SOME NATURAL FLORISTIC AREAS IN BOREAL AMERICA

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IN A SYMPOSIUM ON

ORIGIN AND DEVELOPMENT OF NATURAL FLORISTIC AREAS WITH SPECIAL REFERENCE TO NORTH AMERICA

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INTRODUCTION

A comprehensive discussion of natural phytogeographic areas in boreal America, even if I were able to produce it, would not be compressible into the time allotted for my contribution to this symposium. I have, therefore, chosen to outline a single problem which has led me into a study of some boreal plant ranges. These ranges, when they are superposed and sorted into patterns, supply evidence of natural floristic areas, and afford some implications of the history and manner of development of these areas.

I have had occasion, during the past few years, to study the vegetation of the southwestern part of the District of Mackenzie, in northwestern Canada. Included in this area are the eastern slopes of the Mackenzie Mountains, a range extending in a great arc northwestward from the Liard River into central Yukon (Fig. 1). The highest altitudes attained in these mountains are as yet unknown, but peaks 7,000-9,000 feet above sea-level are not uncommon. Timber line in the southern part of the range is at about 4,500 feet, but is somewhat lower at the north. The range as a whole is separated from the Rockies, Cassiars, Coast Ranges and Richardson Mountains by forested valleys and plateaus.

The flora of the Mackenzie Mountains is still very incompletely known. Prior to our own collections only a handful of plants had ever been gathered there. In 1939 we spent two months at Glacier or Brintnell Lake, in the central part of the range, and in 1944 the route of the Canol pipeline road was examined by Mr. A. E. Porsild who made extensive collections (Porsild 1945). Also in 1944 Dr. V. C. Wynn-Edwards made some notable collections in the eastern fringes of the mountains, and also along the eastern part of the pipeline road. The only place, however, in which anything like a comprehensive collection has been made on the eastern side of the mountains is at Brintnell Lake. The vascular flora of this area proved to be comparatively small—283 species and varieties—with a certain amount of rather poorly defined endemism.

GEOGRAPHIC AFFINITIES OF THE BRINTNELL LAKE FLORA

Preliminary Remarks, Including Notes on Local and Cosmopolitan Species

In order to study the geographic affinities of the Brintnell Lake flora I have mapped the ranges, in Alaska, Canada and the northern States, of 271 of the 283 species and varieties collected there.[1]

When the maps are superposed it becomes possible to designate a number of rather well-defined patterns. The actual number of these patterns depends of course upon the degree of refinement that enters into the selection of criteria. Needless to say, the scanty existing knowledge of geographic factors in boreal America makes it impossible to carry the refinement very far. Comparison of the maps soon brings out, however, two phytogeographic transition zones which appear to overshadow any others that appear. These are the arctic timber line, and the coastal mountains of southeastern Alaska, British Columbia, and western Washington. Some indication of the significance of these "boundaries" may be had from the following figures. Of the 271 species considered in the maps 199 approach or cross the arctic timber line, and 164 of them are either stopped by it or cross it to a limited distance. Nearly all 283 of the Brintnell Lake plants extend *to* the western coastal mountains or forests, but about 196 of them avoid all or part of these habitats. In view of the obvious phytogeographic importance of the coast range and the arctic timber line, I have drawn up a tentative classification of range patterns based in large part upon the plants' behavior with relation to them. A third geographic boundary is not so well defined in all cases, but is sufficiently clear to necessitate recognition. This is marked by the eastern ranges of the Cordillera. About 25 percent of the Brintnell Lake flora does not extend east of the Rocky Mountains, or has limited extensions into the northern great plain of the continent.

About 4.2 percent of the flora at Brintnell Lake (12 spp. and vars.) is composed of plants recently described as new, recently described from the lower Mackenzie district, or known in North America from this single area (Raup 1947). Tentative ranges can be drawn for a few of these, but so little has been discovered about them that I have preferred to keep them in a separate category, and I have not included maps of them. They are as follows:

Picea glauca var. *Porsildii* Raup, *Poa Brintnellii* Raup, *Carex Soperi* Raup, *Salix Barrattiana* var. *marcescens* Raup, *Salix Bebbiana* var. *depilis* Raup, *Salix glauca* var. *perstipula* Raup, *Lychnis brachycalyx* Raup, *Saxifraga sibirica* L., *Rosa acicularis* var. *cucurbiformis* Raup, *Arnica alpina* (L.) Olin, *Arnica Snyderi* Raup, *Antennaria* sp.

At the other extreme in range extension are three cosmopolitan species: *Cystopteris fragilis, Equisetum arvense,* and *Carex aquatilis* s. l. These are among the most wide-ranging plants in boreal America, and the first two are cosmopolitan throughout much of the world. In Canada and Alaska they thrive in nearly all parts of the arctic, alpine, and forest regions, without regard to boundaries that are limiting to most other plants. Of the three, *Equisetum arvense* seems to have the most varied stations.

[1] The base map used for these ranges is by J. Paul Goode, and is copyrighted and published by the University of Chicago Press.

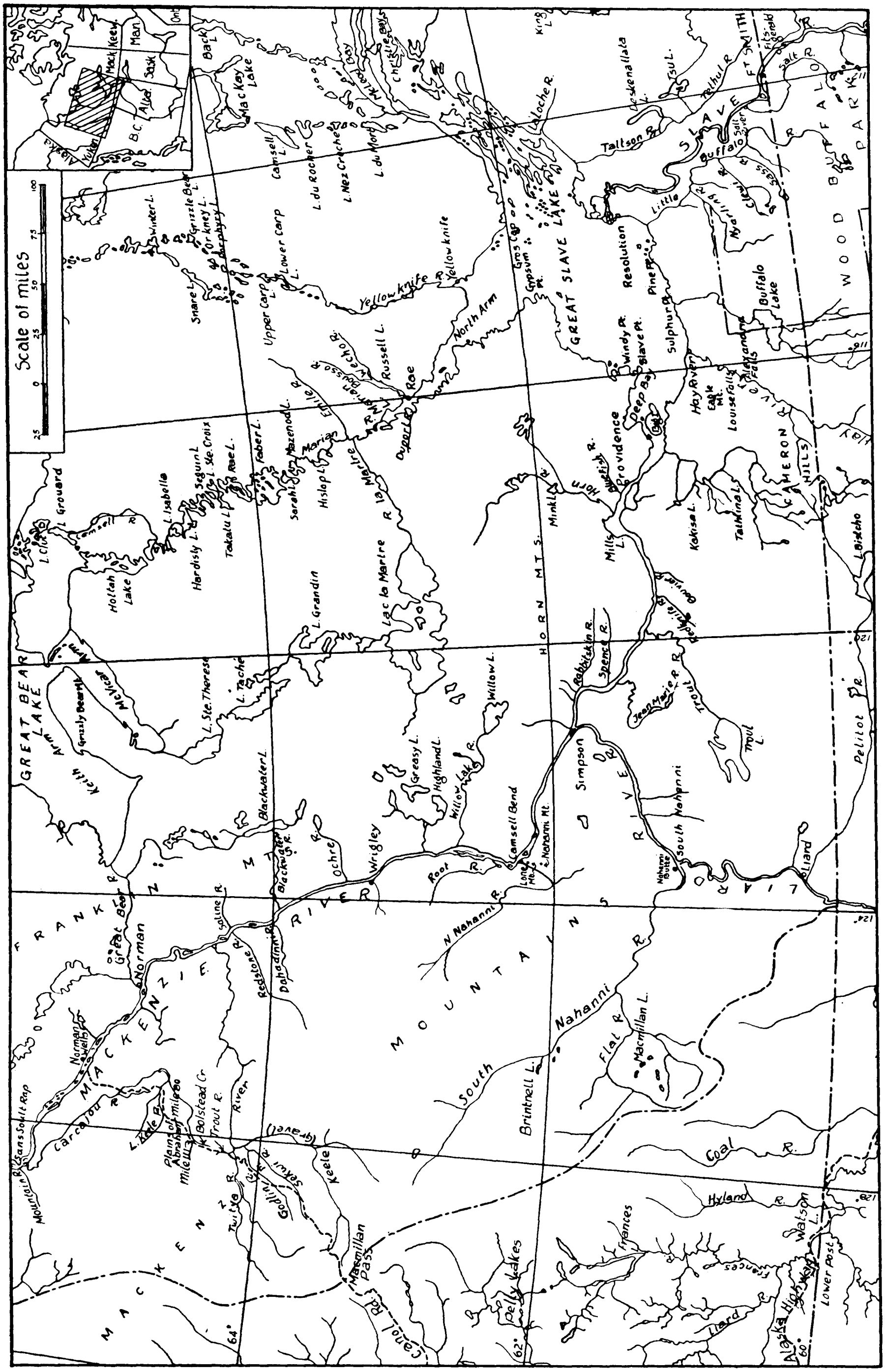

FIG. 1. Map of southwestern Mackenzie and adjacent regions.

The remaining 268 species and varieties can be arranged in five general categories: (1) species whose principal areas are in the region of the Canadian coniferous forest, and whose ranges are wide in this region, extending for the most part all the way across the continent; (2) arctic or artic-alpine wide-ranging species with ranges concentrated north of the arctic timber line, or in both the arctic lowland and in the cordilleran alpine areas; (3) an intermediate group of wide-ranging subarctic species which cannot be placed with either of the above, but which appear to have their greatest concentration on or near the arctic timber line; (4) a group of Alaskan-cordilleran species which have only limited extensions east of the

Rocky and Mackenzie Mountains, and most of which are arctic-alpine in general affinities; (5) a cordilleran group, most of which are alpine but not arctic, and whose ranges are concentrated in the Rocky Mountains and coast ranges. Further subdivisions of these five categories can be made by noting first the actual relation of the wider ranges to the arctic timber line, and second the relation of the ranges to the western coastal mountains or the Pacific slope forests. The following discussion will follow the above outline.

In order to compare the range maps more easily I have drawn lines connecting marginal stations in such a way as to outline the limits to which the various species are now known to extend. For common, much collected plants this can be done without difficulty, but in cases of rare or poorly collected species the outlines of geographic limits must be regarded as tentative. The most difficult cases are those with stations separated by hundreds of miles. Here it is often impossible to decide whether to consider the ranges as continuous or disjunct. Of the ranges mapped in this study I have designated only nine as being discontinuous, although it is possible that a few others might be included. In defense of my tendency to reduce the number of disjunct ranges as much as possible I can only say that one of the results of the collecting and exploration in arctic and subarctic America during the past twenty years has been to fill in and make continuous many ranges that were formerly thought to have separate eastern and western components.

WIDE-RANGING FOREST SPECIES

The most extensive plant ranges in Canada and Alaska, with the exception of the three cosmopolitans already mentioned, are exhibited by a small group of about 19 species. These plants do not stop at the arctic timber line, but reach far out into the tundra, particularly in the eastern arctic. Most of them are spread throughout the timbered parts of Alaska. Eight of them (Fig. 2A) have the widest ranges because they also enter the forests of the Pacific slope from southern Alaska to western Washington:

Equisetum scirpoides, Poa pratensis s. l., *Corallorrhiza trifida, Alnus crispa* s. l., *Rubus Chamaemorus, Epilobium angustifolium* s. l., *Pyrola secunda, Ledum groenlandicum.*

The other 11 species either avoid the coastal forests altogether, or enter them only in southern Alaska or Washington. Thus they are more strictly continental in the far west (Fig. 2B):

Calamagrostis neglecta, Carex vaginata, Habenaria obtusata, Salix planifolia, Betula glandulosa, Ranunculus Gmelini var. *Purshii, Ranunculus lapponicus, Draba lanceolata, Potentilla fruticosa, Hedysarum alpinum* var. *americanum, Vaccinium Vitis-Idaea* var. *minus.*

The remainder of the widespread forest species are more rigorously limited by the timber line, though some of them occur far north on the Labrador coasts, southern Baffin Island, or in Greenland. There are 80 of them, divisible into four groups on the basis of their geographic relation to the Pacific slope forests. The first of these groups (Fig. 3A) contains 30 species that appear in the coastal forests both in southern Alaska and in British Columbia and western Washington. Several of them, perhaps half a dozen, do not appear to reach the western coast of Alaska.

Dryopteris Linnaeana, Equisetum fluviatile, Equisetum palustre, Lycopodium annotinum s. l., *Selaginella selaginoides, Juniperus communis* var. *montana, Agrostis scabra, Poa nemoralis, Carex leptalea, Carex canescens, Carex Garberi* s. l., *Juncus balticus* s. l., *Smilacina stellata, Habenaria hyperborea, Salix Bebbiana, Arenaria lateriflora, Stellaria calycantha* s. l., *Actaea rubra, Ribes lacustre, Ribes triste, Shepherdia canadensis, Cornus canadensis, Cornus stolonifera, Moneses uniflora, Pyrola asarifolia* var. *incarnata, Pyrola minor, Heracleum lanatum, Arctostaphylos Uva-ursi* (incl. var. *coactilis*), *Linnaea borealis* s. l., *Viburnum edule.*

The second group, of 13 species (Fig. 3B), occurs in some of the coastal forests of southeastern Alaska, but becomes more continental in British Columbia and Washington. A few of them, probably not more than four, fail to reach the western Alaskan Coast.

Equisetum sylvaticum s. l., *Lycopodium clavatum* var. *monostachyon, Lycopodium complanatum* s. l., *Carex gynocrates, Eriophorum brachyantherum, Cypripedium passerinum, Populus Tacamahacca, Populus tremuloides, Geocaulon lividum, Parnassia palustris* var. *neogaea, Ribes hudsonianum, Dryas Drummondii, Rosa acicularis* s. l.

A third group of 14 species (Fig. 3C) is still more continental in range, reaching the coast timber only in southwestern British Columbia and western Washington. They avoid the wet slope forests of southern

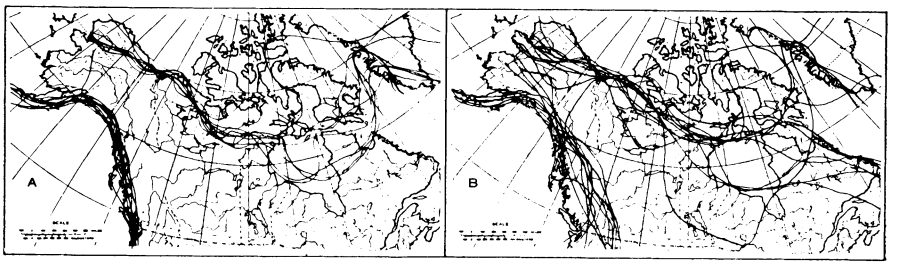

FIG. 2. Wide-ranging forest species extending north of the arctic timber line.

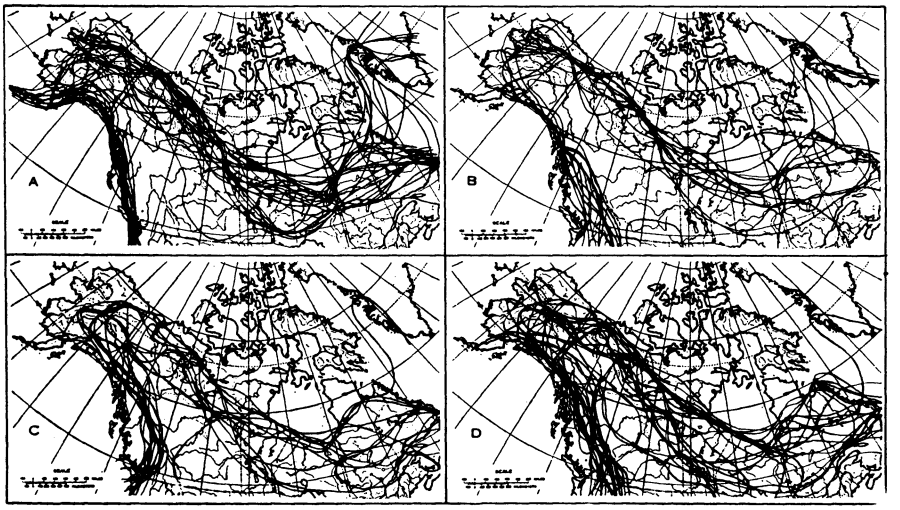

FIG. 3. Wide-ranging forest species whose northern limits are at or near the arctic timber line.

Alaska, and none of them extends to the western coasts of Alaska. Four of these plants seem to have disjunct ranges: *Arctostaphylos Uva-ursi* var. *adenotricha, Betula papyrifera* var. *commutata, Arabis Holboellii, Antennaria subviscosa.* I have included them here because a hypothetical joining of their parts would result in ranges similar to the others in Fig. 3C.

Carex aurea, Betula papyrifera var. *commutata, Arenaria dawsonensis, Arabis Drummondii* s. l., *Arabis Holboellii, Geum macrophyllum* var. *perincisum, Potentilla norvegica, Pyrola virens, Arctostaphylos Uva-ursi* var. *adenotricha, Erigeron angulosus* var. *kamtschaticus, Erigeron elatus, Antennaria subviscosa, Senecio indecorus, Senecio pauperculus.*

The fourth, and almost strictly continental, group contains 23 species (Fig. 3D). With one or two possible exceptions these plants avoid the Pacific slope forests entirely, and all but five of them fail to reach the west coasts of Alaska. A few are even more restricted and do not extend west of the northern Rocky Mountains.

Picea glauca s. l., *Picea mariana, Agropyron trachycaulum* var. *novae-angliae, Agropyron trachycaulum* var. *unilaterale, Calamagrostis canadensis* var. *robusta, Carex concinna, Carex diandra, Carex media, Goodyera repens* s. l., *Listera borealis, Salix myrtillifolia, Alnus tenuifolia, Betula occidentalis, Aquilegia brevistyla, Rorippa islandica* var. *microcarpa, Ribes glandulosum, Ribes oxyacanthoides, Amelanchier florida* (incl. *A. humilis*), *Fragaria glauca, Rubus acaulis, Rubus strigosus, Mertensia paniculata, Valeriana septentrionalis.*

WIDE-RANGING ARCTIC-ALPINE PLANTS

There are 66 wide-ranging arctic-alpine plants in the Brintnell Lake flora. As among the forest species, one can first divide them into two groups according to their actual relation to the arctic timber line. In spite of the fact that the principal ranges of nearly all of them extend throughout much of the arctic archipelago, 26 of them are commonly found far south of the arctic limit of trees (Fig. 4). In so doing they achieve the most extensive ranges of all our arctic-alpine plants and, as did the forest species that crossed the timber line, they approach a cosmopolitan distribution in Canada and Alaska.

The most extensive ranges are those of 7 species (Fig. 4A) which occur not only on the Rocky and Mackenzie Mountains but also on the coastal ranges all the way from the Alaska Peninsula to Washington. They extend southward in the central plains at least as far as Lake Athabaska.

Equisetum variegatum, Lycopodium Selago, Festuca brachyphylla, Poa alpina s. l., *Carex scirpoidea, Salix arctica* s. l., *Empetrum nigrum.*

Another group, of 8 species, is predominantly continental south of the mountains in southeastern Alaska (Fig. 4B). They occur on the coast and Alaska ranges of southern Yukon and Alaska, as well as on the mountains around the Lynn Canal, but in British Columbia and Alberta they are largely confined to the Rockies and Selkirks.

Poa glauca, Trisetum spicatum s. l., *Carex capillaris* s. l., *Juncus castaneus, Polygonum viviparum, Saxifraga tricuspidata, Dryas integrifolia, Astragalus alpinus.*

A third group of these extremely wide-ranging arctic-alpine plants contains 11 species (Fig. 4C) and is almost completely continental in the west. Southeast of the Prince William Sound region of Alaska these plants are confined to the more northerly ranges of the coastal mountains, and to the Rockies and Selkirks. Only two of them come out to the coast in northwestern Washington.

Dryopteris fragrans s. str., *Calamagrostis purpurascens, Arenaria verna* var. *pubescens, Ranunculus hyperboreus, Cardamine pratensis* s. l., *Draba cinerea, Chrysosplenium tetrandrum, Saxifraga aizoides, Potentilla nivea* s. l., *Pyrola grandiflora* s. l., *Taraxacum lacerum.*

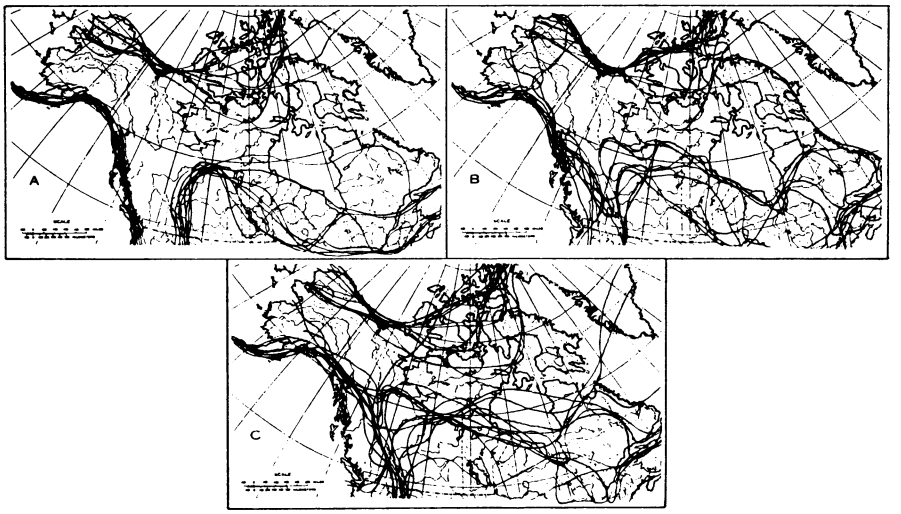

FIG. 4 Wide-ranging arctic and arctic-alpine species which extend far south of the arctic timber line.

For the remaining 40 arctic-alpine plants the arctic timber line appears to be a more formidable barrier. They either stop at the timber line or come only a short distance south of it. Like the preceding group they can be arranged in three divisions depending upon whether they extend to the mountains of the Pacific coast.

First are 12 species of wide range on the coastal mountains (Fig. 5A). One of these, *Dryas octopetala,* has a broken range. It is widespread in the Cordillera and reappears in northwestern Greenland.

Agropyron latiglume, Poa arctica, Luzula spicata, Oxyria digyna, Silene acaulis var. *exscapa, Cardamine bellidifolia, Saxifraga oppositifolia, Saxifraga rivularis, Dryas octopetala, Epilobium latifolium, Epilobium anagallidifolium, Erigeron unalaschkensis.*

Another group of 10 species ranges the coastal mountains only in southern and southeastern Alaska (Fig. 5B). In British Columbia and Alberta they reach their southern limits in the Rockies and Selkirks, and are strictly continental.

Hierochloë alpina, Carex bipartita, Eriophorum Scheuchzeri, Luzula Wahlenbergii, Salix reticulata, Salix Richardsonii, Oxytropis foliolosa, Cassiope tetragona, Pedicularis capitata, Pedicularis sudetica.

Finally, a group of 18 arctic-alpine plants, with one exception in western Washington, avoid the coastal mountains entirely (Fig. 5C).

Calamagrostis lapponica s. l., *Carex membranacea, Luzula confusa, Arenaria humifusa, Arenaria Rossii, Lychnis apetala, Stellaria longipes* var. *Edwardsii, Ranuncu-*

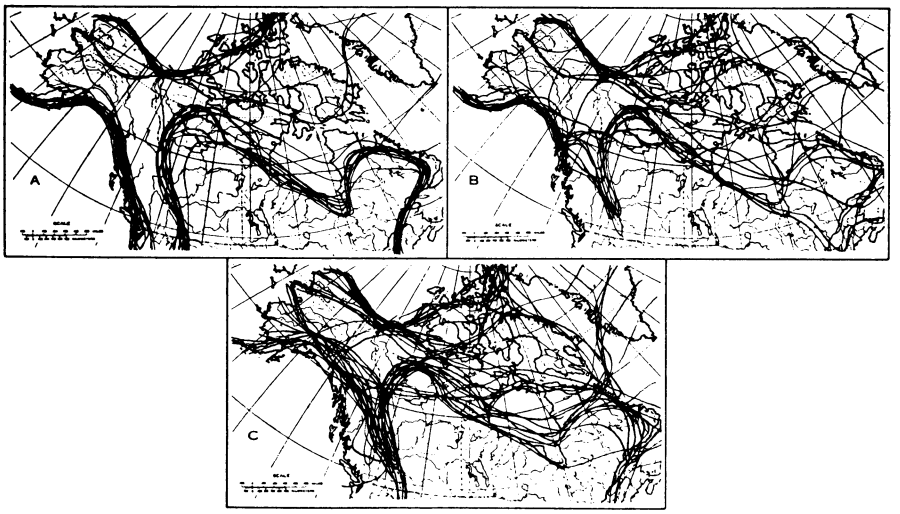

FIG. 5. Wide-ranging arctice and arctic-alpine species whose southern limits are at or near the arctic timber line.

lus nivalis, Draba fladnizensis var. *heterotricha, Draba glabella, Saxifraga nivalis, Potentilla emarginata, Oxytropis Maydelliana, Epilobium davuricum, Vaccinium uliginosum* var. *alpinum, Pedicularis lanata, Erigeron eriocephalus, Crepis nana.*

Two features of the arctic-alpine plant ranges should be noted especially. Nearly all of them extend to the western Alaskan coasts, in contrast to the forest plants among which 39 do not accomplish this. Second, there are a few of the arctic plants, probably not more than 8, which do not occur in the Rocky Mountains at all, but find their southern limits in the Mackenzie Mountains and in southern Yukon or Alaska.

PLANTS OF THE TIMBER LINE REGION

There are 31 species which constitute something of an enigma in that, although they have wide subarctic ranges across most of the continent, they cannot properly be classed either with forest or arctic-alpine categories. They extend into the tundra, but avoid most of the high arctic regions. At the same time they are common to abundant in the northern part of the forest. They occupy a wide range of habitats, although none of them is characteristic of rich woods, and about two-thirds of them are perhaps most abundant in muskegs or wet tundra. Most of them appear in the northern Rockies, but two or three do not come south of the 60th parallel. All but two or three reach the western Alaskan coasts.

A glance at Fig. 6 will show that most of these "timber line" species are continental in the more southern parts of their ranges. I have arranged them in two groups, carrying out the plan used in other categories. The first group contains 10 species which occur in the coastal strip as far south as southeastern Alaska, while beyond that area all but 3 retreat inland (Fig. 6A). One species of disjunct range is included here, *Lycopodium alpinum.*

Woodsia ilvensis, Lycopodium alpinum, Calamagrostis canadensis var. *Langsdorfii, Cerastium Beeringianum, Anemone parviflora, Anemone Richardsonii, Sibbaldia procumbens, Andromeda Polifolia, Vaccinium microcarpum, Vaccinium uliginosum.*

A second group, of 21 species, avoids the coastal strip except in southwestern British Columbia, where four of them come out to Vancouver Island (Fig. 6B). Three species with discontinuous ranges are in this group: *Sagina Linnaei, Epilobium lactiflorum, Oxytropis ixodes, Carex deflexa, Carex microglochin, Tofieldia palustris, Salix glauca* s. l., *Arenaria sajanensis, Sagina Linnaei, Parnassia Kotzebuei, Hedysarum Mackenzii, Oxytropis hudsonica, Oxytropis ixodes, Epilobium lactiflorum, Cornus canadensis* f. *purpurascens, Arctostaphylos rubra, Gentiana propinqua, Pedicularis labradorica, Veronica alpina* var. *unalaschcensis, Pinguicula villosa, Solidago multiradiata, Antennaria isolepis, Taraxacum ceratophorum, Taraxacum lapponicum.*

ALASKAN-CORDILLERAN SPECIES

An arrangement of Alaskan and cordilleran components of the Brintnell Lake flora on the basis of their relation to timber line proves to be impracticable. Of the 72 species counted in these categories, only ten can be regarded as forest plants, and most of these ten are likely to be found far above or beyond the timber line. All the others are plants commonly found in the alpine or western arctic tundra. However, a great many alpine plants of the Mackenzie and northern Rocky Mountains are commonly found in the timbered areas at low levels. About half of the western alpine plants were found below timber line at Brintnell Lake, and no doubt further search would yield more of them. It is not possible, therefore, safely to classify them in relation to timber line.

I have arranged the 72 species in two main groups, the first of which ranges throughout central and western Alaska, many of them north to the arctic coast. Most of them come into the mountains farther south, so that I have called them the Alaskan-cordilleran group. There are 45 of these, 16 of which (Fig. 7A, C) range southward into the western United States. The whole group can be separated on the basis of its coastal extensions. First is a wide-ranging series of 11 species, all of which occur on the coastal mountains of southeastern Alaska, and many of them on the coast ranges farther south (Fig. 7A).

Carex physocarpa, Luzula arcuata, Lloydia serotina, Zygadenus elegans, Arabis lyrata var. *kamchatica, Sedum roseum* var. *integrifolium, Viola epipsila, Gentiana glauca, Aster sibiricus, Artemisia arctica* s. l., *Petasites frigidus.*

Allied to these, but with their southern extensions terminating in Yukon or the Alberta and British Columbia Rockies, are 15 species, all of which are coastal in southern or southeastern Alaska (Fig 7B).

Cryptogramma crispa var. *sitchensis, Arctagrostis arundinacea, Festuca altaica, Poa paucispicula, Carex loliacea,*

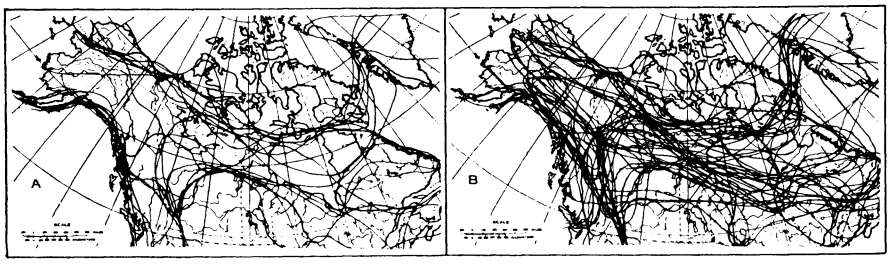

FIG. 6. "Timber-line species."

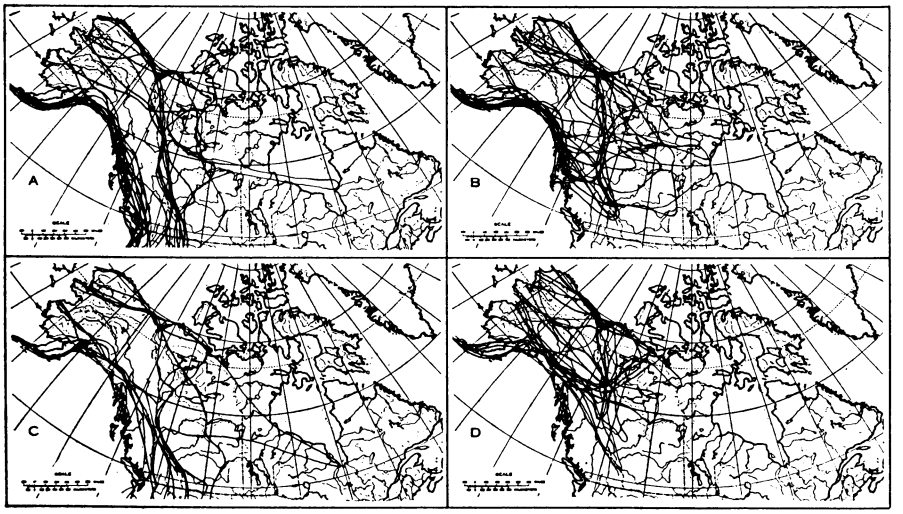

FIG. 7. Alaskan-cordilleran species.

Salix alaxensis s. l., *Salix arbusculoides, Salix pulchra, Betula papyrifera* var. *humilis, Aconitum delphinifolium, Anemone narcissiflora, Saxifraga punctata* s. l., *Boschniakia rossica, Campanula lasiocarpa, Arnica Lessingii.*

Two groups are more strictly continental in the region southeast of Prince William Sound, although a couple of species appear at the coast in the Puget Sound area. Five species range southward into the United States (Fig. 7C).

Delphinium glaucum, Potentilla uniflora, Myosotis alpestris s. l., *Artemisia Tilesii* s. l., *Senecio lugens.*

The remainder, 14 species, extend from Alaska to the northern Rocky Mountains, and avoid the coastal mountains except west of Prince William Sound (Fig. 7D).

Larix laricina var. *alaskensis, Carex nesophila, Carex podocarpa, Corydalis pauciflora, Draba longipes, Saxifraga radiata, Astragalus frigidus* var. *littoralis, Lupinus arcticus, Oxytropis hyperborea, Oxytropis pygmaea, Gentiana arctophila, Polemonium acutiflorum, Antennaria monocephala, Taraxacum alaskanum.*

CORDILLERAN SPECIES

The last category of ranges to be considered involves 27 plants that are more strictly cordilleran than any of the above. They do not reach the arctic coast proper, either in Alaska or Mackenzie, and their eastward extensions into the northern plains are less numerous and less pronounced. All of them range southward into the western United States. They fall rather clearly into two groups: one with a strong coastal relationship and the other just as strongly continental.

Sixteen of the 27 follow the coastal mountains from the Alaska Peninsula to western Washington, although a couple of them retreat inland a short distance in the latter region. They extend throughout the northern Rocky Mountains, but most of them are confined to the southern ranges of Alaska. None of them reaches the lower Yukon valley (Fig. 8A), although two have been found at the Mackenzie River delta. Our Mackenzie Mountain collections have constituted northeastern range extensions for most of these species.

Abies lasiocarpa, Carex nardina var. *Hepburnii, Carex phaeocephala, Carex pyrenaica, Juncus Drummondii, Salix Barclayi, Salix commutata, Salix Scouleriana* s. l., *Ranunculus Eschscholtzii, Draba nivalis* var. *elongata, Parnassia fimbriata, Saxifraga Lyallii, Hippuris montana, Phyllodoce glanduliflora, Senecio triangularis, Hieracium gracile.*

The other 11 cordilleran plants avoid the coastal strip except in the south, where four of them appear

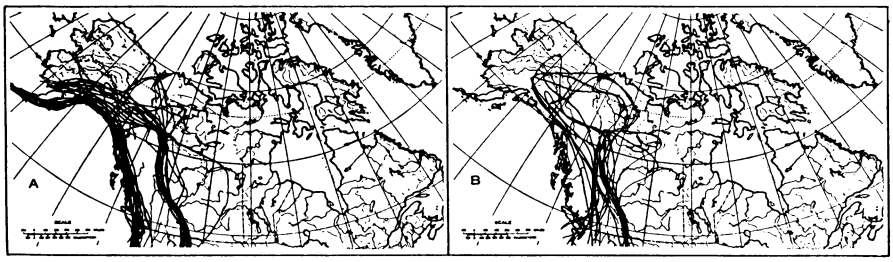

FIG. 8. Cordilleran species.

in the Puget Sound region. A few of them (4) reach central Alaska, and two are found at the Mackenzie delta (Fig. 8B). This group contains the very few Rocky Mountain plants which have their known northern limits in the Mackenzie Mountains.

Poa Buckleyana, Carex albonigra, Carex atrata ssp. *atrosquama, Salix Barrattiana, Draba McCallae, Draba praealta, Potentilla diversifolia* s. l., *Erigeron jucundus, Antennaria media, Arnica mollis, Arnica alpina* ssp. *tomentosa.*

DISCUSSION

Table 1 gives a summary of the range patterns just described. Some generalizations from these figures will serve to bring out further the regional characteristics and affinities of the Brintnell Lake Flora. Fully 70 percent or about 199 of the species, have wide ranges across the continent, most of them extending from Alaska to the Gulf of St. Lawrence. Approximately 25.4 percent are Alaskan or cordilleran, while the remaining 4.2 percent are endemic or local.

TABLE 1

	No. of spp. and vars.	Percent
Endemics and plants of limited known range	12	4.2
Cosmopolitan in Canada and Alaska	3	1.0
Wide-ranging forest species		
Reaching coasts of Alaska, B.C., and western Washington	38	13.4
Reaching coasts of southeastern Alaska	13	4.6
Avoiding coasts, southeastern Alaska to Washington	48	17.0
Wide-ranging arctic or arctic-alpine species		
Reaching coastal mountains, Alaska to Washington	19	6.7
Reaching coastal mountains of southeastern Alaska	18	6.4
Avoiding coastal mountains, S.E. Alaska to Washington	29	10.2
Wide-ranging "timber-line" species		
Reaching coast of S.E. Alaska	10	3.5
Avoiding coasts, S.E. Alaska to Washington	21	7.4
Alaskan-cordilleran species		
Reaching coasts, Alaska to Washington	11	3.9
Reaching coasts of southern and southeastern Alaska	15	5.3
Avoiding coasts, S.E. Alaska to Washington	19	6.7
Cordilleran species		
Reaching coasts, southern Alaska to Washington	16	5.6
Avoiding coasts, southern Alaska to Washington	11	3.9
TOTALS	283	99.8

The wide-ranging plants fall into two main groups, arctic-alpine and forest species. In the first there are 66 species, while in the second there are 99. A third group of 31 species (10.9 percent) are intermediate between the first two, and three (1 percent) are cosmopolitan. This is not a complete statement of the proportions of arctic-alpine and forest elements, however, because approximately 62 of the 72 Alaskan and cordilleran plants are of prevailingly alpine or arctic affinity and should be added to the wide-ranging ones. Thus the total of arctic, arctic-alpine, and alpine plants is about 128, or about 45 percent of the total vascular flora, and that of forest species is 109, or about 38 percent of the whole.

Although the flora as a whole is strongly continental in character, a great many of its species are able to live in the damp forests of the north Pacific slopes or on the coastal mountains. The range maps give a rough index to the degree of continentality which is achieved by the Brintnell Lake flora. There are about 140 species (49.4 percent) which avoid the coastal forests and mountains completely or nearly so, and are the most rigorously continental plants in our flora so far as the west is concerned. Another 56 (19.8 percent) avoid the British Columbia and Washington coasts, but occur in southeastern Alaska. The remaining 87 (30.7 percent) inhabit, in addition to the continental ranges, the coastal strip from Alaska to Washington.

Table 2 will summarize the above generalizations.

TABLE 2

	No. of spp. and vars.	Percent
Endemics and plants of limited known range	12	4.2
Cosmopolitan species	3	1.0
Plants of wide range across the continent	199	70.3
Plants with ranges mainly in Alaska and the Cordillera	72	25.4
Plants of the forested country	109	38.0
Arctic, arctic-alpine, or alpine species	128	45.0
"Timber-line" ranges	31	10.9
Strictly continental with regard to S.E. Alaska, B. C., and Washington	140	49.4
Plants that avoid the coasts of B. C. and Washington, but occur in S. E. Alaska	56	19.3
Plants whose ranges extend into the coastal strip of S.E. Alaska, B. C., and Washington	87	30.7
Plants that do not reach the western coasts of Alaska	83	30.0

APPLICATION OF HULTÉN'S HYPOTHESIS

In view of the geographic position of the Mackenzie Mountains in northwestern America, their recent botanical exploration, the present isolation of their alpine flora by the development of surrounding forests, and the simplicity and apparently incipient endemism in their flora, it has occurred to me that this flora might be used as a test of theories advanced some years ago (1937) by Dr. Eric Hultén concerning the origin and development of all our boreal biota.

Whether or not there were ice-free land surfaces in the Mackenzie Mountains during the Late Wisconsin (W_3) glacial episode is not certain, although there is some evidence, both geological and botanical, that suggests them. If ice-free summits were present, their flora must have been composed of the arctic-alpine remnants of a wide pre-Late Wisconsin dispersal of these plants. A few species found at Brintnell Lake suggest this. There are three that

have extensive ranges in Eurasia but are not known elsewhere in North America, and there are eight rather poorly defined endemics or suspected endemics. Considering the small number of these unique plants, and the paucity of the Brintnell Lake flora as a whole, it is hardly justifiable to set up the Mackenzie Mountain area, at least so far as the eastern slopes are concerned, as a refuge equivalent to those of Beringia, the North Pacific coasts, or the Yukon Plateau. It seems more reasonable to assume that although a few alpine plants may have persisted at Brintnell Lake through Late Wisconsin time, most of the flora has arrived during and since the retreat of the last valley glaciers. The findings of Porsild on the western slopes of the mountains may require modification of this view.

It is unnecessary to review in detail all of the reasoning and implications of the theories advanced by Hultén, for this has already been done by several students (see Stebbins 1942, Raup 1941, Halliday and Brown 1943, Cain 1944). The following is a brief outline of the broader geographic aspects, with a few critical notes that have grown out of the present investigation.

In connection with his floristic studies of Kamtchatka and the Aleutian Islands, Hultén mapped, sometimes in detail and sometimes by limits, the ranges of hundreds of arctic and boreal species. He organized this factual material on the basis of what he called "equiformal areas." That is, when large numbers of ranges are superposed they fall into a group of patterns which are more or less clearly defined geographically, and "equiformal" within themselves. Each equiformal area shows a region of concentration in number of species, which is called its "centre." Since it is assumed that each species has acquired its present range by dispersal from a point of origin or survival, the regions of concentration within the equiformal areas are regarded as fundamental centers of origin for the various major elements in the flora; and the "equiformal areas" become "equiformal progressive areas" that are thought to indicate the general patterns of dispersal among the major elements. The species are termed "radiants" from the various "centra."

The geographic arrangement of centra as worked out by Hultén is as follows: They are " . . . in North-Eastern Siberia and in the Amur-Manchurian region. Another occurs in the Altai-Sajan region, sending out radiants towards the Arctic shore. A third centre is northern Japan, whence numerous plants radiate to the north and to the coast of the Asiatic Continent. A centre of great importance is the region around the northern part of the Bering Sea. It sends out progressive radiants reaching symmetrically as well to the west into arctic Asia and Europe as to the east to Eastern America, and also often extends arms along both the Asiatic and American Pacific coast. In America radiants proceed from the Yukon valley along the Arctic American coast, others centre around the Arctic Archipelago, and others again have the centre of their progressive figures in the State of Washington and radiate along the American coast or along the Rocky Mts. to Alaska. Of the plants discussed . . . no groups could be formed having their centres in northern Europe or western Siberia, or in North-Eastern America or in the country between Yukon Valley and the Great Lakes" (Hultén 1937, p. 25).

Hultén immediately draws a correlation between the distribution of his centra and the distribution of ice during the Pleistocene. No centra could be found in areas that were covered by ice during the maximum advance of the glaciers; and the existing floras have all been derived from areas of refuge close to the ice. It is maintained, on genetical grounds, that the ability of the species to disperse themselves from their refugia has not been uniform. Those confined to small refugia, under difficult climatic conditions and in small populations, are considered to have been so depauperated of biotypes that they have been exceedingly slow to spread. Others had large areas and populations, either within the generally glaciated regions or south of the ice, so that they retained their inherent variability and aggressiveness and could quickly invade lands freed of ice.

It is thought that the so-called "Linnaean species" of the present boreal flora originated in the last great interglacial or earlier, and that large numbers of them achieved wide dispersals during that time. Their present areas are looked upon as reductions from these wide ranges, with post-Glacial re-expansions that have been conditioned by the amount of depauperation suffered during the maximum ice advance.

Hultén's arrangement of equiformal areas is open to modification or criticism along three lines. First, it is possible to make additions to his lists, at least in the American boreal flora. The Brintnell Lake region is found to have approximately 45 species not discussed by him at all. When these are sorted into patterns they have a distribution among the equiformal areas, however, that makes no serious modification in the latter. Second, there are apparent gaps in the ranges of boreal American plants which are gaps in exploration rather than in the actual ranges. Lacunae in our knowledge of the more uniform floras of eastern glaciated regions are not so troublesome; but the gaps in northern British Columbia and Yukon are more serious, for the distribution of species into equiformal areas sometimes depends upon their behavior in this region. Some of Hultén's dispositions of species are therefore open to modification due to range extensions discovered since his study was made. Third, Hultén's original sorting of species among his equiformal areas can be questioned in many cases. This is particularly notable in his treatment of wide-ranging forms.

I have found it necessary to make a number of changes in Hultén's lists along the three lines just mentioned. The changes are in many cases matters of judgment, and even when all are taken together they make no serious modification in his general sorting of ranges.

If the general thesis outlined by Hultén is tenable,

then the flora of the Mackenzie Mountains should show affinities with his various centra which, within the general limits of accessibility, are directly proportional to the size of the relic populations, and presumably inversely proportional to their degree of biotype depauperation.

It should be possible to draw up a sequence showing the relative availability of plants for the colonization of the Brintnell Lake area during the retreat of the glaciers. It is presumed that for a time after the disappearance of the ice the mountains and adjacent valleys and plains had free access to the alpine and tundra floras of the Rockies, the Cassiars, the Yukon Plateau, the Richardson Mountains, and the arctic lowlands. With the amelioration of the climate coniferous forests eventually covered the valleys of the Mackenzie, upper Liard, Peel, and Wind Rivers, and finally the divides between these streams and the Yukon system. In so doing they effected the isolation of the alpine and arctic elements of the Mackenzie Mountain flora.

The time intervals are conjectural, but probably can be brought within reasonably definite limits. There is fairly good evidence that forests did not appear in the central Mackenzie basin until after the final retreat of the ice from Great Slave Lake and until after the last of the post-Glacial lakes in the Athabaska-Great Slave Lake region had been drained. Forests probably did not enter southwestern Mackenzie until the period of the climatic optimum, as late as 7,000 years ago. They can hardly have reached the higher, interior valleys and divides until somewhat later.

According to Hultén's theory the first aggressive floristic elements to invade the glaciated lands were the Arctic-Montane plants, and such parts of the Beringian and other groups as are supposed to have reached refugia south of the ice before the maximum advance. In both cases these plants were able to maintain large populations during the last great ice advance, and to maintain their genetic plasticity. The most plastic of all Hultén's groups, and certainly the most wide-ranging species, are among the Boreal Circumpolar plants, but since a very large proportion of this group is of forest species, it cannot be expected to show so high a representation in the Mackenzie Mountains as the arctic-alpine group.

Next to the Arctic-Montane plants in a decreasing scale of availability would come the Continental West American Radiants. These are thought to have survived in the Yukon valley and the northern Rocky Mountains, many of them below the ice boundary. Since they contain a large arctic-alpine element they can be expected to be well represented in the Mackenzie Mountains. Furthermore a part of their refuge areas are directly adjacent to the Mackenzie Mountains.

The various Beringian radiants of Hultén should be rather poorly represented, not only because many of them are thought to have lost their spreading capacity, but also because they, like other alpine elements, were eventually stopped by the advance of the forests. Another small part of the Mackenzie Mountain flora should be derived from the coastal radiants, for they could not be expected to spread far outside the habitats of the relatively warm and wet north Pacific shores. It is true that Hultén allows many of these coastal species to spread widely across the continent, but they are more southern types that would not be expected at high latitudes.

In Table 3 I have compared Hultén's floristic elements of the Brintnell Lake area in two ways. First the percentages of the total know flora which are derived from the various sources are compared, and second, the percentages of the total numbers of radiants (as revised) from the various sources that are represented in the mountains. Approximately the same results are reached by both methods. The Arctic-Montane group is present in largest numbers. Over 42 percent of all the plants listed in the group have been found at Brintnell Lake, and they make up about 35 percent of the local flora there. Next are the Continental Western American plants, and third, the Boreal Circumpolar group. The Beringian groups, taken together, and the western American Coast Radiants have each supplied only 8.1 percent of the flora. The most strictly coastal group set up by Hultén, of Atlantic-Pacific plants, is not represented at all.

It will be seen at once that these results correlate very well with the series expected on the basis of Hultén's theory. They lend considerable support to his general concept. It should be noted that the results from similar comparisons made with Hultén's unrevised figures are not far different from the above. The positions of the Boreal Circumpolar and Continental West American groups are reversed, but they are not far apart in any case.

Hultén's method of handling his data, however, leaves a great deal to be desired. The success achieved by him probably can be attributed to his perspicacity in "sensing" the geographic relationships of American plants rather than to an objective treatment of his information. This is best shown in his sorting of wide-ranging species into his several groups. It is virtually impossible, for instance, to say whether a wide-ranging arctic-alpine species should be placed among the arctic-montane, boreal circumpolar, or continental western American radiants. The equiformal progressive areas are clear so long as their individual plant ranges are relatively small. The larger ones disappear in the great "pools" of species whose ranges extend all the way across the continent. A few doubtful decisions of this sort would not be serious, but Hultén had to make hundreds of them in order to relate all the ranges to his equiformal areas.

With these difficulties in mind I have tried to sort the actual ranges of the species, so far as they are known, into natural patterns without regard to hypothetical centers of dispersal. Using the maps presented here and the genetic reasoning employed by Hultén, it is possible to arrange a sequence of floristic influences similar to that described above. The size

TABLE 3

	Hultén's totals (amended)	Found at Brintnell Lake	Percentage of total Brintnell L. plants	Percentage of Hultén's amended totals
Local plants, or plants of limited known range		12	4.2	
Beringia Radiants	248	23	8.1	9.3
Atlantic-Pacific plants	16	0	0	0
W. American Coast Radiants	267	23	8.1	8.6
Continental W. American Radiants	190	73	25.8	38.4
Arctic-Montane plants	235	100	35.3	42.6
Boreal Circumpolar plants	262	52	18.3	19.9
TOTALS	1218	283		

and character of existing ranges can be used as indicators of the success with which plants have migrated from the Pleistocene refugia.

Considering first the alpine flora, by far the largest single group (66 spp.) is derived from wide-ranging arctic-alpine plants—51.5 percent of the alpines, or about 23 percent of the total flora. These are the species that are thought to have maintained comparatively large populations during the Pleistocene, and to have been able to migrate during that time.

Second in extent of range are the species that have occupied wide areas in Alaska or the northern Cordillera or both, some of them extending eastward toward Hudson Bay (maps, Fig. 7A, B, C; Fig. 8). There are 49 of these—about 38.2 percent of the alpines. Finally there are 13 species of far northwestern range (map, Fig. 7D), only a few of which extend south of the 60th parallel. They comprise about 10.1 percent of the alpine plants at Brintnell Lake.

The plants of wide range on the mountains of Alaska, Yukon, British Columbia, and Alberta may well have had access to the large refuge of the Yukon Plateau and to possible refugia in the northern Rocky Mountains and eastern foothills, as well as to those of Beringia. The smallest ranges are those of the Alaskan species which were probably limited to Beringian refugia.

Nearly all of the forest plants at Brintnell Lake are derived from wide-ranging species in boreal America. I have already noted that only ten of the western plants represented are typically forest types. The Brintnell Lake forest flora is clearly derived from lands to the southeastward and has undoubtedly come up from the Liard valley. That of the central Mackenzie region, in turn, as I have suggested in an earlier paper, has probably developed from the amalgamation of populations that persisted through Late Wisconsin time in the East and in the valleys and foothills of the Rocky Mountains. All of these species could have maintained fairly large ranges during that time, and have no doubt increased their spreading capacity by subsequent fusion of populations.

ORIGINS OF THE BRINTNELL LAKE FLORA

By way of summary of the foregoing we may picture the Mackenzie Mountains as having been one of the latest montaine areas to lose its glaciers (remnants of them still exist). While the glaciers were retreating there was a period of time during which the lower slopes were tundra-covered, with the tundra more or less continuous across the neighboring valleys and to neighboring mountain ranges. The length of the period is problematical. There is some evidence, however, that forests did not come into the lower valleys until about 7,000 years ago, and that they did not cover the divides until somewhat later. In any case the tundra period must have been one in which arctic and alpine plants of all the northwestern refugia had open routes of migration to the Mackenzie Mountains. There is evidence that they availed themselves of these routes in differing proportions, depending first upon their broad habitat preferences, and second upon their inherent abilities to migrate. Their success at colonizing the mountains was conditioned also by the remoteness of the various refugia. Plants of continental habitat preferences were of course most successful; and of these the wide-ranging Arctic-Montane group were outstanding because of both accessibility and lack of biotype depauperation. Survivors in the Yukon valley and the northern Rockies were second in numbers, for they were only partially depauperated and were near at hand. Northern Beringian and Coastal radiants were next in importance, probably held in check by distance and lack of plasticity.

The process of alpine colonization appears to have been checked, at least for the Brintnell Lake region, before it had reached anything like completion. Evidence for this is to be found in the general paucity of species in the alpine plant cover. The "partial" nature of the flora is to be seen in all the common arctic families and genera. Such groups as Potentilla, Senecio, Arnica, and Pedicularis, all represented in surrounding regions by half a dozen or so species, have only 2 to 4 species each in the Brintnell Lake district. The colonization appears to have been stopped by the advance of forests into the surrounding valleys. These forests brought a new element to the mountain flora, derived from refugia south of the ice or on the slopes of the more southern mountains. Whether any of it came from the Yukon valley is uncertain. It was derived from Hultén's Boreal Circumpolar, Continental western American and possibly in part from his western coastal groups. In terms of range patterns outlined in this paper it was drawn chiefly from wide-ranging forest species and in part from the "timber-line" group. By nature it is aggressive, but probably shows so small a portion of the total Brintnell Lake flora as it does only because of the short time available for its invasion, and because of the subarctic situation of the Mackenzie Mountains.

GENERAL CONSIDERATIONS

I would be bold indeed if I were to attempt a detailed correlation of these geobotanical events with those in other boreal and temperate parts of North America. It is impossible, however, to resist the temptation to do a little speculating.

As I have said previously, there is good evidence that there were no forests in most of Alberta, northern Saskatchewan or Mackenzie until the last of the great post-Glacial lakes of the central Mackenzie basin were drained. Using Antevs' chronology, this did not occur until approximately the advent of the post-Glacial optimum, or toward the close of his "younger Late Glacial" period. Similar evidence indicates that there were no forests in the Saskatchewan River basin until Glacial Lake Agassiz had reached nearly the modern level of Lake Winnepeg. The latter event may have occurred somewhat earlier than the drainage of the last Mackenzie basin lakes, but Antevs places it also in the "younger Late Glacial." He suggests that the period of Lake Agassiz may have been 10,000 to 15,000 years in length, and that it corresponded to the period of ice recession from northern New England north to beyond Lake Timiskaming.

If these chronologies are reasonable then it seems necessary to recognize a wide gap in the continuity of the northern coniferous forest, beginning with the advance of the Mankato or Wisconsin$_3$ ice, and lasting at least until 7,000 or 9,000 years ago. The wide ranges of the forest species described in this paper must have been achieved since that time. In Mackenzie and Yukon we probably are seeing the last stages of this achievement, with the amalgamation of eastern and western relic elements, and the advance of newly aggregated forests into the mountain valleys and adjacent plateaus. When prairies were developing in Ohio, therefore, and when there was, we suppose, a warmer climate in southern New England, forests were just beginning to cover the upper Saskatchewan and southern Mackenzie watersheds, and the alpine areas of the Mackenzie Mountains still had floristic access to the Rockies, Coast Ranges, and the Arctic.

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