Geographical Affinities of the Flora of North Dakota*

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Introduction

The state of North Dakota, like most political units, has political boundaries rather than geographic barriers to delimit its area. Plants, ignoring such divisions, continue their migrations until stopped by climatic extremes, unfavorable edaphic conditions or biotic interference.

In North Dakota some species may reach their northern limits because of temperature extremes, others their western limits because of precipitation deficiencies. Many species, moving eastward, are checked when they meet the competition of others more aggressive. Biotic interference has been especially severe since the plow of the white man broke the plains.

The available flora acted upon by physical and biotic factors has resulted in a prairie vegetation of short grass in the western part of the state, tall grass in the east, with a transition zone of mixed prairie lying between. Locally, edaphic conditions permit the occurrence of more mesic plants or restrict the vegetation to a few hardy desert species.

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Physiography

North Dakota extends into two physiographic provinces (Fenneman, 1931, 1938), the Central Lowland and the Great Plains. The relief of the entire state is relatively low. The highest point is Black Butte, in Slope County, 3468 feet above sea level. The general elevation is approximately 3000 feet in the southwest corner of the state, sloping gradually to less than 800 feet in the northeast corner (fig. 1).

The two provinces are divided by a low indefinite east-facing escarpment, five to twenty miles wide, 300 to 600 feet high.

West of the line lies the Missouri Plateau section of the Great Plains province, which extends from the Pine Ridge escarpment in southern South Dakota northward to an undetermined boundary in Canada. It is a wide-

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spread rolling upland beveling Upper Cretaceous and Tertiary strata which apparently represent a once continuous surface from which newer and sharper relief has been carved. Along its eastern edge it is being consumed by the gradual westward spread of the Central Lowland.

A number of monadnocks, such as Sentinel Butte, Black Butte and others, rise to an almost uniform level 400 to 600 feet above the peneplain. These buttes are characteristically flat topped and protected by strong sandstone. Still higher beds once covered them and at least 1000 feet of rock were eroded away in forming the peneplain which surrounds them. A number of eminences, presumably identical in character, stand out on the plains of Montana, like giant stepping stones westward toward the Rocky Mountains.

"Badlands" are developing upstream along the Little Missouri River in southwestern North Dakota due to vigorous renewed erosion of the peneplain.

East of the boundary is the western Young Drift section of the Central Lowland province. The elevation is lower than west of the line due to the approximate completion of a more recent cycle of erosion. The gently rolling underlying rock surface is chiefly Cretaceous, overlain by relatively smooth glacial deposits, mostly ground moraine. Bedrock is exposed only occasionally where streams cut through the drift. About 25 miles from the eastern border of the state, the land levels off to the flat Red River Valley, once the bed of glacial Lake Agassiz.

Along the west edge of the Red River Valley at the International Boundary lie the Pembina Mountains. They comprise an escarpment ex-

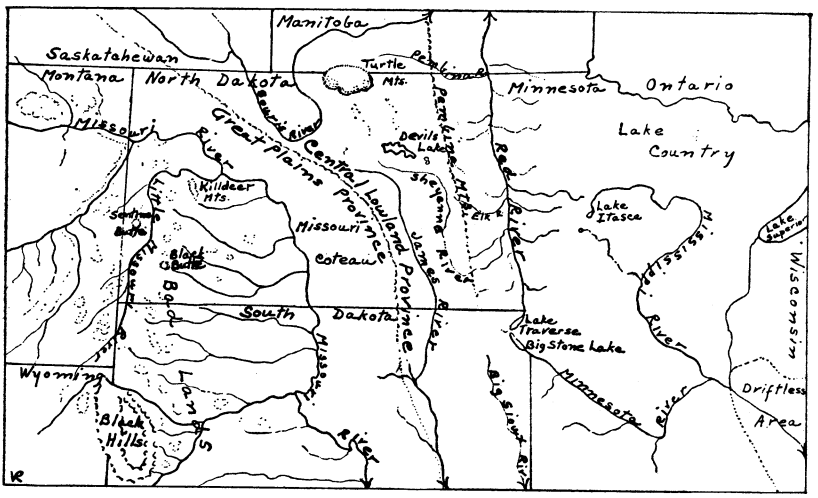

Fig. 1.—Physiographic map of North Dakota and adjacent areas.

posing outcrops of Upper Cretaceous chalk and shale, and rise 300 to 500 feet above the glacial filling of the valley. The elevation decreases southward and increases northward into Canada.

The Turtle Mountains are located at the point where the 100th meridian crosses the International Boundary. They cover an area of about 800 square miles and consist of hills, lakes and ponds. They are overlain by an estimated 100 feet of drift. The slopes are not steep but the highland is relatively prominent, rising 400 to 600 feet above the surrounding plain.

Glaciation occurred more than once in North Dakota. West and south of the Missouri River, in a belt about 25 miles wide, can be found remains of glacial drift of Iowan age. The deposit presumably was thin and the time since its deposition has been so long that an erosion topography has been fairly well reestablished.

The topographic effects of the most recent glaciation, the Late Wisconsin, are far more important, not only because of the larger amount of drift deposited but because of the recency of the event.

Like all previous glacial advances over North Dakota, its origin was at the Keewatin center, west of Hudson Bay, and it moved southward in lobes which intermittently progressed and regressed over the entire eastern part of the state. To the westward the ice mass climbed the escarpment of the Missouri Plateau, but having done so, lost its energy and was unable to proceed much farther. In successive small advances and retreats it built its reduplicated terminal moraines. In places, there remained several hundred feet of uneroded, stony glacial debris, on top of the plateau and in the valleys which formerly indented its slopes. This strip of moraine mantled plateau, 15 to 25 miles wide, bounded on the west by the Missouri River whose northward flow it deflected, overlooking the Central Lowland on the east, is known as the Missouri Coteau.

Eastward on the Lowland as far as the shoreline of glacial Lake Agassiz (fig. 2) the area is chiefly covered by ground moraine. The effect of glaciation was principally smoothing of the surface by abrading hills and filling valleys.

As the ice moved southward it effectively dammed northflowing river systems. Thus was formed Lake Agassiz, in the valleys of the present Red, Saskatchewan, and upper Nelson rivers, flooding an area of 110,000 square miles, which is greater than the combined areas of the present Great Lakes. Of that area, 6800 square miles is now North Dakota. Lake Agassiz was more than 400 feet deep at the International Boundary and rose to 650 feet higher than the present level of Lake Winnepeg, its remnant and successor.

Lake Agassiz overflowed at the lowest col in the divide between the basins of the present Red and Minnesota rivers. Its outlet, glacial River Warren, flowed to the Mississippi in a course now marked by Lake Traverse, Big Stone Lake and the Minnesota River. The large volume of

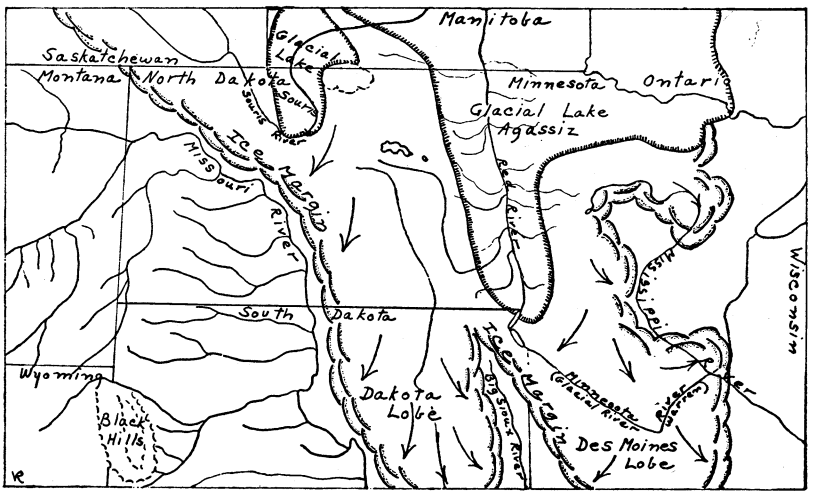

Fig. 2.—Map of North Dakota and adjacent areas showing maximum extent of late Wisconsin glaciation and location of glacial lakes Agassiz and Souris. In part after Leverett and Sardeson, 1932.

water it carried cut a trench 200 feet deep and one-half to four miles wide.

In the lake bed, a deep silt layer was deposited. Along the western shore where the Elk, Pembina and Sheyenne rivers entered the lake, sandy deltas developed and today remain as dune areas.

Ultimately the ice dam retreated northward and disappeared, revealing a sinking of the land. Drainage to Hudson Bay resumed.

Between the Turtle Mountains and the Missouri Plateau is the flat valley of the Souris River which enters the state southward from Saskatchewan, forms a loop and then flows northward into Manitoba. In glacial time this ponded to form Lake Souris.

Drainage of the glaciated portions of North Dakota is still young. Except near large rivers, streams are widely spaced. Few channels have been developed except along lines of depressions which were ready made when the ice vanished. Partly on account of the young drift topography and partly by reason of less rainfall, many small areas have only internal drainage. Brackish Devils Lake, formerly 40 miles long and draining into the Sheyenne River, is now the hydrographic center of an area of 3500 square miles.

Preglacial drainage of the Dakotas was apparently almost all northward. During glaciation all major streams were deflected southward because of ice dams and morainic barriers. Postglacial adjustments have permitted all except the Missouri River and its tributaries to resume approximately their original channels toward Hudson Bay.

PRESENT CLIMATE

North Dakota, situated at the geographic center of North America, is subject to a rigorous continental climate. With possible temperature extremes of —60°F. in winter and 120°F. in summer, and an annual average precipitation which some years may be as low as eight inches, the floristic population is restricted to hardy species with great resistance to climatic stress and those relicts or pioneers which are established in locally suitable edaphic areas.

Following the classification of Thornthwaite (1931), the temperature-efficiency rates as microthermal. The annual mean temperature for North Dakota ranges from about 36°F. to 44°F. (U.S.D.A. 1941). The average number of days a year when the temperature reaches 90°F. or higher is 14, and the average number with zero or lower is 53. The average growing season has about 121 days without severe frosts. However, killing frosts have occurred as late as the first part of June, and as early as the first days of September. The long duration of extreme weather and the short growing season undoubtedly prevents many species from becoming established.

On the basis of precipitation-effectiveness (Thornthwaite, 1931), the climate may be classified as subhumid in approximately the eastern third of the state and semiarid in the western two-thirds. Moisture is deficient at all seasons of the year. Annual precipitation averages 19.53 inches in the eastern part, 16.32 inches in the middle, and 15.38 inches in the west.

The boundary between the subhumid and semiarid prairie is transitional and variable. In the subhumid lands, one to ten years out of 20 are likely to be so deficient in rainfall as to be designated as dry or semiarid (U.S.D.A., 1941). The semiarid region has occasional humid years and not infrequent desert periods. The fickleness of precipitation is illustrated by data from Jamestown, N. D., near the western edge of the subhumid zone. In the course of 35 years, 15 years have been moist subhumid, 13 dry subhumid, five semiarid, one humid and one arid.

Such fickleness effects instability in the floristic pattern. In moist years, mesophytes make gains, only to be repulsed by a series of dry years and replaced by deeper rooted or otherwise better adapted xerophytic species.

SOILS

The soils which have developed as products of the subhumid to semiarid climate and prairie vegetation interacting on the parent material are predominantly Pedocals, lime accumulating soils (U.S.D.A., 1938).

The most striking are the Chernozems, black earths, which exhibit a darker surface layer than any other upland soils. They develop in temperate subhumid grasslands and are found in North Dakota on the glacial drift and lacustrine deposits of approximately the eastern third of the state.

In the western part of the state, where the climate is drier and the vegetation more sparse, Chestnut soils occur. They are less dark than the Chernozems and have developed on unglaciated sandstone and shale as well as on glacial drift.

In addition to the Pedocals, there are a few localized exceptions. Podzol has developed on the relatively small area of the Turtle Mountains, which are overlaid by poorly drained glacial drift supporting bog and forest vegetation. Dune sands occupy the Sheyenne River delta and similar deposits. The rough, broken lands of steeply eroded clays and soft shales along the Little Missouri River and the alluvial soils along the Missouri River are so recent that they are characteristic of the parent material, unchanged by environment.

Small areas, such as many of the lower buttes, are capped by scoria, a slag-like substance due to the partial fusion of clays by the natural burning of coal beds. The soil bordering many of the poorly drained lakes and ponds becomes excessively saline, especially in dry years. These are locally known as "alkali beds."

The exceptional areas are interesting floristically because they support the more unusual species, particularly the relicts.

VEGETATIONAL HISTORY

In the distant past the climate of North Dakota was much more clement than today and permitted a vegetation of luxuriant forest. Fossil records show that during Cretaceous and Early Tertiary time palms, *Metasequoia, Gingo, Cercidiphyllum, Fagus, Sassafras* and other associated warm temperate and subtropical mesophytes ranged well up into the area (R. W. Brown, 1949, personal communication).

Elevation of the western mountains, the Rockies and particularly the Cascades, begun at the close of the Cretaceous, continuing nearly to present height in Miocene, with a general regional uplift in Pliocene, induced drier mid-continent conditions by cutting off the inflow of humid air and precipitation from the Pacific Ocean. Gradually the great plains east of the Rockies became semiarid and forest land gave way to prairie (Schuchert and Dunbar, 1933).

With the onset of glaciation in Pleistocene time, the climate became cooler and more humid. And, as Sears states (1935), "the general theory is that tundra, scrub, conifers and deciduous forest shifted as belts before the advancing ice, then followed back in its wake as it melted." There is no evidence, however, to suggest that such succession occurred in North Dakota.

But, as Sears continues, "actually, of course, the ice extended into the interior grasslands as well as into the forest regions." Tyrrell (1910), referring to the grassland region of Canada just north of North Dakota, pointed out that the ice spread southward and later retired northward over plains and prairies and that "the whole known climatic history of these grassy plains is therefore included in the statement that a cold climate was succeeded by a dry continental climate, under neither of which conditions was a forest growth possible." Such was the case in North Dakota. The great plains then, as now, were in the rain shadow of the western mountains. For example, suggesting that at that period the vegetation, the cli-

mate, and edaphic conditions must have been essentially the same as at present, deposits of pre-Wisconsin Peorian interglacial age from Bronson, in northern Minnesota, about 25 miles east of the North Dakota line, have yielded plant materials, the majority of which are specifically the same as are found there today (Rosendahl, 1948).

The cool, humid periods of glacial advance, alternating with warm, drier interludes of retreat, resulted in successive destruction and reestablishment of vegetation. The most recent advance, the late Wisconsin, overwhelmed all of North and South Dakota east of the Missouri River, most of Minnesota, and extended southward over Iowa as far as Des Moines (fig. 2). The axis of glacial movement was from the Keewatin center southward along the Red River valley. At approximately the North-South Dakota border, the ice mass separated into two lobes, commonly referred to as the Dakota and the Des Moines. Ice free areas remained west of the Missouri River, south of the aforementioned lobes, with a wedge protruding northward between them in the present valley of the Big Sioux River, and in central Minnesota within about 75 miles of the North Dakota line (Leverett and Sardeson, 1932).

Presumably, the ice moved southward from a region of tundra and boreal conifer forest. Along its western flank it progressed across transition aspen woodland, into the prairie area of Canada and the Dakotas. Southeastward across Minnesota, conifer forest maintained a vanguard position and ultimately extended considerably beyond its present range.

As the encroaching ice obstructed the north flowing drainage systems, increased moisture due to ponding of streams must have permitted invasion of a few pioneer forest species. Aspen woods probably developed in mesic situations in North Dakota, with willow thickets and wet meadows occupying the lowlands and prairie remaining on the drier hilltops. Further stages in forest succession probably did not occur because cooling of the climate was causing temperate deciduous forest to migrate southward and the boreal conifer forest in Minnesota was unable to expand westward into North Dakota because of the ice barrier in the Red River valley.

Cooler conditions during glaciation also depressed montane vegetation to lower altitudes and Rocky Mountain flora, along with an intermingling of boreal species which were moving southward in the mountains, spread eastward onto the Black Hills and the Missouri Plateau section of western North and South Dakota. There are a number of such species persisting in that area today, apparently as relicts.

Finally, when the ice began to wane, its recession was back toward the Red River axis, with the final phase, or substage, of late Wisconsin represented by an ice lobe mainly in the Red River drainage basin. Melting of the southern tip of this lobe marked the preliminary stage of glacial Lake Agassiz. With continued northward melting of the ice, water ponded until it rose sufficiently to flow southward, as the glacial River Warren, to the Mississippi River.

On the basis of the rate of erosion of the Minnesota River valley by

the River Warren and the rate of recession of St. Anthony Falls at Minneapolis, Leverett has estimated the beginning of Lake Agassiz to have been about 18,000 years ago. Drainage southward is believed to have continued until about 9000 years ago at which time the ice had receded so far northward as to permit resumption of drainage northeastward to Hudson Bay.

This chronology would indicate that since glaciation there has been considerable time for reinvasion of vegetation into North Dakota, but somewhat less than has been available for migration into other states farther south and east. The turning point in glaciation, when the ice sheets began their last retreat from the upper Mississippi valley and southern New England is believed to have occurred some 25,000 or 30,000 years ago (Schuchert and Dunbar, 1933).

Because of widespread lake and swampland, hydrophytes were probably the first reentrants into North Dakota. There was doubtless an early return of willow, aspen, and birch. The onset of the postulated xerothermic period (Gleason, 1922, and others) would have favored return of prairie, the northeastward migration of southwest desert species, and a decline of the more mesic montane species.

Eastern deciduous forest migrated northward in the river valleys, especially along the Minnesota and the Big Sioux, up into southeastern North Dakota (fig. 3). The deep rooted, xeric bur oak, the quick growing boxelder, green ash, and American elm were among the vanguard and today have a wider distribution than the more requirant species such as basswood and hornbeam.

There is no evidence to suggest that North Dakota underwent any postglacial spruce to pine to deciduous forest succession as did the eastern states (Sears, 1948). Boreal conifers continue to be absent from the native vegetation although a number of their associates do occur. Some of the more mobile species, such as aspen and birch, apparently preceded the ice across the state and then followed it northward as it withdrew. Other northern or Canadian species, because of their limited distribution, so far as available records indicate, appear to have invaded North Dakota from the northeast relatively recently, perhaps only since the removal of the Lake Agassiz barrier.

Tundra has left no traces, if it ever existed in North Dakota. Rosendahl (1948), after examination of plant materials deposited "in the early stages of Lake Agassiz" at Moorhead, Minnesota, just across the line from North Dakota, states, "it is significant that none of the species found are tundra plants and there is no supporting evidence for assuming a tundra stage in the revegetation of the area." Rather, some 30 vascular species identified are "all characteristic components of the present day flora of the region."

PRESENT FLORA

The present flora of North Dakota includes about 900 native species (Stevens, 1922, 1950). Those of the prairie are predominant but also represented are many species whose affinities are with other formations, for-

est or desert, or are so widespread geographically as to be essentially cosmopolitan.*

Those well within their normal distribution, the intraneous species, comprise about 55 percent of the total flora. The remaining 45 percent, extraneous species, which are at or near the margin of their ranges, forms a slightly smaller group, of diverse origin and apparently restricted both by climate and physiographic history.

Introductions, which add roughly 150 species to the present flora, chiefly from Europe, are not considered in this paper.

The following outline presents the approximate percentage of species included in each of the various elements, broadly delimited, of the native flora of North Dakota.

I. Intraneous Flora	55
A. Widespread species	15
B. Prairie species	40
II. Extraneous Flora	45
A. Eastern deciduous forest species	20
B. Northern coniferous forest species	15
C. Rocky mountain species	5
D. Southwestern desert species	5

I. INTRANEOUS FLORA

A. WIDESPREAD SPECIES

Approximately 15 percent of the native flora of North Dakota is composed of widespread species. Many of these are transoceanic and range not only widely over North America but extend over other continents as well. Their occurrence in North Dakota is not unexpected. In most cases point of origin as well as lines of migration have become obscured. A number are aquatics, which find their localized habitats in any or all plant formations, forest, grassland or desert, and probably were among the early entrants into deglaciated territory.

Representative of the more or less cosmopolitan species found in North Dakota are: *Botrychium virginianum, Cystopteris fragilis, Pteridium aquilinum, Potamogeton pectinatus, Ruppia maritima, Zannichellia palustris, Phragmites communis, Cyperus esculentus, Lemna minor, L. trisulca, Spirodela polyrhiza, Juncus bufonius, Atriplex patula, Ceratophyllum demersum, Myosurus minimus, Centunculus minimus.*

Others, widespread around the northern hemisphere but not established on the southern continents, include: *Naias flexilis, Eleocharis acicularis,*

* Floristic data in this paper, including the distribution records in figures 3, 4, and 5, are supported by specimens in the herbarium of the North Dakota Agricultural College at Fargo and in the United States National Herbarium, Washington, D. C.

Ranunculus pensylvanicus, R. scleratus, Rorippa islandica, Humulus lupulus, Monotropa uniflora, Utricularia vulgaris.

A third group is found rather widely distributed over temperate North America, with many of the species ranging north to Alaska or south into Central America but not crossing to other continents. Among such are: *Sparganium eurycarpum, Potamogeton foliosus, Sagittaria latifolia, Sphenopholis intermedia, Scirpus validus, Heteranthera dubia, Juncus torreyi, J. nodosus, Corallorhiza maculata, Parietaria pennsylvanica, Urtica gracilis, Polygonum ramosissimum, Silene antirrhina, Geranium carolinianum, Rhus radicans, Heracleum lanatum, Sium suave, Verbena bracteosa, V. hastata, Ambrosia artemisiifolia.*

B. PRAIRIE SPECIES

Since North Dakota lies entirely within the grassland formation (Shantz and Zon, 1924), it is not surprising to find that a comparatively large portion of the flora, about 40 percent, is composed of prairie species. Climatic conditions over the state are most conducive to prairie development. Only the exceptional, localized situations favor maintenance of other types of vegetation.

The sub-humid eastern part of the state and a few moist valleys, or draws, farther west permit the development of tall grass prairie with *Andropogon furcatus, Sorghastrum nutans,* and *Stipa spartea* as dominants. Accompanying them are mid grasses such as *Andropogon scoparius, A. paucifloras, Bouteloua curtipendula, Elymus canadensis, E. glaucus, Koeleria cristata, Panicum virgatum, Sporobolus heterolepis* and numerous forbs including *Lilium umbellatum, Anemone cylindrica, Glycyrrhiza lepidotum, Linum sulcatum, Gentiana puberula, Lithospermum canescens, Gerardia aspera, Penstemon gracilis, Campanula rotundifolia, Aster laevis, Helianthus maximilliana, H. subrhomboideus, Kuhnia glutinosa, Liatris scariosa.* Actually, such communities have been much reduced by the encroachment of agriculture.

Over the western part of the state where arid conditions prevail, and eastward on dry slopes and overgrazed areas, short grass predominates. Most important is *Bouteloua gracilis,* with *Buchloë dactyloides, Agropyron smithii, Bouteloua hirsuta, Stipa comata, Carex filifolia, Allium reticulatum, Draba nemorosa, Psoralea argophylla, Linum rigidum, Sphaeralcea coccinia, Viola nuttallii, Gaura coccinia, Phlox hoodii, Collomia linearis, Plantago purshii* and other prairie species with relatively low moisture requirements.

Between these extreme prairie types lies the intermediate mixed prairie. This is characterized by the bunch habit of the dominants, *Andropogon scoparius, Bouteloua curtipendula,* and *Koeleria cristata.* Shorter grasses, particularly *Bouteloua gracilis,* and *Buchloë dactyloides,* occupy the interspaces. Other frequent species include *Festuca octoflora, Muhlenbergia racemosa, Panicum capillare, P. scribnerianum, P. virgatum, Sporobolus cryptandrus, Rumex mexicanus, Anemone cylindrica, Erigeron ramosus,* and *Solidago serotina.*

Here conditions in general are not sufficiently humid to permit the taller grasses to crowd out the xerophytic short grass species nor arid enough to eliminate the mesophytic grasses. A series of drought years, several successive humid years, or slight variations in elevation, exposure, soil texture, or grazing will considerably weight the floristic balance in favor of one group or the other. Studies by Weaver and his associates (1934, 1939), Hanson and Whitman (1938) and others have contributed greatly toward understanding of these interrelationships.

The mixed prairie species, both grasses and forbs, are sufficiently adaptable and so easily disseminated that they occur not only in more than one type of prairie in North Dakota but also in meadow, prarie, forest openings and disturbed areas almost throughout North America, lacking, in most cases, only in the high mountains of the west and in the southern Appalachians.

Geographically, the tall prairie species tend to show relationship to mesophytes of the humid east and the short grass to the xerophytes of the arid southwest. Some of the mid species are circumboreal components of montane and boreal meadows. However, the mobility of the species involved and the wide distribution apparently achieved during the postglacial xerothermic period somewhat obscures such affinities. Nevertheless, several major distribution patterns are evident in addition to the widespread range of the mixed prairie species.

The first group, comprising about one-fourth of the prairie species, has a range eastward from the Rocky Mountains, extending across the Mississippi River into the Prairie Peninsula of Illinois, Indiana, and Ohio. Included are: *Andropogon furcatus, Sorghastrum nutans, Stipa spartea, Astragalus plattensis, Dalea alopecuroides, Linum sulcatum, Asclepias syriaca, Gentiana puberula, Phlox pilosa, Lithospermum canescens, Houstonia longifolia, Helianthus rigidus, H. tuberosus, Solidago rigida.* Found in this group are the dominants of the tall grass prairie and many species of the mixed prairie.

A second pattern is shown by a group of species whose range extends from the Mississippi River westward into the intermontane prairies of the Rockies. About one-half of the total prairie species are included here. Mostly they are of the short grass plains, among them: *Agropyron hallii, A. smithii, Aristida longiseta, Bouteloua gracilis, Buchloë dactyloides, Allium reticulatum, Leucocrinum montanum, Comandra pallida, Rosa fendleri, R. woodsii, Lupinus argenteus, L. pusillus, Polygala alba, Sphaeralcea coccinea, Viola nuttallii, Gaura coccinea, Oenothera serrulata, Mentzelia decapetala, Penstemon angustifolium, Gilia minima, Solanum rostratum, Plantago purshii, Aster pauciflorus, Cirsium megacephalum, Helianthus annua, H. maximilliana, H. petiolaris, Liatris punctata, Ratibida annua, H. maximilliani, H. petiolaris, Liatris punctata, Ratibida columnaris.* In a few cases, especially among the short grasses, the easternmost stations of this group may be recent introductions.

A third group, comprising most of the remaining 25 percent of the prairie flora, are more or less limited to the strip of states lying between the Mississippi River and the Rockies. Mostly these species are found in sandy areas. A few such are: *Petalostemon villosum, Psoralea argophylla, P. esculenta, Linum rigidum, Euphorbia geyeri, E. marginata, E. missurica* var. *intermedia, Eriogonum annum, Oenothera caespitosa, Penstemon gracilis, P. grandiflorus, Plantago spinulosa, Brauneria angustifolia, Senecio plattensis, Solidago mollis.*

A few prairie species are restricted in range to the north central states, roughly the area between the Mississippi River and the Rocky Mountains, from Kansas northward. This may be because the species are younger or, in some cases, at least, because narrower specific limits have been applied. A few examples of this group are: *Calamagrostis montanensis, Carex assiniboinensis, Lesquerella arenosa, Rosa arkansana, Astragalus bisulcatus, A. flexuosus, Phlox hoodii, P. andicola, Lygodesmia rostrata.*

The amount of endemism in North Dakota is uncertain. A number of new species have been described from the region but almost all have been reduced to synonymy, usually, for being merely environmentally induced variations.

II. EXTRANEOUS FLORA

The 45 percent of the flora classified as extraneous to North Dakota includes those species which are at the edges of their ranges and are, in fact, beyond the margins of the formations to which they belong. In general, they are either more mesic or more xeric than the prairie species. Those advancing from the west are checked when they meet and fail to withstand the competition of the eastern species. The mesic eastern species are as effectively eliminated where they encounter the unfavorable conditions that only xerophytes can withstand.

A. EASTERN DECIDUOUS FOREST SPECIES

Forest, in North Dakota, occurs almost exclusively in the Turtle, Pembina, and Killdeer Mountains and as narrow strips, a few hundred feet wide, along the larger streams.

Of the eastern deciduous forest dominants, which northwestward diminish to maple-basswood climax (Braun, 1947), only basswood (*Tilia americana*) reaches North Dakota. The sugar maple (*Acer saccharophorum*) disappears about 50 miles east of the North Dakota-Minnesota line. There was an early collection at Rutland, Sargent county, in the southeastern part of the state, reputedly from two native trees, which, however, have never been relocated. A few cultivated specimens occur in Fargo but their growth seems retarded.

In spite of the relatively small area suitable for the eastern mesophytes, they constitute about 20 percent of the total native species of North Dakota. The largest number are found along the Red River and a few miles to the west where they probably became established at the margin of

glacial Lake Agassiz. They apparently arrived via the Warren-Minnesota River valley and the Big Sioux River system of eastern South Dakota (fig. 3). In the group so limited are, for example: *Onoclea sensibilis, Allium tricoccum, Smilacina racemosa, Trillium cernuum, Arisaema triphyllum, Pilea pumila, Anemone quinquefolia, Clematis virginiana, Dicentra cucullaria, Penthorum sedioides, Ribes cynosbati, Crataegus mollis, Desmodium acuminatum, Xanthoxylum americanum, Impatiens pallida, Orobanche uniflora, Veronica virginica, Eupatorium rugosum, Cirsium altissimum. Ulmus fulva* is grown as a shade tree but its native occurrence has not been verified.

An additional number of eastern mesophytes occur not only in the Red River valley but also a little farther west along the James River and in the Devils Lake region. Among these are: *Uvularia grandiflora, Hypoxis hirsuta, Ostrya virginiana, Laportea canadensis, Menispermum canadense, Ribes missouriensis, Geum canadense, Rhus glabra, Tilia americana, Gentiana andrewsii, Verbena urticaefolia, Mimulus ringens.*

While none of the preceding species has been found in the Turtle Mountains, the following have reached their present western limits in that area: *Festuca obtusa, Hystrix patula, Corylus americana, Sanguinaria canadensis, Impatiens biflora, Stachys aspera, Gerardia tenuifolia, Prenanthes alba, Rudbeckia laciniata.*

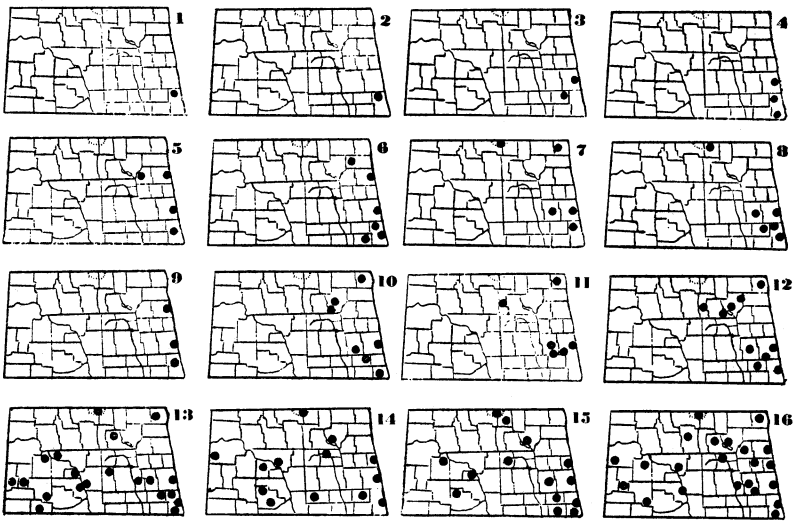

Fig. 3.—Eastern deciduous forest species in North Dakota, at or near their northwestern limits of distribution. (1) *Onoclea sensibilis.* (2) *Ribes cynosbati.* (3) *Allium tricoccum.* (4) *Eupatorium rugosum.* (5) *Caulophyllum thalictroides.* (6) *Arisaema triphyllum.* (7) *Hystrix patula.* (8) *Sanguinaria canadensis.* (9) *Xanthoxylum americanum.* (10) *Rhus glabra.* (11) *Ostrya virginiana.* (12) *Tilia americana.* (13) *Quercus macrocarpa.* (14) *Ulmus americana.* (15) *Prunus americana.* (16) *Ribes americanum.*

Some of the eastern species, better adapted to withstand drought, range across the Missouri River to western North Dakota and into eastern Montana. These include: *Polygonatum commutatum, Ulmus americana, Celtis occidentalis, Quercus macrocarpa, Polygonum scandens, Anemone virginiana, Ribes americanum, Fragaria virginiana, Prunus americana, P. pensylvanica, Amphicarpa bracteata, Desmodium canadensis, Lathyrus venosus, Celastrus scandens, Acer negundo, Vitis vulpina, Fraxinus pennsylvanica* var. *lanceolata, Monarda fistulosa, Viburnum lentago, Lactuca canadensis.*

About one-fourth of the eastern deciduous forest species in North Dakota are of Canadian-Alleghenian origin, including such examples as: *Anacharis planchoni, Scirpus fluviatilis, Juncus brachycephalus, Cypripedium candidum, C. reginae, Salix discolor, S. serrissima, Asarum canadense, Anemone canadensis, A. hudsoniana, Caulophyllum thalictroides, Viola pubescens, Hydrophyllum virginicum, Fraxinus nigra, Mentha canadensis, Pedicularis lanceolata, Scrophularia lanceolata.*

Their ranges, like those of the foregoing, vary somewhat in westward extension depending on their moisture requirements as well as rate of migration (fig. 3).

Absent from North Dakota, although found no more than 50 miles to the east in Minnesota are, in addition to *Acer saccharophorum,* such species as *Taxus canadensis, Populus grandidentata, Carpinus caroliniana, Ulmus thomasi, Quercus borealis, Hepatica americana,* and *Dirca palustris.*

B. NORTHERN CONIFEROUS FOREST SPECIES

Northern conifer forest is lacking from North Dakota. None of the boreal coniferous trees, *Abies balsama, Picea glauca, P. mariana, Larix laricina, Pinus banksiana, P. resinosa,* or *P. strobus,* are found native in the state although within about 50 miles east and northeast they are important in the vegetation of Minnesota and Canada.

Nevertheless, many associated species are present, composing about 15 percent of the total North Dakota flora. As mentioned earlier in this paper, there evidently was no migration of tundra or conifer forest across the state either before, or after, the late Wisconsin glacial advance. However, modification of the prairie region by increased humidity and soil moisture as the ice began to move southward must have favored some forest development. Aspen-birch woods probably became rather widespread but further stages in forest succession did not occur because the cooling climate was not conducive to temperate forest expansion northward and boreal conifer migration into North Dakota was cut off by the ice barrier. The aspen-birch woods persisted for some time, representing a subclimax to a boreal conifer forest climax which failed to materialize.

Subsequent xerothermic climate influenced the disappearance of boreal species. Only those in protected areas such as moist shaded locations in the Turtle, Pembina, and Killdeer Mountains and in spring-fed depressions in sand hills of the Sheyenne delta were able to persist, as relicts (fig. 4).

More recently, westward migrating species of the eastern deciduous forest have found suitable habitats in the same locations so that the resulting vegetation is an intermingling of mesophytes of diverse geographic origin.

The trees of the boreal forest which do range into North Dakota are: *Populus tacamahaca, P. tremuloides,* and *Betula papyrifera.* As understory or as dominants in treeless situations are various shrubs, such as: *Salix bebbiana, S. candida, Betula glandulosa, Ribes triste, Amelanchier alnifolia, Elaeagnus argentea, Shepherdia canadensis,* and *Cornus stolonifera.* Among the boreal semi-shrub and herbaceous plants have been found: *Carex aurea, Arabis holboellii, Drosera rotundifolia, Parnassia palustris, Potentilla fruticosa, Rubus pubescens, Viola rugulosa, Epilobium angustifolium, Cornus canadensis, Pyrola asarifolia, P. secunda, Arctostaphylos uva-ursi, Menyanthes trifoliata, Linnaea borealis,* and *Petasites sagittata.*

C. Rocky Mountain Species

Rocky Mountain species, which comprise about five percent of the North Dakota flora, are principally found in the unglaciated southwestern part of the state (fig. 5). The presence of some may be the result of recent migration. The majority probably are relicts of former more extensive communities. The monadonocks on which these species are chiefly found are themselves relicts, left behind in the westward retreat of the old Tertiary upland. As erosion has progressed, the upland has diminished to a few rocky buttes and dissected bad lands. The developing peneplain, the ultimate product of this erosion cycle, provides a new and favorable habitat for prairie species, which soon acquire dominance.

During glacial periods, because of the prevailing cool, moist climate,

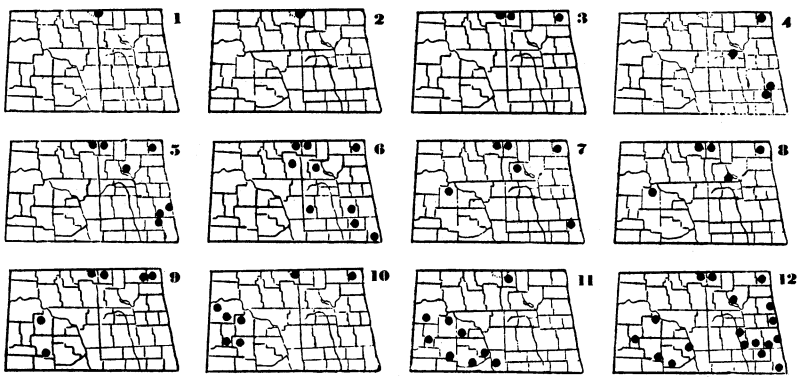

Fig. 4.—Northern coniferous forest species in North Dakota. Most also occur, as relicts, in South Dakota. (1) *Drosera rotundifolia.* (2) *Linnaea borealis.* (3) *Cornus canadensis.* (4) *Betula glandulosa.* (5) *Rubus pubescens.* (6) *Parnassia palustris.* (7) *Betula papyrifera.* (8) *Pyrola asarifolia.* (9) *Elaeagnus canadensis.* (10) *Arctostaphylos uva-ursi.* (11) *Arabis holboellii.* (12) *Viola rugulosa.*

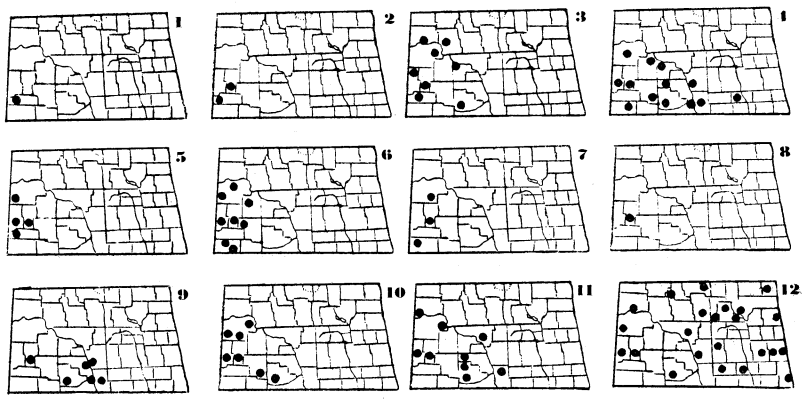

Fig. 5.—Rocky Mountain species. (1) *Pinus flexilis.* (2) *Pinus ponderosa* var. *scopulorum.* (3) *Juniperus scopulorum.* (4) *Rhus trilobata.* (5) *Calochortus nuttallii.* (6) *Lesquerella alpina.* Southwestern desert species. (7) *Artemisia tridentata.* (8) *Atriplex confertifolia.* (9) *Yucca glauca.* (10) *Sarcobatus vermiculatus.* (11) *Eurotia lanata.* (12) *Suaeda depressa.*

montane and alpine vegetation zones were depressed and there probably was considerable migration of Rocky Mountain species into western North Dakota. But in this case, as with the boreal flora, the increase of aridity, during and following deglaciation, would have been responsible for the decline of such vegetation and the increase of prairie and desert species. Only in a few localities, on buttes and in cañons of the badlands have a limited number of montane species been able to survive the climate and competition.

Most striking are three conifers, *Pinus flexilis, P. ponderosa* var. *scopulorum,* and *Juniperus scopulorum.* Other characteristic, though less conspicuous, species are: *Calochortus nuttallii, Disporum trachycarpum, Delphinium bicolor, Ranunculus glaberrimus* var. *ellipticus, Lesquerella alpina, Hedysarum cinerascens, Rhus trilobata, Androsace septentrionalis* var. *puberulenta, Gilia congesta,* and *Lappula texana* var. *columbiana.*

D. SOUTHWESTERN DESERT SPECIES

Another five percent of the North Dakota flora is made up of migrants from the deserts of southwestern United States. Locally, they may be observed to dominate sizeable areas. Dry hillsides are studded with cactus, flats along streams may appear silvery with sagebrush, and saline spots, the "alkali beds," are populated almost entirely by halophytes from the Great Basin region.

In general, these species, although not restricted to the western part of the state, are most abundant there (fig. 5). Dry years tend to favor their eastward extension by reducing their competitors, principally the grasses.

Atriplex confertifolia and *Artemisia tridentata,* dominants in the Great Basin Desert (Shreve, 1942), occur in North Dakota but only in the western part of the state. Much more abundant are other species of these two genera, viz. the saltbushes, *Atriplex argentea, A. dioica, A. hastata,* and *A. nuttallii* and other sagebrushes, *Artemisia cana, A. dracunculoides, A. frigida, A. glauca, A. gnaphalodes,* and *A. longifolia.*

Additional species whose affinities are with the southwest deserts or have, since glaciation, reinvaded North Dakota from such areas are *Yucca glauca, Franseria acanthicarpa, Mamillaria missouriensis, M. vivipara,* and *Opuntia fragilis,* all of which occur on dry sandy or gravelly soils, and the halophytes, *Distichlis stricta, Eurotia lanata, Monolepis nuttalliana, Sarcobatus vermiculatus, Salicornia rubra, Suaeda depressa,* and *Allocarya californica,* which are found in and about the numerous saline areas of the state.

E. COASTAL PLAIN SPECIES

With the exception of *Juncus balticus* var. *littoralis,* none of Peattie's list of Atlantic coastal plain plants in the flora of the Great Lakes (Peattie, 1922) has been found to occur in North Dakota. "True" *Polygonum pennsylvanicum* L. may possibly be present but all collections, to date, have been identified as var. *laevigatum.*

In Minnesota, however, a third or more of the listed species have been found, on sandstone, in sand dune areas near Minneapolis, along the Minnesota River as far as Mankato, and up the Mississippi, some as far as its source at Lake Itasca, only about 75 miles east of North Dakota. Westward, in the Lake Agassiz bed and beyond, the calcareous nature of the soil may be a limiting factor in the distribution of coastal plain flora, but, presumably, migration is in progress and will proceed northward and westward where suitable habitats are available.

SUMMARY

The vegetation of North Dakota is a part of the North American grassland formation, reflecting the influence of climate, physiographic history, and biotic factors upon the available flora. In localized areas, edaphic conditions permit the occurrence of more mesic plants or restrict the vegetation to a few hardy xeric species.

Approximately 55 percent of the flora is intraneous, of which 40 percent comprises prairie species and 15 percent species of widespread distribution.

The remaining 45 percent is composed of extraneous species: 20 percent are immigrants from the eastern deciduous forest; 15 percent are relicts of the northern coniferous forest; and five percent, each, are from the Rocky Mountains and from the deserts of southwestern United States.

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