedrock is deeply buried under the drift except where exposed along the banks of the major streams—usually near the margins of the lobe.

The soils of the region are mostly derived from the glacial drift and the overlying loess, but sand terrace soils occur along the Cedar and Wapsipinicon Rivers, and narrow strips of alluvial soils are found along all rivers.

Shimek (3) believed that the native vegetation is generally little affected by minor variations in soil type in this region of relatively new and fertile soils. I am in agreement with this view. Probably the edaphic factor of most significance to the vegetation is the moisture-holding capacity of the soil. Thus loam, sandy and rocky soils all harbor different plant communities. From field observations of plant communities in the Iowan lobe, it appears that the other major ecological factors which determine the habitat and thus the local flora are elevation, slope, protection and available moisture.

Analysis of Discontinuous Species Distribution Patterns

Procedure of Investigation.

In searching for evidence of the postglacial migrations in the present plant distributions in the Iowan lobe, I reasoned that

little useful information would be derived from a study of plants with continuous general distributions in the Iowan area, e.g., *Fraxinus pennsylvanica* Marsh. (Figure 1). Rather, if the present

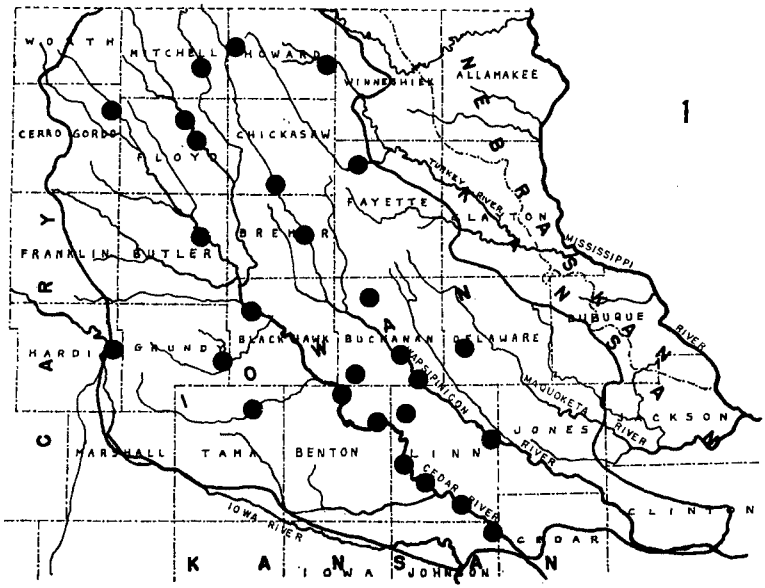

Figure 1. *Fraxinus Pennsylvanica* Marsh.

flora is still in a state of flux, one would expect to find discontinuities in species distributions which cannot be attributed to climatic gradients, edaphic differences or variations in other ecological factors.

Consequently, the first step in this investigation was to campare the floras of the adjacent areas—the Cary lobe by Monson (15), the Driftless Area by Hartley (16), and Johnson County by Thorne (17)—with the flora of the Iowan lobe, searching for discontinuities in distributions of the component species. On the basis of this comparative study, a list was compiled of approximately 350 species appearing to have discontinuous distributions in the Iowan lobe. During the summer of 1963 a special search was made for these species in the field. The herbaria at the University of Iowa, Iowa State University and the State College of Iowa were checked for previous collections of these plants and regional monographs and floristic studies were searched for additional distribution data. I selected for further study those species on which the most complete distribution data were available.

As one might expect, the plants associated in a particular

habitat also had similar distribution patterns. For this reason they are grouped together in the following discussion.

Plants of Wooded Rocky Bluffs and Slopes.

The map of *Pellaea glabella* Mett. (Figure 2) illustrates the distribution pattern of many plants inhabiting wooded rocky places of considerable relief. These habitats are generally absent from the interior of the Iowan lobe; consequently, so are the plants.

Other species with similar but more restricted distributions in the Iowan lobe are:

Lycopodium lucidulum Michx.
Cryptogramma stelleri (Gmel.) Prantl.
Dryopteris goldiana (Hook.) Gray
D. marginalis (L.) Gray
Gymnocarpium dryopteris (L) Newm.
Woodsia obtusa (Spreng.) Torr.
Asplenium rhizophyllum L.
Pinus strobus L.
Taxus canadensis Marsh.
Carex eburnea Boott
C. hitchcockiana Dew.
C. pedunculata Muhl.
Adoxa moschatellina L.
Betula lutea Michx. f.
B. papyrifera Marsh.
Campanula rotundifolia L.
Diervilla lonicera Mill.
Cornus rugosa Lam.

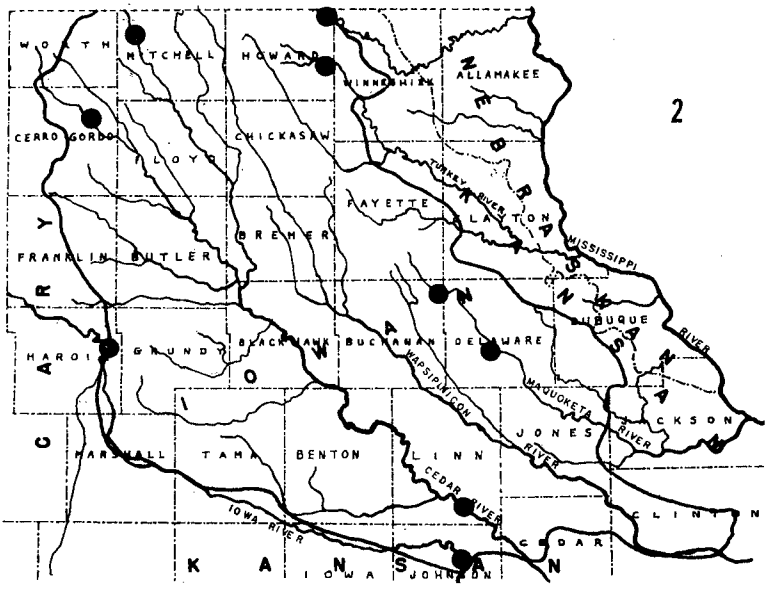

Figure 2. *Pellaea glabella* Mett.

These species also have very similar general distributions, chiefly centered in the northeastern United States and southeastern Canada. Many of these plants are not found west of the Iowan lobe. The probable explanation for this is that there are few rocky bluffs in central or western Iowa. The mean annual precipitation also decreases westward.

Plants of Moist Wooded Slopes and Ravines.

Carpinus caroliniana Walt. (Figure 3) is a species restricted to these habitats.

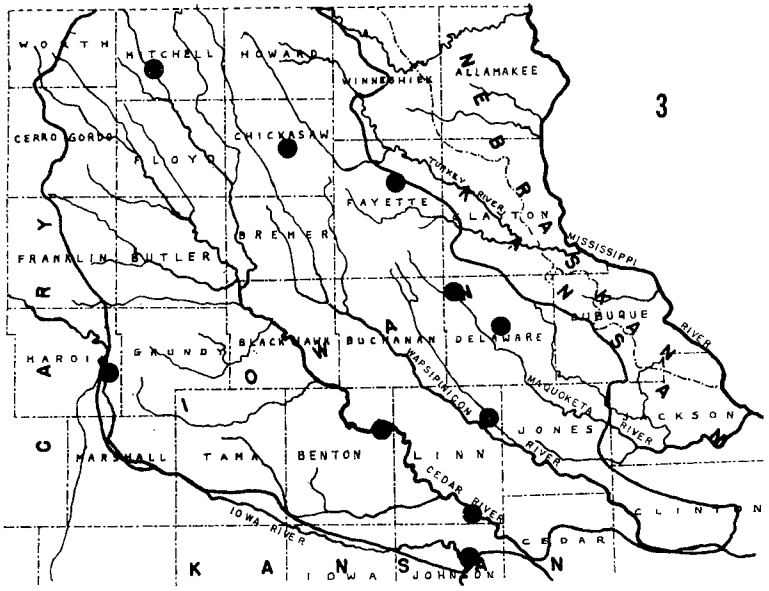

Figure 3. *Carpinus caroliniana* Walt.

Other species with similar but more restricted distributions are:

Lycopodium complanatum L.
Athyrium pycnocarpon (Spreng.) Tidest.
A. thelypteroides (Michx.) Desv.
Dryopteris spinulosa (O. F. Muell.) Sw.
Matteuccia struthiopteris (L.) Todaro
Polystichum acrostichoides (Michx.) Schott
Thelypteris hexagonoptera (Michx.) Weatherby
Asplenium platyneuron (L.) Oakes
Carex gracillima Schw.
C. hirtifolia Mack.
C. jamesii Schw.
C. oligocarpa Schkuhr
Maianthemum canadense Desf.
Trillium flexipes Raf.
Aplectrum hyemale (Muhl.) Torr.
Corallorhiza odontorhiza (Willd.) Nutt.
Cypripedium reginae Walt.
Goodyera pubescens (Wild.) R. Br.

These species have local and general distributions similar to those inhabiting rocky places. This is to be expected, because both habitats are associated with areas of deeply dissected topography, although the two differ ecologically.

As pointed out in the discussion of physical features, the Iowan drift is an area of low relief with few bedrock exposures. Most of the steep rock outcrops and sheltered ravines are located along the periphery of the Iowan drift. The few outcrops that do occur in the interior are along the major rivers and are usually isolated, of low relief and of small extent.

Isolated communities of plants in the Iowan lobe which contain many species having centers of distribution in northeastern U.S. have been referred to as boreal communities (18). This is a misuse of the term "boreal," for these communities contain no spruce or fir, which are characteristic of the boreal forests of the northern U.S. and Canada. Rather, the majority of the species present are constituents of the "Eastern Deciduous Forest Province" discussed in Gleason and Cronquist (19). An unusual number of these plants with northeastern affinities are found on the rocky wooded ravines, slopes and bluffs of Des Moinian sandstone bordering the Iowa River north of Eldora in Hardin County. It has been postulated that isolated plant communities of this kind are relicts of a more contonuous, early postglacial vegetation (12). It can also be argued that these communities are not relicts, but have become established in late postglacial time (3). The reason given is that the last few thousand years have been sufficient for the disseminules (seeds, fruits, spores etc.) of these northeastern plants to have reached nearly every available habitat and to have become established.

Several facts should be considered before drawing conclusions as to the probable age of the plant community at Eldora. First, no endemic species, subspecies or varieties have been found there. Second, analysis of the distributions of the plants making up this community shows that only four species, *Dryopteris goldiana, Dryopteris marginalis, Carex pedunculata* and *Mainthemum canadense* have not been found anywhere else in the Iowan lobe. (These four species have been collected in White Pine Hollow Forest Reserve approximately 100 air miles east of Eldora and in several other localities in the Kansan area east of the Iowan lobe.)

It is possible that other populations of these four species existed in the Iowan lobe before their habitats were destroyed by cultivation, pasturing or lumbering; possibly some undiscovered populations still exist. For many years the only place in the Iowan lobe that *Betula papyrifera* had been found was near

Eldora, until it was collected in Linn County by R. V. Drexler in 1951.

A third factor which must be considered is that it is rather unlikely that this plant community, requiring a microenvironment which is cooler and moister than the prevailing climate of the area, could have persisted during the Hypsithermal time, when conditions were warmer and drier than at present.

Taking these factors into account, I think it is reasonable to assume that the plants making up the community at Eldora moved there as a part of the northward migration of deciduous forests following the Hypsithermal interval. These plants, which required a specialized environment, probably moved by a step-by-step migration between habitats which were more numerous before the land was settled. Some dispersal over greater distances may also have occurred.

Plants of Moist Alluvial Woods.

Representative species illustrating the discontinuous distributions of a number of plants inhabiting flood plains and terraces of rivers and streams are: *Cornus drummondi* C. A. Meyer and *Gymnocladus dioica* (L.) K. Koch (Figures 4 and 5).

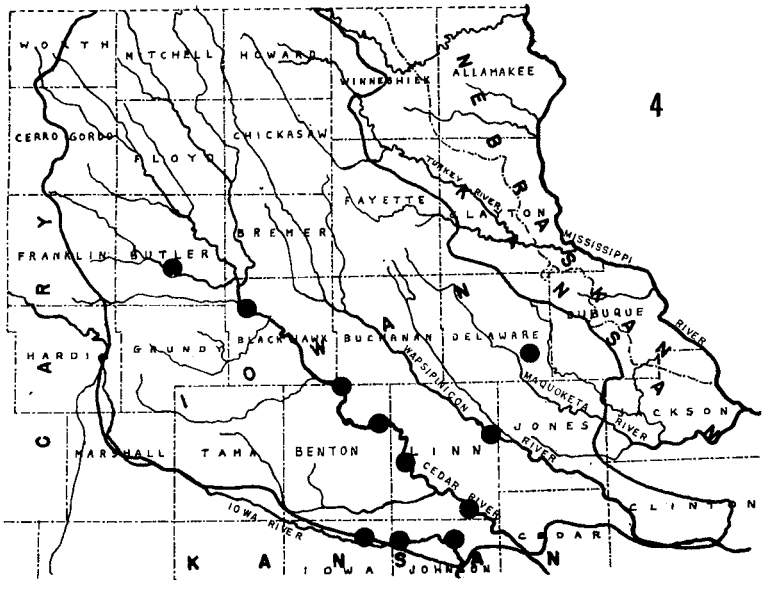

Figure 4. *Cornus drummondi* C. A. Meyer

Other species with similar distributions are:

Carex grayii Carey
C. muskingumensis Schw.
C. shortiana Dew.
Trillium recurvatum Beck
Betula nigra L.

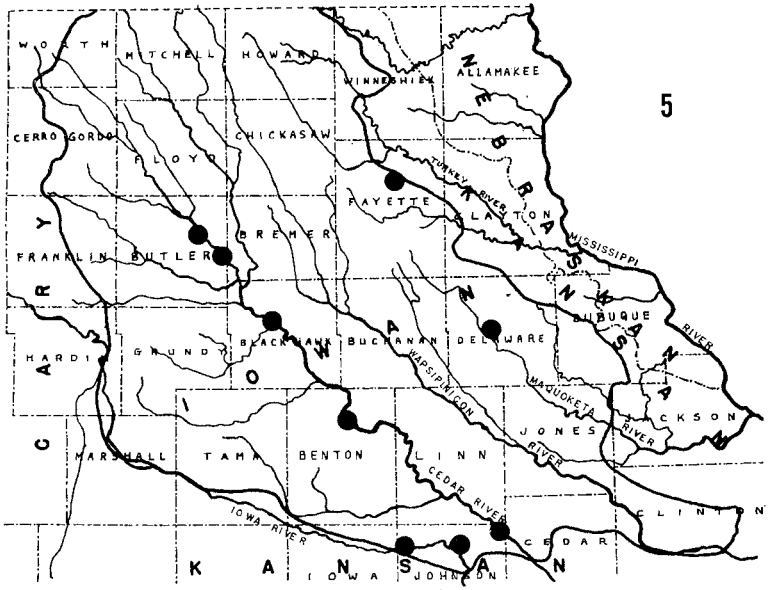

Figure 5. *Gymnocladus dioica* (L.) K. Koch

Cacalia muhlenbergii (Sch.-Bip.) Fern.
Cardamine douglassii (Torr.) Britt.
Quercus bicolor Willd.
Stachys tenuifolia Willd.
Cassia marilandica L.
Platanus occidentalis L.
Ulmus thomasi Sarg.
Chaerophyllum procumbens (L.) Crantz
Heracleum lanatum Michx.

The over-all ranges of these plants are most often centered in northeastern and eastern United States. A few of these species are widely dispersed in certain river systems in the Iowan lobe, but appear to be totally absent from adjacent systems. *Cornus drummondi* and *Gymnocladus dioica*, for example, are found only along the Cedar River drainage basin. One might assume from their distribution patterns that these species have migrated into the Iowan lobe so recently that they have attained only a limited "foothold".

A second possible explanation for these distribution patterns is that there are ecological differences in adjacent river valleys and that species near the limits of their ranges are sensitive to these differences. An argument for the migration hypothesis, however, is that most other alluvial species are widely distributed in all the river valleys of the Iowan lobe, indicating that these valleys are ecologically similar. It is clear that additional evidence is needed before conclusions can be drawn.

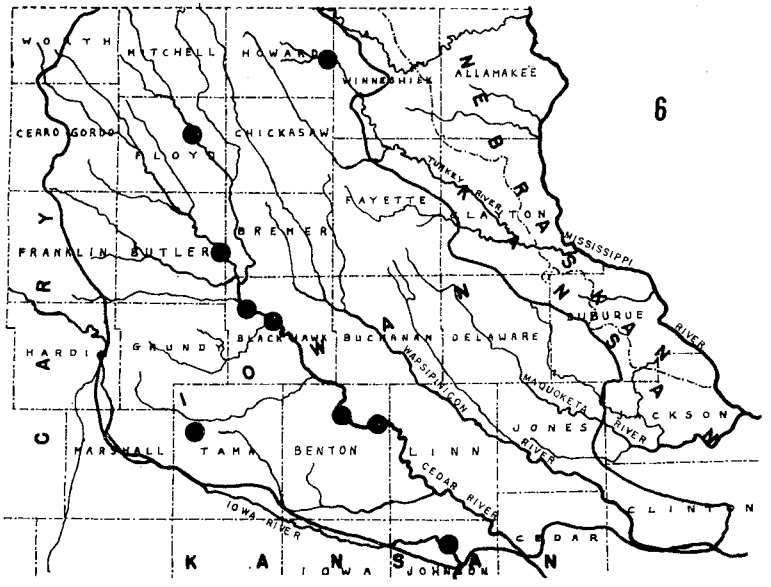

Figure 6. *Eupatorium altissimum* L.

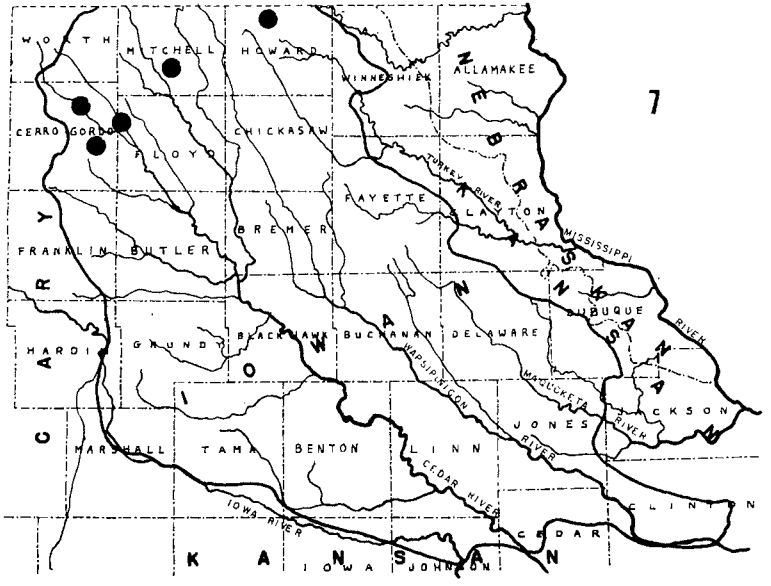

Figure 7. *Psoralea argophylla* Pursh

Plants of Sandy Open Soil.

Most of the sandy soils in the Iowan area are found in the flood plains and terraces along the major rivers. For this reason

the distribution patterns of plants restricted to these habitats are very similar to those of the plants inhabiting alluvial woods. Their general distributions are centered in the eastern and central United States. *Eupatorium altissimum* L. (Figure 6) has a distribution of this type.

Species having similar distributions, but mostly limited to the southern counties, are:

Selaginella rupestris (L.) Spring
Myosotis verna Nutt.
Symphoricarpos orbiculatus Moench.
Paronychia canadense (L.) Wood
P. fastigiata (Raf.) Fern.
Helianthus occidentalis Riddell
Kuhnia eupatorioides L.
Croton glandulosus L.
Euphorbia dictyosperma Fisch. & Mey.
E. geyeri Engelm.
E. supina Raf.
Geranium carolinianum L.
Astragalus distortus T. & G.
Petalostemum villosum Nutt.
Tephrosia virginiana (L.) Pers.
Anemone caroliniana Walt.
Myosurus minimus L.

Plants of Upland Prairies.

There are few prairie plants whose distributions are discontinuous in the Iowan lobe. The probable reason for this is that the prairies spread into the Midwest during the Hypsithermal; consequently prairie plants have had sufficient time to become widely established.

Two western species whose distributions terminate in the Iowan lobe are *Psoralea argophylla* Pursh (Figure 7) and *Ratibida columnifera* (Mett.) Wooton & Standl. They have been found only in the northwestern corner of the Iowan lobe. *Erigeron pulchellus* Michx. (Figure 8) is a species with an eastern distribution. The western terminus of its range is in the eastern counties of the lobe.

Plants of Moist Prairie Swales, Marshes and Margins of Ponds and Lakes.

The over-all distribution patterns of these plants do not possess the similarity noted in the communities previously discussed. For this reason, they have been further subdivided.

1. *Cicuta bulbifera* L. (Figure 9) represents a group of plants with northern affinities. Other species are:

Equisetum fluviatile L.
Sagittaria cuneata Sheldon
Carex rostrata Stokes
Heteranthera dubia (Jacq.) MacM.
Pontederia cordata L.
Potamogeton natans L.
P. richardsonii (A. Benn.) Rydb.

P. zosteriformis Fern.
Alnus rugosa (DuRoi) Spreng.
Helianthus maximiliani Schrad.
Utricularia vulgaris L.

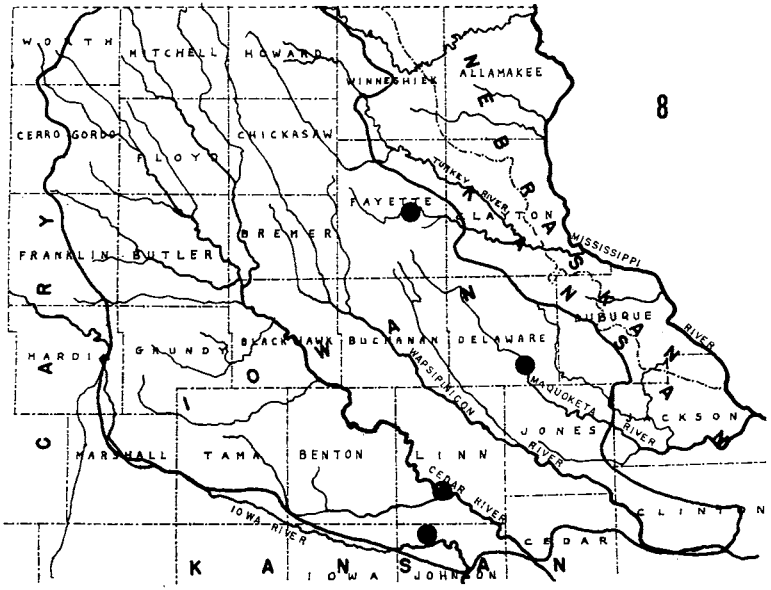

Figure 8. *Erigeron pulchellus* Michx.

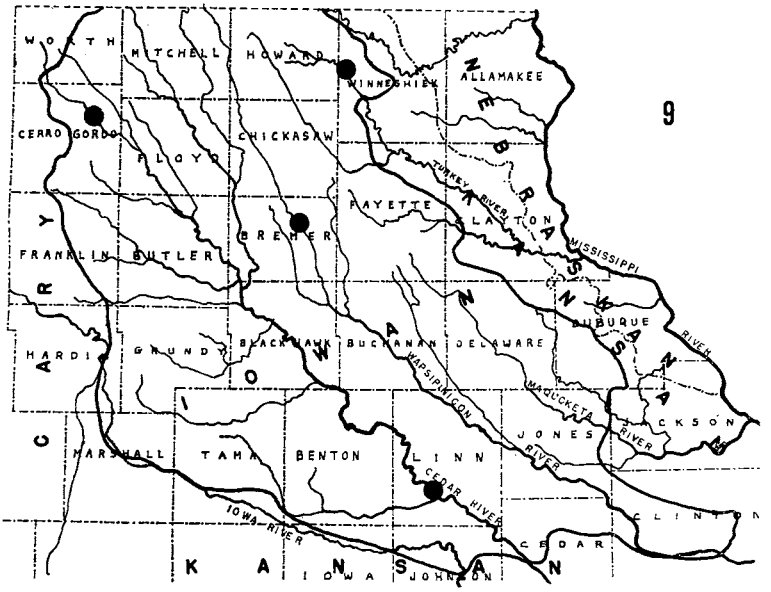

Figure 9. *Cicuta bulbifera* L.

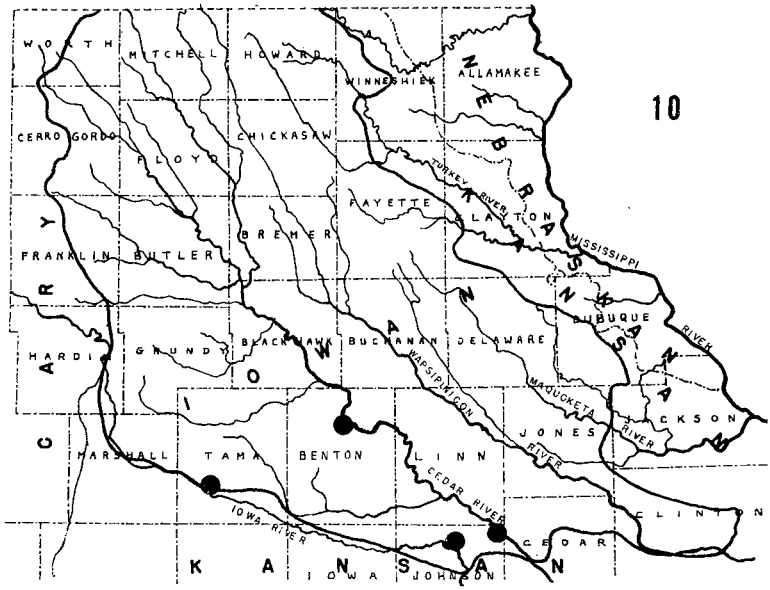

Figure 10. *Rorippa sessiliflora* (Nutt.) Hitchc.

Lysimachia thyrsiflora L.
Galium trifidum L.

2. *Rorippa sessiliflora* (Nutt.) Hitchc. (Figure 10), a species with a general southern distribution, has been observed only in the southern part of the lobe.

3. *Calopogan pulchellus* (Salisb.) R. Br. (Figure 11) is an eastern plant. Other species with similar distributions are:

Scleria triglomerata Michx.
Juncus acuminatus Michx.
Asclepias sullivantii Engelm.
Gentiana crinita Froel.
Ludwigia alternifolia L.

Although aquatic or semi-aquatic habitats are usually isolated from one another, hydrophyllic plants appear to migrate readily. Gravel pits and spring-fed roadside ditches quickly acquire a marsh or pond flora. It seems likely that the wind and migrating water birds and animals serve as vectors in the transportation of the plant disseminules from one locality to another (3).

These plant communities were widely distributed in the Midwest prior to the Hypsithermal interval and likely persisted during the Hypsithermal interval along the major streams and lakes. As precipitation increased following that interval, it is probable that the plants rapidly colonized the newly-created moist habitats.

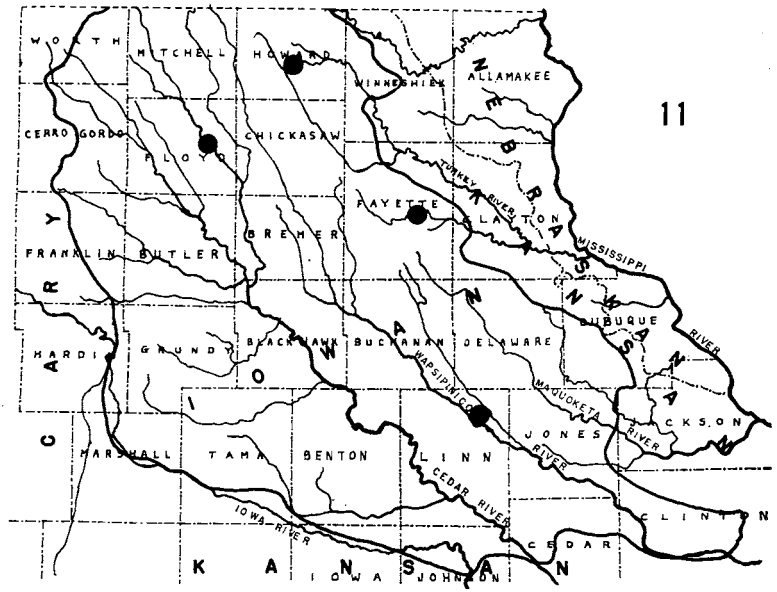

Figure 11. *Calopogon pulchellus* (Salisb.) R. Br.

Conclusions

Most of the discontinuous plant distributions in the Iowan lobe can be attributed to factors other than continuing postglacial migration. It appears that these plant distributions are almost entirely a function of the distribution of suitable habitats. The eastern and northeastern deciduous forests have their westtern terminus in eastern Iowa because of insufficient rainfall and the dearth of bluffs, slopes and moist sheltered ravines in central and western Iowa. A few species inhabiting alluvial places may be migrating northward along the major rivers, but in general I believe that there has been sufficient time since the Hypsithermal interval for plants to have become established in most of the habitats suitable to their requirements.

More definite conclusions cannot be drawn until additional paleobotanical evidence is available on the species composition of the successive floras which occupied this region during the Pleistocene glacial and interglacial stages. There are many exposed or buried peat beds in Iowa. Careful analysis of both their microfossil and macrofossil contents are needed. Radiocarbon dating of these fossils would add immeasurably to the usefulness of the information obtained.

There is also a need for detailed studies of species which, from their distribution patterns, appear to be invading new territory. Among other things, these studies would require the

development of objective criteria for measuring the direction and rate of migration. One would have to determine the physiological requirements of each species during all of its ontogenetic phases, from seed to mature plant. It would also be necessary to make an ecological study of habitats in which the species are established, comparing them to seemingly similar habitats beyond the limits of range of the species.

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Distribution Patterns of Eastern Red-Cedar *Juniperus virginiana L.* in Henry County, Iowa

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Abstract: The distribution patterns of Eastern red-cedar were studied in Henry County, Iowa, in a general survey and also in three intensive study areas in Marion, Jackson, and Wayne townships. It was found that the abundant seed sources of red-cedar and the predominantly rolling land in Henry County make extensive establishment of red-cedars possible. In the northern tier of townships red-cedars are restricted to fence lines and roadsides whereas in the hilly southern three tiers of townships they are much more abundant.

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