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BOTANICAL PROBLEMS IN BOREAL AMERICA. II

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THE DEVELOPMENT AND DISTRIBUTION OF PLANT COMMUNITIES

Introductory—Static and Dynamic Concepts

It has already been stated that the description of plant communities in boreal America has lagged far behind that of the flora. Sparse though it is, the available material may be divided into two categories, depending upon the point of view from which it has been presented: an earlier "static" view and a later "dynamic" one. Chronologically, the division should have occurred in the early 1900's when dynamic concepts in the study of vegetation were being developed by such men as Clements, Cowles, and Transeau. Scarcely any application of such concepts to boreal American vegetation was seen until 1923 when Cooper published his first paper on the Glacier Bay region of Alaska.[1]

Sir John Richardson prepared the first general description of vegetation types for our region ('51). He proposed 5 provinces in northern America each of which had "a peculiar physiognomical character" in its vegetation: the "eastern woodland" (with its northwestern extension), the "Barren Grounds," the "prairie slope," the "Rocky Mountain chain," and the "lower woodland country on the Pacific side of the range." He worked out the main features of the northern boundaries of many common forest trees, as well as those of many other plants. Similar pioneer work was done in British Columbia by G. M. Dawson ('81*a*, '88) and John Macoun ('77), and in eastern Canada by Robert Bell ('84), A. P. Low ('06), and J. M. Macoun ('96). Except for the addition of some details, no further outstanding contribution was made until the Preble expeditions to Hudson Bay and the Mackenzie basin ('02, '08).

[1] The plant communities of Greenland are far better known than those in much of the Arctic Archipelago or the boreal parts of the continent. Some of the more important papers dealing with them are by Warming ('88), M. P. Porsild ('01), Sørensen ('35), Gelting ('34), and Böcher ('33b).

Preble applied the life zone classification of Merriam ('95, '98) to much of western and arctic Canada, setting off as Arctic all the country north of the limit of trees. The northern boundary of his Hudsonian Zone reached from the valley of the Liard River to Great Slave Lake, with an extension down the Mackenzie valley to about lat. 65°. South of Great Slave Lake it followed the eastern rim of the Slave River valley, crossed Athabaska Lake, and extended southeastward so as to pass to the south of Reindeer Lake. Thence it turned eastward to James Bay. Both Hudsonian and Arctic, of course, reappear on the higher mountains in the Canadian Zone to the southward.

It is unnecessary to describe in detail all the general classifications of boreal vegetation that have been published. Harshberger ('11) returned to a concept not far different from that of Richardson, recognizing tundra, prairie, an eastern forest region (Great Lakes-St. Lawrence region), a subarctic coniferous forest, Rocky Mountain forest, and northwest coast forest. Richardson had noted the change in character of the coniferous forests northwest of the Lake Winnipeg, but had not set up a separate province for them. Harshberger correlated his entire subarctic, northern coniferous forest with Merriam's Hudsonian, thus greatly broadening the concept of the latter as outlined by Preble. Weaver and Clements' recent map is essentially that of Harshberger, so far as boreal America is concerned, except that their northern boundaries for the Lake Forest and the grasslands are not so far northward ('38). Rydberg, in his discussions of Rocky Mountain vegetation, used the Merriam classification as a point of departure ('13–'21).

The Merriam system was utilized in recent years by Harper in his studies east of the Slave River ('31). Here he attempted to set up a faunal subregion between the Canadian and Hudsonian of Preble, which he designated as the "Tazin Highlands." This is considered a part of the Canadian Zone, differentiated from the Hudsonian by the temperature factor, and from the rest of the Canadian by a complex of climatic and edaphic factors.

The extent to which the Merriam system will remain useful in boreal America is uncertain. Its weaknesses for the classification of plant communities are legion as has been shown by Livingston and Shreve ('21). To adjust it to a dynamic viewpoint is particularly difficult. Western biologists have maintained it as a working basis far more consistently than eastern students, probably because of the sharper biotic contrasts in the climatically and physiographically more diverse west. After sorting the whole flora of the Olympic Peninsula into life zones, Jones ('36, p. 17) found "that less than 5 per cent of the total number of species known to occur . . . show an anomalous zonal distribution." Jones has produced some illuminating results in his analyses of the floras of the Olympic Peninsula and Mt. Rainier by attempting a fusion of the Merriam system, Raunkiaer's classification of biological life-forms, and a dynamic viewpoint involving certain climax forest types in the Transition Zone ('36, '38). His comments on the Merriam-Raunkiaer combination are worthy of note: "The significance of the Raunkiaer system of life-forms as applied to the flora of the Olympic Peninsula is threefold. By means of this system a statistical analysis can be made of the flora of the whole region, or of the flora of each of the four life-zones taken separately. By whichever method used the results are comparable with the flora of other regions, and a simple but biologically sound summary of the phytoclimate thus can be obtained. As applied to Merriam's life-zones the Raunkiaer system yields valuable corroborative data. Merriam was concerned chiefly with the factors of climate which are effective during the season of growth and reproduction, whereas the Raunkiaer system is based on the adjustment of plants to the unfavorable, which is usually the dormant, season. By the application of both of these systems, a much clearer characterization of the life-zones or climatic formations may be obtained" ('36, p. 61). So far as the present writer knows, the application of such a scheme to any large part of boreal America has not been tried.

A recent and exceedingly useful map of Canadian forest regions has been drawn up by Halliday ('37). His basic scheme follows that of Weaver and Clements, recognizing three climax formations for Canada: tundra, forest, and grassland. The forests are subdivided into 8 regions or formations. "The recognition of such subdivisions is governed by the principles outlining the climax formation, and takes into consideration evolution and the relationship of species and genera. It is necessarily objective, indicating climate through the nature of the climax and reflecting it through the geographical position" (p. 6). A further subdivision into "Forest Sections" is "based on floristic considerations and the result of physiographic, edaphic, and local climatic conditions" (p. 11). Within the sections some effort is made to correlate probable successional trends with the general character of the forest. Halliday's work is of particular interest for two reasons: first, it involves a far greater volume of information on Canadian forest types than has ever been brought together; and second, the basis for classification, though still static in many respects, contains the idea of development both in local situations and in terms of broad geographic entities. Through his division of "Forest Regions" into "Sections," he has found expression, in the region west of Hudson Bay, for the boundary between Hudsonian and Canadian noted by Preble. This boundary is a striking one to any one travelling across it, and was unrecognized in the more general classifications.

Certain phases of a developmental concept are to be found in the writings of Richardson. He reported, for instance, some evidence of recent changes in the position of the arctic tree-line ('51), and must have sensed the instability of many arctic and subarctic plant communities. Preble ('08) described the development of flood plain forests along the great northern Rivers, and John Macoun ('77) has a vivid description of the delta vegetation of the lower Athabaska and Peace Rivers. But the theory of vegetational succession has only recently been applied to whole sections of the plant cover.

The dynamic point of view has been a part of the reasoning in floristic plant geography for many years, dealing with the problems of glacial and post-glacial changes of climate and terraine. If common ground is to be found for these two methods of approach, the plant communities must, like the floras, be analyzed in terms of age, stability, and their relation to the events of recent geologic time. The patterns of distribution noted above, which have engaged the attention of vegetational geographers for so long, require dimensions for time and analyses in terms of species potentiality if they are to appear in their true perspective.

The evolution of plant communities on bare areas involves migration, establishment, competition, and the consummation of systems of communal interdependence. Current theories of speciation and of the inherent abilities of species to accomplish these things must also be taken in account. The analysis of boreal American plant communities therefore presents an endless series of problems which are particularly intriguing because of the varying ages of the land surfaces and the probable varying potentialities among the species. Most of these problems are hardly more than sensed, much less stated and solved. Such beginnings as have been made in studies of the dynamics of boreal American vegetation will be summarized in the following pages.

Plant Formations of Boreal America

By far the greater part of boreal America is covered by two plant formations. The first of these is the Canadian coniferous forest, or Taiga, which extends from the Gulf of St. Lawrence to Alaska, and covers most of the slopes of the western mountains. North of this, and above it in mountainous country, is the formation commonly known as tundra. A third formation, of smaller areal extent, is represented by the natural grass lands of the central and southwestern parts of the Mackenzie basin which have their closest counterpart in the park lands of central Alberta and Saskatchewan.

The vegetation in all of this region was, beyond question, either completely destroyed by the Pleistocene ice, or highly modified if it managed to survive in unglaciated areas. It has acquired its present form, therefore, since the land surfaces of the north have become available, a process which has been progressive, and the sequence in which is still controversial. Except for the unglaciated areas, the sequence outlined by Antevs ('38) would place the oldest surfaces in the southeastern portion of our region, and the youngest in the Great Slave Lake country. Just how young the latter are is not yet known, but, as stated earlier in this paper, the matter is complicated by the great extent of post-glacial lakes. These lakes may have greatly reduced the interval available for the establishment of the modern plant communities. Likewise the effects of intense soil frost cannot yet be measured in terms of post-glacial time.

The Tundra. No adequate botanical descriptions, either floristic or phytosociological, of most of the treeless plains between the northern limits of forest and the arctic coast have ever been published. Many travellers have noted superficial differences among the types of vegetation to be seen in this vast area. There are moss and sedge tundra which are more or less wet throughout the year but there are also broad plains which are comparatively dry and covered with grasses and sedges. The region has been the principal grazing ground of countless caribou which still remain in enormous numbers.

Griggs ('36) has described the tundra in some detail in the Katmai district of Alaska, and has discussed the definition of the term "tundra" ('34*a*, pp. 157–9), showing that in a vegetational sense it is ambiguous, and should probably be used only in a geographical sense to cover all the vegetation of the treeless arctic. His discussion of Middendorf's concepts ('64) brings out the fact that the latter found some difficulty in differentiating, ecologically, the tundra and steppe of northern and central Asia. Similar problems will undoubtedly develop in boreal America. A more recent treatment of this question as it applies to Eurasia, and particularly in its historical aspects, will be found in a paper by Steffen ('38, pp. 177–95).

Porsild has published ('37*a*) a brief description of the tundra vegetation north of Great Bear Lake and west of the Coppermine River. He distinguishes first, heath associations over wide areas of rolling till-covered plain; second, meadows or prairies (of grasses and sedges) in the bottom lands between the low hills, "of greatest extent in the low alluvial plains bordering the Arctic ocean, west of the Anderson river, and in central Keewatin"; third, a sparse sand ridge type, relieved here and there by patches of green caused by manuring around ground-squirrel burrows; fourth, rock-face and rock-crevice types; and fifth, a rocky slope type. He considers that the meadows are "transitional," and are being invaded by the heath. Blanchet has also noted the contrast between heath and meadow types in the region northeast of Great Slave Lake, relating them to topography and soil ('26).

It is to be inferred from both Porsild's and Blanchet's descriptions, that the meadows are not necessarily stages in pond successions, but rather that many of them have developed upon relatively well-drained soils. Porsild suggests ('37*a*, p. 137) that "these plains were perhaps the last places to become available to plant life upon the recession of the Keewatin ice-sheet and the subsequent emergence of land from the sea and the draining of former lakes." Polunin has described some areas on Akpatok Island which are dominated by grasses, sedges, and other herbs ('34–'35). These occur in both xeroseres and hydroseres. Polunin also suggests that such vegetation is temporary, leading to a heath shrub type. Hultén describes a comparatively narrow "alpine meadow" zone on the Aleutian mountains ('37*a*, pp. 37–39). He says it is being invaded from below by subalpine shrubs and from above by heaths which cover wide areas. "The heaths are found on all exposed places, while the meadows occur in more sheltered valleys or hollows between the small hills, ridges or plateaus."

The areal extent of these various types of tundra is unknown. It is probable that they have some broad correlation with major natural divisions of soil, topography and climate. Polunin has shown the importance of solifluction in determining the development of vegetation at Akpatok ('34) but its relation to the distribution of vegetation over wide areas, with diverse soils and climates, is still to be worked out.

The Forested Region. Although the Canadian forest is similar in life form throughout its area, it varies extensively from east to west in species composition, and from north to south in general aspect. In the east it involves mainly the white spruce, *Picea glauca,* and the balsam fir, *Abies balsamea.* In the Rocky Mountains *P. glauca,* represented to a large extent by western varieties, is associated with another fir, *Abies lasiocarpa.* The coast ranges are characterized by the western hemlock, *Tsuga heterophylla,* Sitcha spruce, *Picea sitchensis,* and giant cedar, *Thuja plicata.* In the far north and northwest the forests are largely reduced to *Picea glauca* or its varieties. Dry soils in the east and in most of the central part are dominated by the jackpine, *Pinus banksiana,* while those of the northern cordillera are characterized by the lodgepole pine, *Pinus contorta.* Muskegs or bogs are everywhere characterized by black spruce, *Picea mariana,* and larch, *Larix laricina.* Throughout this region the only deciduous trees of consequence are the white birches, *Betula papyrifera* and its varieties, and the aspens and poplars, *Populus tremuloides* and *P. tacamahacca.* From south to north, in the central part of our region, while there is some modification in species composition, a very noticeable difference is to be found in the general aspect of the forests. In the southern part they are relatively dense, with a rich ground cover of mosses and ferns. Near timber line they become open and park-like, with very little undergrowth or groundcover. The latter often consist of lichens and trailing heaths. The local distribution of these various types within the Canadian forest gives rise to many problems. They are not easily arranged geographically, but seem to be interrelated in a complex manner due to present and past differences of soil and climate.

Within the forested region the most prominent vegetation boundary is coincident with the southern and southwestern margin of the crystalline rocks of the Canadian Shield. This was the boundary between the Canadian and Hudsonian life zones as laid down for the region west of Hudson Bay by Preble. To the east and north of the boundary the forest is greatly reduced in stature and density, and there are large areas of rock covered only by mosses, lichens, and such higher plants as can find space and soil in crevices and depressions. To the south and west the forests resemble superficially those of eastern Canada in having trees of good growth form, and a more or less rich cover of duff and humus beneath them.

In northern Alberta, northeastern British Columbia, and in the district of Mackenzie, these richer forests rest upon rocks of Paleozoic or Cretaceous age. Most of the Cretaceous rocks here exist in the form of erosion plateaus, isolated, or toward the southwestern part of the district, more or less continuous and forming the high plains of north central Alberta. The northern boundary of the continuous Cretaceous plateau marks another vegetational and floristic province. There are modified recurrences of it farther north on the isolated Cretaceous plateaus mentioned above. As noted previously, the more mesophytic, eastern Canadian forests are dominated by white spruce and balsam fir. As one passes northwestward through these forests the fir disappears at approximately the northern boundary of the Cretaceous plateau. Many other species also disappear in the same way, so that the far northwestern coniferous forest becomes greatly simplified in species composition, and the white spruce *Picea glauca,* becomes the most important tree except on very light soils or in muskegs. In the Mackenzie drainage basin the boundary of the Cretaceous plateau lies on the lower Athabaska and Peace Rivers. The balsam fir has been found in the Athabaska River delta, but north of this point it is extremely rare or nonexistent. Records of it are in the literature as reappearing on the Mackenzie and near the sixtieth parallel west of the Slave River, but neither of these records has ever been verified. Many of the species which disappear at the northern margin of the plateau are to be found far westward in the Rocky Mountains and some even northward in the cordilleran region to Alaska, but they have never been found in the comparatively simple forest of the lower and central parts of the Mackenzie basin (Raup, '30).

To the southwest the margin of the Cretaceous plateau continues to be a significant boundary, although with different species involved. Here a cordilleran influence is felt, with the northeastern extension of such trees as the lodgepole pine, *Pinus contorta* var. *latifolia,* and the balsam fir of the Rocky Mountains, *Abies lasiocarpa.* Many other characteristic cordilleran species accompany them.

The contrast in soils between the pre-Cambrian and younger formations is striking, and sufficient to account for such wide vegetational differences as occur. Edaphic differences between the Cretaceous areas and the lower, Paleozoic surfaces, most of which are till-covered, are not so clear. The present writer ('30) has tried to account for the absence or rarity of many species in the lowland and northern forests of the Mackenzie basin by postulating extreme immaturity in the forest communities and soils. "The most profitable line of inquiry appears to be in the edaphic factors of the environment, especially in so far as they are affected by the rigorous climate and the short time available since much of the vegetation had its inception" ('30, p. 207).

Further anomalies appear when the "simple" forests of the lower, northern country, both on Paleozoic and pre-Cambrian formations, are analyzed. The ultimate in simplification is reached in some of the jack pine woods on dry sandy soils about Lake Athabaska. Here is rather open timber whose trees are 70 years old or more, with a close ground cover of lichens. After careful examination of a large area only half a dozen vascular secondary species could be found; and there are whole acres whose only vascular plants are the pines.

The white spruce forests occur in three phases which are geographically rather distinct. On the great river flood plains the trees grow to large size (75–100 ft. high, 2–3 ft. in diameter), and in close, nearly pure stands. The undergrowth is relatively thick, but the ground flora is sparse, with a rather thin carpet of mosses. Stages in the development of this type are to be seen everywhere in the flood plain and delta country, and have been described in some detail (Raup, '35). Closely related to the forests on alluvial soils are those on the better drained glacial soils of the uplands. Here the stands are not quite so dense and the undergrowth is thinner. The ground is covered, however, with a mat of mosses and duff 4–8 inches thick. Some of these forests appear to have developed from a jack pine type (Raup, '33*a,* '35), but others may have come from a third kind of spruce wood. This third phase is quite different from the other two, and consists of an open, park-like stand of timber with practically no undergrowth. The ground is usually covered with a lichen-heath mat, and the soils are light and sandy. This type is best developed in the pre-Cambrian parts of the region, but representatives of it are occasionally met with in the country farther west and south. It is the spruce forest that appears at arctic timber line.

No specific differences among the spruces of the three types have been found. It is not impossible that there are some racial variations whose outward manifestations are physiological rather than structural. We have to deal, therefore, with a single species which forms and dominates, side-by-side in the same region, three different kinds of forest communities, all of them with different origins and stages of development. Here, apparently, is a wide range of tolerance in the white spruce, brought about by a system of controls and releases about which we know almost nothing. The species is not far from the margin of its range; and as Griggs has pointed out repeatedly ('14, '34*a,* '34*b*), the solution of many of our geographic problems may hinge upon more intimate knowledge of the behavior of plants under such conditions.

Working upon the hypothesis that there has been only an amelioration of climate since the land surfaces became available, the present writer has suggested ('33*a*) that the earliest post-lacustrine and post-glacial forests were of white spruce arranged in an open, park-like association similar to the third type noted above. With the warming of the climate and the decrease of ground frost the less tolerant jack pine could migrate into some parts of the country, where it could compete successfully with the spruce on the dry sandy soils. An increased growing season, more available moisture, and more rapid decay then permitted the accumulation of humus; and a forest succession was set up by which the spruce followed the pine again to form the second type. The youngest of the three is on the new flood plains at the lowest levels. Remnants of the original open spruce type still persist within the areas of the other two, on sites which the pine cannot invade due to local conditions. Some support for this concept is to be found in Pulling's studies of root flexibility among northern trees ('18).

Some evidence for the immaturity of boreal vegetation in the glaciated regions is to be found also in pond shore communities. During the writer's botanical exploration in the Athabaska-Great Slave Lake district, notes in more or less detail have been made on some 70 ponds. In the pre-Cambrian parts of the district 161 species of vascular plants were listed in these habitats. No less than 58 of them (36%) were put down as primary species in at least one association, and they appeared in 83 different associations within which they dominated. This lack of uniformity and continuity in the distribution of primary species is one of the most striking aspects of the pond vegetation of the region. The writer makes no pretense to having exhausted the possibilities, and he suspects that the examination of more ponds would only increase the number of combinations to be recognized. It looks as though the marginal communities of the ponds were just becoming aggregated out of migrating species. Even if a uniform series of pond habitats were available, a wide variability among the communities could be expected on this basis alone.

With such figures as those just given it has been impossible to set up any kind of successional series applicable to more than a very few ponds. The only organization of the data which has so far proved feasible is on a geological basis. There seems to be some correlation between the distribution of species and communities, and that of the major rock formations. In fact only 10 species could be listed in all of the geological divisions set up.

Subarctic Prairies. Another set of problems which has appeared in the study of the forested country pertains to the semi-open prairies which extend from the Upper Peace River far to the northeastward. They are known to occur throughout the Lower Peace River country, to have large extensions in the Wood Buffalo Park west of the Slave River, and are thought to have representatives on the northwest side of Great Slave Lake and west of the upper Mackenzie. These prairies have been studied in a few places on the Upper Peace River (Raup, '34), and in the southern part of Wood Buffalo Park (Raup, '33*b,* '35), but otherwise they are yet to be investigated. Their presence scattered through nearly the entire breadth of the forest zone is a somewhat anomalous situation, since the belt of coniferous forest is generally regarded as a climatic formation, and the general conditions of temperature and rainfall throughout the year suitable for the growth of trees. The influences determining the presence of this semi-open prairie country are, therefore, yet to be determined.

The "Chinook" winds of Alberta, northeastern British Columbia, and western Mackenzie create rather distinctive local climates in those regions (Raup, '34). They might be related to the occurrence of the prairies, although it can be shown that some of the prairies extend far outside the probable range of effectiveness of the "Chinooks" (Raup, '35). If these winds are to be effective in keeping down tree growth, the damage is probably done by winter-killing, since the winds are a feature of the winter climate. Local foehn winds have been noted elsewhere, such as on the north shore of Lake Athabaska, but their biological significance is unknown.

Certain essential facts concerning the prairies are: first, so far as they are known at present, they are confined to dark loamy soils of post-glacial lacustrine origin; second, they occur on land surfaces which have a fairly efficient surface drainage; third, the grass land seems to represent a virgin type of vegetation on the soils which it occupies, using the term "type" in a broad sense; fourth, aspen and occasionally spruce forests are slowly encroaching upon the prairies although in many places but little progress has been made; and fifth, grassland soils on the uppermost of the ancient lake bottoms show the most advanced (chernozem) development of soils (Raup, '34).

Floristically the prairies of the central and southern parts of the Mackenzie basin closely resemble those of central Alberta. But those still farther north appear to be different, involving fewer xerophytic grasses and more sedges. One of the most intriguing botanical problems in the north is the discovery of the floristic and structural relationship between these northern grasslands and those of the arctic tundra. Is there an unbroken series of transition types that will give us clues to the formation and history of all our prairies? And if so, what will be the evolution of soils under such a series?

It is suggested that the Mackenzie basin prairies developed as such directly upon the new soils exposed at the drainage of the post-glacial lakes, or that they followed some sort of tundra which in turn originated on these soils. (Raup, '34, '35.) At least two other interpretations might be advanced. It was originally thought that both the Peace River prairies and those of much of the park land of central Alberta and Saskatchewan were caused by fire. It was supposed that repeated burnings of the timber during dry periods kept the grass lands open. Recent studies by Moss, however, in central Alberta ('32) have shown that all of the aspen park land and the so called poplar belt have developed on dark soils which must have had their early history under grass land. Moss has shown that fire can be reckoned only as a deterrent in the development of timber on what were originally grass lands. A second interpretation involves a post-glacial warm period during which prairies may have pushed northward, to be later cut off by a deterioration of the climate. There is yet no other evidence in the region to support such a theory. The study of peat deposits may throw some light on it, but no remains of forests have yet been found in the prairie soils. It must be emphasized again that our post-glacial chronology for this region is not comparable with that of many other parts of the glaciated country, and that such a climatic optimum may have occurred before much of the present land surface was exposed.

Timber-line Problems

The position of the tree-line, its causes, and its possible fluctuations have been studied in a few places, and commented upon by many travellers. On the older maps it was shown by a fairly even line; but with increasing information the boundary becomes more and more ragged. There are long northward extensions down the valleys of the Coppermine, Thelon, Dubawnt, and Kazan Rivers, with isolated areas in the upper Lockhart basin and upper Back River valley, and in the country between Point Lake and Bathurst Inlet (Halliday, '37). Clarke has recently described its convolutions in the country east of Great Slave Lake ('40). Whatever its causes, the northern limit of trees is a biotic boundary of major significance, equivalent in its way to the transition from forest to prairie in middle latitudes.

Griggs presents rather convincing evidence that the timberline in Alaska is moving into the tundra: "(1) All the trees near the edge of the forest are young—less than 100 years old, whereas three miles back from the edge they exceed a meter in thickness and are over three hundred years old. (2) Many old trees now in a dense forest of younger growth are 'open ground' trees with branches, now killed by over-shading, clear to the base. (3) The rate of growth at the forest edge compares favorably with that of the same species, Sitka spruce, in southeastern Alaska many hundred miles behind the edge. (4) Records left by early Russian settlers explicitly describe as treeless, areas now covered with heavy forest. (5) Peat from the bogs contains only a few scattering grains of spruce pollen such as would be blown a long distance, thus demonstrating that the present is the first forest that has occupied the ground since the beginning of the bogs, *i.e.*, since the glacial period" ('34*a*, p. 163). Griggs also quotes Robert Marshall, who studied timberline conditions in northern Alaska, to the effect that the youngest, and outermost trees at the edge of the tundra have as good a growth rate as those many miles to the southward. Several other observers have reached similar conclusions for other parts of Alaska (see Griggs, '34*b*).

Using this apparently active advance of timberline as evidence, Griggs concludes that it is not now a climatically determined boundary in Alaska although timberlines generally are thought to be climatically fixed. He suggests that the timber is far behind an amelioration of climate that took place sometime ago, and is now finding no great difficulty in invading the neighboring tundra.

The northern forest boundary east of Hudson Bay has not been studied so extensively at any point as it has been by Griggs in Alaska. Nevertheless it is probable that here the line is retreating instead of advancing. Abbe has reviewed the scanty data on recent changes of climate in northern Labrador and Greenland ('36, '38), citing the excavations of old Norse colonies in the latter region (Nörlund, '24). There seems to be incontrovertible evidence that beginning in the latter part of the 10th century a deterioration of climate began in southwestern Greenland. It did not become serious until the latter part of the 12th century; but after that the Norse colonies rapidly declined under the influence of increasing cold, and finally perished. The present writer ('37) has gathered evidence from the fields of botany, zoology, paleontology, and archaeology which strongly suggests that there has been a deterioration in the climate of New England within the past 3000 years or less. Fernald found some indication of a retreat of coniferous forests at the Straits of Belle Isle ('11). It is therefore not unreasonable to expect that shifting of the tree-line in the east has been in the opposite direction from that in Alaska.

Between Hudson Bay and the Mackenzie delta, on the other hand, evidence of change is variable. J. B. Tyrrell, one of the keenest and most widely travelled observers ever to visit the north, could find no evidence of anything other than an amelioration of post-glacial climate in the regions east of Athabaska and Great Slave Lakes ('10*b*). He found many dead trees in the outer northern groves, but noted that most were alive. The absence of *Sphagnum* bogs in the tundra districts was used as evidence that forests had never grown there, since these bogs are now limited to the forested regions. Clarke has recently published what appears to be an exhaustive study of the timber line east of Great Slave Lake, and finds it relatively stable ('40). "Many traces can be found of clumps that have perished, leaving only bleached sticks to tell the tale, and there are others obviously new. On the whole there seems to be a very slight gain in these clumps more often than the contrary, and the writer believes that they are not sterile" ('40, p. 22) ; and "The Thelon must have looked much as it does now for hundreds of years, and similar climatic and physical conditions have prevailed for a couple of thousand years anyway" (p. 21). Clarke thinks that the line is now actually to be correlated with existing climatic phenomena, rather than by historical interpretation as Griggs found necessary in Alaska.

Richardson found evidence on the lower Coppermine River that the forest line was retreating southward ('51). This was mainly in the form of many isolated clumps of dead trees scattered over the "barren grounds," unaccompanied by any living ones. He made the significant observation that while the living clumps were confined to sheltered places, many of the dead ones were on exposed hillsides where they could have grown only if the climate were more congenial. Johansen has confirmed this observation ('19, '24), also maintaining that there has been a recent deterioration of climate. Porsild presents some evidence from the Mackenzie District, as follows: "We have no proof that the climate of the Mackenzie District is becoming colder or that the limit of perpetually frozen ground is extending downward, but we have botanical evidence favoring this view. On Richards Island, for example, 60 or 70 miles north of the present limit of trees, well preserved roots and stumps of a former spruce forest are found *in situ,* now covered with a peat deposit many feet thick. In peat deposits presumably of still greater age, on the east branch of the Mackenzie Delta, the writer discovered larch cones more than 50 miles north of the present range of this tree. *Potamogeton epihydrus* var. *Nuttallii,* discovered in the peat deposits in Pingorssarajuk, is not now found anywhere in the Northwest Territories.

"As regards recent botanical evidence, there are in the Eskimo Lakes basin isolated occurrences of several boreal or even temperate species such as the duck weed (*Lemna trisulca*), water arum (*Calla palustris*), yellow water lily (*Nymphozanthus variegatus*), sedges (*Carex norvegica* and *C. petricosa*), *Agoseris cuspidata,* pondweeds (*Potamogeton pectinatus, P. Friesii*), *Lappula Redowskii,* and several others that may be considered relics from a milder, postglacial period" ('38, p. 57).

To sum up, the tree line seems to be advancing in Alaska, retreating in northwestern Mackenzie, approximately stable in southeastern Mackenzie, and apparently retreating in eastern Canada.

The northern limit of trees is generally thought to be determined by climate, whether in an immediate sense or on a broader historical basis. Observers in the interior of the continent are agreed that exposure to cold dry winds, particularly those with a northern component, is a determining influence at the tree line: Porsild ('37*a*), Blanchet ('26, '30), Clarke ('40). Clarke thinks that outliers of timber are in part edaphically determined, growing in sheltered positions, on soils that are unfavorable to the tundra type. Just why the line should be where it is, however, is not clear. Blanchet has expressed the problem quite clearly: "It is difficult to conceive of a line drawn across a plain on one side of which trees grow while on the other they cannot. However, such a line does exist, modified by variations of soil and shelter. . . ." ('25). There is a rough correlation between the tree line and the July isotherm for + 10° C., as noted previously (Nordenskjold, '28), but Griggs has pointed out the rather serious discrepancies that appear when the matter is examined in detail ('34*a*, p. 161). According to his figures the forest is 250 miles below the isotherm on the Alaska peninsula, about on it in northeastern Alaska, nearly 150 miles north of it east of the Mackenzie, 350 miles south of it on the west coast of Hudson Bay, and nearly 400 miles north of it again in northern Labrador. Recent climatic maps (Brooks and Connor, '36) greatly reduce the discrepancy on the west coast of Hudson Bay, and eliminate most of it in northern Labrador.

Stupart ('28) has suggested that in northeastern Canada (Labrador Peninsula) the northern limits of trees and agriculture may be correlated with the position of the country in reference to the mean path of cyclonic storms. "Over all this region the prevailing winds have a northerly component in summer as well as in winter, this owing not to abnormally high pressure in the north, but to the fact that in all seasons the mean path of cyclonic areas lies to the southward of this region," and "In the northern portion of this northeastern territory there are vast tracts of land where the climate is so completely dominated by Arctic influences that the country is treeless and agriculture is impossible" ('28, p. 41). Maps of the tracks of cyclones have been published by Connor ('38) for boreal and north temperate America, and by Shaw ('36) for the circumpolar area. An earlier map of circumpolar storm tracks was published by Loomis ('85). So little is known, however, of the actual arrangement, both in time and space, of these major influences that to draw up such a broad correlation with the tree line as is suggested above would be hazardous.

A series of challenging problems should be found in attempted correlations between changing climates and vegetations on one hand, and on the other the migrations of aboriginal populations. Recent papers by Jenness ('33, '37) have described extensive migrations, among both northern Indians and Eskimos, during the Christian era. He divides the existing Canadian Eskimos into three groups: (1) those of the Mackenzie delta (and formerly of Southampton Island); (2) those on the treeless plains west of Hudson Bay; and (3) those of the arctic coasts from Coronation Gulf to Labrador. The first are considered to be descendants from an ancient ("Thule") people who migrated from Alaska "to the eastern Arctic about 1000 or more years ago, dropping colonies all along their route." The second group are known as the Caribou Eskimo, and are the remnants of a "second great reservoir of the race—the inland Eskimo, now shrunken to a fast vanishing pool." The third group, as it now exists, "flowed out of this inland reservoir about 1200 A.D., overwhelmed the earlier coast-dwellers, and in their new environment gained a fresh lease of life and vigor."

The Indians of the northwestern interior of Canada and Alaska are of Athapaskan stock. They have always been a race of non-agricultural, land hunters, having very little contact with the sea, but utilizing fresh-water fish. With but few exceptions they have stayed within the boundaries of the forested country. Jenness has outlined their migrations as follows: "If now we contemplate these late movements of the Athapaskans, and the distribution of their tribes at the opening of the historical period, we seem justified in assuming that at the beginning of the first millenium A.D. they were still massed in the northwest corner of the continent, but had already begun their southward trek. One division occupied the basin of the Mackenzie river to the edge of the Barren Grounds, where the lack of timber halted them, and perhaps also the hostility of the inland Eskimo. It was partly the lack of timber, too, that checked their expansion onto the prairies, for even in later times the Sarcee clung to the forest border until they obtained horses from the Blackfoot. Most of the migrants, however, did not cross the Rockies, but drifted far down the western plateau, travelling, like the early Navaho, in small bands of two or three families that here and there, in favorable localities, concentrated to form new tribes" ('37, p. 36).

Causes for these migrations have not been determined. Dr. Jenness suggests fluctuations in the supply of game, wars over tribal hunting grounds, and a sheer spirit of adventure. To anyone thinking in terms of vegetational change, the question naturally arises as to whether coincidences might be established between the two series of events. Two groups of people are involved, Indians and Eskimos, whose cultures have been closely related, respectively, to the wooded country and the tundra, and whose separation has been, from time immemorial, at the arctic timber line. Could it have been a northward movement of the forest border that started the inland Eskimo toward the coast about 1200 A.D., either by narrowing their hunting grounds or by increasing the pressure from migrant Athapaskan peoples to the south and west? Again, is it possible that the movement of Athapaskan Indians southeastward from Alaska was coincident with the actual arrival of forests in the lower Mackenzie region and the northern Rocky Mountains?

We are woefully lacking in vegetational chronology for the regions in question. About all that can be said now is that the timber line shows a tendency to fluctuate (at an unknown rate), and that the plant cover as a whole appears to be very "young" and "immature." Some evidence for the youth of the vegetation is noted elsewhere. It should be remembered that the time interval is not a post-glacial one, but rather a shorter, post-lacustrine period.

Aboriginal legend, unless it can be checked from other sources, is a notoriously unsubstantial basis upon which to build history. Nevertheless a few legends that involve changes of climate and biota in western Canada are worthy of note. David Thompson's Indian guides, while travelling with him through the Athabaska Pass in 1811, expressed a firm belief in the existence of the mammoth, a tundra animal, in that region ('16, p. 445). The Eskimo have myths and a word in their language for the mammoth (Jenness, '24). By far the most interesting story that has yet come to light, however, was reported by Mackenzie, in 1793. Mackenzie was at his winter quarters along the Peace River near the mouth of the Smoky, and one day interviewed an old Indian who tried to tell how old he was. "An Indian in some measure explained his age to me, by relating that he remembered the opposite hills and plains, now interspersed with groves of poplars, when they were covered with moss, and without any animal inhabitant but the reindeer. By degrees, he said, the face of the country changed to its present appearance, when the elk came from the East, and was followed by the buffalo; the reindeer then retired to the long range of high lands that, at a considerable distance, run parallel with this river" ('01, p. 143). It is hardly conceivable that this Indian was actually relating personal experience; but it is not impossible that he was drawing upon tribal history that was sufficiently recent to contain considerable detail. The change from tundra to grass land described by him in the Peace River region is precisely that which recent studies of the prairies suggest (Raup, '34, '35).

Ground Frost

Most of boreal America has a permanently frozen subsoil, the botanical consequences of which are far-reaching. Data on the depth to which the soil is frozen and the amount thawed each year are exceedingly meager. Harshberger ('28) and Cooper ('23, '37) have noted some features of the problem in Alaska, and the present writer has discussed some of the effects of frozen soils in the Mackenzie basin ('33*a*, '35). Porsild has noted that the ground in unglaciated parts of Alaska is not frozen to as great depths as it is in most of the north ('38). Pulling's studies in northern Manitoba ('18) are of particular interest because he attempted an actual correlation of the root-habits of trees with frozen subsoil. Porsild's investigation of "Pingoes" in western arctic Canada should also be noted ('38). Smith ('39) has a discussion of permanently frozen ground in Alaska in his paper on the areal geology of Alaska, with a map of localities from which data are available. There is also a map of the extent of Quaternary glaciation in Alaska (see also Capps, '32).

Light sandy soils may have no permanent frost in them, or they may thaw to great depths each year; while immediately adjacent, heavier soils remain frozen near the surface. The prevalence of muskegs or bogs in the north is due in many cases to impervious frozen strata beneath the surface. The wide-spread uniformity in muskeg floras may be ascribed at least in part to the abundance of such habitats. The maintenance of so much ponded water has undoubtedly served to retard the processes of erosion even further than they are already retarded by the shortness of the open season. Thus the maturing of stream drainage systems, even in comparatively friable materials, is slowed down; and all the resulting developmental processes in the vegetation are correspondingly slow. No measure of these retarding influences has been found, nor has it been possible to calibrate them in terms of past events.

Pulling has set up a classification of the common northern forest trees on the basis of their inherent flexibility of root-habit. Black spruce, tamarack and canoe birch are regarded as having a "rigid shallow root habit"; white spruce a "flexible shallow root habit"; balsam poplar a "deep flexible root habit"; and jack pine and white pine a "deep rigid root habit" ('18). Pulling suggested that the northern extent to which these trees might go was determined by their ability to live in soils made shallow either by frost or by the thinness of deposits over much of the Canadian Shield. The present writer has utilized the classification in accounting for some features of forest distribution in the Mackenzie basin ('33*a*); but a wider application of the idea, to embrace other elements of the woody flora, would no doubt prove worth while.

The difficulty of studying the rates of vegetational change in relation to stream erosion and deposition, previously discussed, applies also to lake and pond shores. The open season during which geomorphic processes can operate is much shorter than in more southern climates, and it differs greatly within the boreal region itself. We speak of the vegetation of the central Mackenzie basin as "young," perhaps "very young" if Antevs' theory of a late rejuvenation of the Keewatin ice is accepted and we take into account the length of time the post-glacial lakes occupied the country. But if the extreme slowness of decay, humus formation, and physiographic processes are considered, the "youth" may be a qualitative rather than quantitative concept. The development of vegetation in a subarctic pond, for instance, or on a receding lake shore, may be rendered so slow by the rigorous climate that the succession effective in more temperate regions are not applicable. It may be necessary to interpret the ordinary stages of development with time intervals so long as to extend over periods of climatic change great enough to change the facies of all the plant associations.

The effects of frost action upon surface soils were noted by Harshberger ('28) as a fruitful source of problems in arctic botany. Their significance in modifying plant communities in the tundra has also been suggested by Griggs ('34*a*). The most extensive studies in the American arctic, however, are probably those of Polunin at Akpatok Island, in Ungava Bay ('34–'35).[2] Here a large part of the surface of the island is characterized by "polygons" of limestone fragments or finer material which are so constantly churned by the action of frost as to be almost sterile of plant life. Only on the more stable portions can a handful of plants find a chance for survival. The geographic and historic meanings of this phenomenon have not been worked out. Although soil polygons and other evidences of intense frost action have been described in many parts of the arctic, yet their actual surface distribution is yet to be outlined and related to other geographic features.

Polunin gives a detailed structural description of the ones he saw, and reviews some of the theories advanced to explain them. It is quite obvious that they occur most abundantly in arctic and alpine climates, and that the availability of moisture and the occurrence of certain types of rock are important conditioning influences. Recent studies by C. S. Denny on central New England mountains ('40) indicate that "the factor which controls the development of stone-rings on mountain summits is the presence or absence of vegetation, provided that suitable rock basins filled with relatively fine debris (till) are also present . . . therefore stone-rings should be found on those summits which are treeless." Other studies on the New

[2] Investigations along this line in Greenland are described in papers by Sørensen ('35) and Seidenfaden ('31).

England Mountains by Antevs ('32) and Goldthwait ('39) have not only defined present day frost-action effects, but also larger "fossil" polygons and stone stripes. The effects of intense frost action have been found to be widespread in southern New England and adjacent New York (Denny, '36, '38; see also Bryan, '28), in regions now in temperate climate and under forest growth. That these last are "fossil" effects, dating from a time of treelessness and arctic climate, has not been conclusively proved though the evidence on the ground, as well as the studies by Denny noted above, point rather clearly in that direction.

From these facts it seems clear that in the arctic and alpine regions of boreal America the manipulation of surface soils by frost is now a phenomenon of considerable significance, and that it may have been significant over much of the country at an earlier time. Its effect upon modern arctic vegetation has been described by Polunin ('34–'35), who considers that this habitat on Akpatok Island is one of long-standing and may continue for a long time: ". . . the climatic, topographic and edaphic conditions on Akpatok are all very unfavourable to plant growth and have combined to keep the vegetation extremely scanty and reduced. These conditions have probably obtained much as they are today for at least one or two thousand years, and there is every reason to suppose that during most of this time the plant communities, being in the majority of cases too miserable to accumulate humus, have also remained substantially unaltered." Studies in temperate alpine regions also strongly suggest that vegetation is closely related to frost action; but here the point of view is reversed, and it is thought that the presence or absence of trees determines whether there shall be frost-heaving or not. Both views are probably correct, and there is a point in the transition between arctic and southern climates where vegetation can actually overcome the churning by frost and finally stabilize the soil.

Another suggestion that comes out of this field of inquiry is that in any historical-vegetational chronology we set up for the glaciated parts of our region, it may be necessary to insert an indefinite interval during which plants could scarcely make any headway at all. This would be the case particularly on soils and surfaces suitable for frost action. Polunin found it difficult to visualize any successional changes on most of Akpatok Island except those that had occurred when the land was first exposed at the retreat of the ice. He set up what he calls a "polygon subclimax" in order to place the vegetation in a hypothetical sere. Theoretically the polygons on Akpatok should eventually be reduced entirely to fine materials, but the vegetation that would then grow on them is conjectural.

In any case, one of the most fruitful fields for botanical research in the north should be this inquiry into the effects of ancient or modern frost action. The surface evidence of solifluction is not always easily recognized by the uninitiated. Consequently the fact that it has not been reported in a region does not indicate that it isn't there. Larger stone polygons are readily recognized but small, temporary stone-rings and stone-stripes, as well as the cumulative effects of small disturbances upon slowly moving slides will be recognized only with practice.

Other frost action phenomena, perhaps of lesser contemporary biological significance, are the "earth mounds" of the western arctic. These are so common and striking in appearance that there is a term for them in the Eskimo language: "Pingo," meaning conical hill. They occur, according to Porsild ('38), "On the otherwise low and featureless coastal plain . . . from Point Barrow eastward past the delta of the Mackenzie River to the first outcrop of rock east of the Horton River." Other mounds have been found on the Seward Peninsula and in the Kotzebue region of Alaska. Porsild has examined a great many in the field and has reviewed the theories advanced to explain them. Some, situated on sloping country where there are previous layers of gravel, may be due to hydraulic pressure. Others, in level country, appear to be "formed by local upheaval due to expansion following the progressive downward freezing of a body or lens of water or semifluid mud or silt enclosed between bedrock and the frozen surface soil, much in the way in which the cork of a bottle filled with water is pushed up by the expansion of the water when freezing" ('38, p. 55). The latter type always occurs "in or near the border of a lake or in the basin of a former lake," and has in the summit a crater-like depression the sides of which show the stratification of the lake bed in which the mound has been formed. Porsild has shown that these fractured and exposed surfaces are excellent places to collect peat samples which should yield valuable evidence of earlier vegetations and climates.

Peat Problems

A promising field of research in boreal vegetation is the study of peat deposits. Bowman has published the results of his pollen studies at Kodiak ('34), and Cooper has investigated the fossil forests at Glacier Bay ('23, '31*a*, '37, '39). Porsild has pointed out the possibilities of such studies in the lower Mackenzie region ('38), and Tyrrell has published valuable notes on the general distribution of peats in the country west of Hudson Bay ('10*b*). Erdtman ('31) has published the results of some studies in the peat bogs of central Alberta. It is safe to say, however, that the field is entirely open, and holds unusual promise as a source of major contributions in boreal American phytogeography. It should also be of value in the solution of many perplexing physiographic problems.

There are large islands in the western part of Great Slave Lake, near the entrance of the Mackenzie River, which seem to be composed entirely of peat. The lake waves have cut terraces in the peat that afford excellent sections from which to take samples. The origin of the deposits is conjectural. If our present concepts of lowering lake levels are correct, then it is possible that during the stages immediately preceding the present there was an immense bog in this western part of the lake which has been excavated by wave action as the water receded, leaving only a few remnants.

If peat analysis in the north is to be effective it must be done with a clear understanding of the physiographic problems involved. It should be remembered that the sequence of post-glacial geomorphic events is only sketchily known. In the Mackenzie basin an excellent starting point would be the existing theory of lake expansion and contraction, with the realization that at best this is only a working hypothesis, subject even to radical changes as new facts appear. Likewise it must be borne in mind constantly that our vegetation boundaries and climates are not stable, but have fluctuated widely in the past, with results which are yet obscure.

Methods and Concepts

Associations and Successions. The ecological description of boreal vegetation bristles with problems of method and concept. Analyses in terms of plant associations, or attempts to arrange the associations in seres, often become so complex and involved as to defeat their own purposes. Griggs, in trying to describe the arctic plant cover of the Katmai region in ordinary ecological units, found it hopelessly complex. "In the temperate zone vegetation is rather clearly segregated into more or less well-marked associations, like beech forests, oak forests, pine woods, swamps, and bogs. . . . When one goes to the arctic he naturally expects to find similar plant associations, but instead he meets a bewildering mixture of plants of all sorts jumbled together in seeming defiance of the principles of plant association learned in low latitudes" ('34*a*, p. 154). He stresses repeatedly the difficulty of setting up a group of associations with which to generalize over any large area, pointing also to the experience of Scandinavian botanists who have set up a multiplicity of associations to describe the occurrence of a very few species. (See also Faegri, '37*b*, for a recent review of European problems in this connection.)

The present writer has had similar difficulties in the forested regions of the interior. The necessity for describing three kinds of white spruce forest in the same district is anomalous in the light of our rather well-defined temperate types. Again, the failure to find any phytosociological basis for generalization among pond floras is an excellent example of the same kind of confusion. Polunin described thirty-odd combinations involving vascular plants on Akpatok Island, with a total vascular flora of only 129 species ('34–'35). He notes particularly the floristic uniformity of the vegetation mixture, and makes no attempt to outline communities until he has described a series of special habitats in which to look for them. A glance at the designations he uses for many of his communities indicates the difficulty he had in defining them: "Carex-grass-forb mat," "Dryas, etc. Fjaeldmark," "Dryas-Salix-herb polygon sub-climax," or just "Forbs." Hultén apparently found similar difficulties on the Aleutian Islands.

Griggs' ('34*a*, p. 174) conclusion is that "Each of the items contributing to the belief that arctic vegetation remains in a state of flux goes to indicate that the plants of the arctic, individually and collectively, are still far from equilibrium with their environment." He thinks that the arctic vegetation "has not yet recovered from the glacial period but is still in process of active readjustment." This is consistent with the writer's own findings in the Mackenzie basin.

Griggs reaches still another significant conclusion: that "a science of arctic ecology cannot be built up on the assumption that the place and mode of occurrence of a plant give reliable indications of its optimum habitat." Here he is in essential agreement with several other students whose work on relic species and communities is reviewed in this paper.

With so much confusion in the *content* of northern plant associations, their organization into developmental series, especially under the existing climatic and physiographic conditions, becomes equally obscure. The difficulties in working out the history of what look like comparatively simple seres on the shores of large northern lakes has already been discussed (pp. 23–4). Similar studies in ponds, alluvial deposits, and upland forest seres suggest that the successions are not conditioned so much by biological factors as by climatic and edaphic ones. That is, the presence of a plant association in a given place is dependent not so much upon the previous existence of another one which prepared the ground, as upon the availability of the ground itself and a suitable climate. For instance, it is suggested that the Banksian pine has invaded the park-like spruce forests because a lowering of the upper limit of ground frost made possible the penetration of the rigid taproot of the pine, rather than because the spruce had modified the soil so that it could be invaded. Competition assumes far less importance in the structure of communities under this concept than it does in more temperate regions.

If the ideas outlined above are accepted, then a central theme of the theory of succession, that of the "climax," becomes difficult of application in boreal regions. One would have to concede that in much of our region no true climax has yet developed in post-glacial time. If we continue to use a concept of climax, it must of necessity be entirely theoretical, or at least highly conditioned.

Polunin seems unwilling to discard the ideas of equilibrium, climax, and seral development, in spite of the troubles he had in defining them. His statement of the problem is worthy of quotation: "Over the exposed limestone plateau which constitutes almost the whole area of the island, the vegetation is so poor as to suggest that hardly any successional advances or even marked changes (except in a few favoured localities) can have taken place since the first colonization after the final ice retreat. Consequently it is to be presumed that the *Dryas* and other main communities now seen, although they may appear to be of almost a pioneer type, will persist at least for a very long time to come. Whether they resemble true climaxes or arrested (sub-climax) stages in an *autogenic main sere,* or merely pioneer or migratory *proseres.* the majority at least of these dwarf and meager plant communities which go to make up the vegetation of Akpatok appear to be in equilibrium with the present conditions and hence relatively stable" ('35, p. 196).

Cooper has been extraordinarily successful in establishing successional series in the Glacier Bay region of Alaska ('37). Here he has a clean-cut history of recent topographic change following the retreat of the glaciers, with an actual time scale covering a considerable part of it. Furthermore the climate of the region is conducive to relatively heavy forest growth. The analysis of plant communities and seral stages under such conditions becomes almost an exact science.

Although a time scale is not available, quite reasonable successional series can be worked out on flood plain and delta deposits in the northern interior (Raup, '35). Here the change is rapid enough to show some of the earlier stages by which the forests develop. Although Cooper can be fairly confident that the forests being produced on the older surfaces at Glacier Bay are parts of the regional climatic climax, it is doubtful if the northern interior forests can be so classified. The relative simplicity of the latter, both in flora and structure, together with their lack of uniformity, suggest that they have not yet reached the equilibrium of a climatic climax. If Polunin's concept is applied, however, with a somewhat broader interpretation of what constitutes a climax, then these forests might be regarded as actually in equilibrium with conditions in general, and could perhaps be called edaphic subclimaxes.

If recent or current fluctuations of the tree line are valid, then it may well be that an analysis of climax vegetation in the eastern arctic or subarctic would produce quite different results from one in the west. The instability and lack of organization in the Katmai vegetation described by Griggs may be replaced by relative stability in other parts of the arctic. Polunin has postulated a degree of stability at Akpatok Island, and Clarke thinks the forest line is stable in the Thelon region. Cooper has abundant proof of recent development at Glacier Bay, and the present writer finds evidence of unstable conditions in the Mackenzie basin.

Here the matter rests at present, with no well defined bases for generalization. Most of those who have attempted ecological description in boreal America are impressed with the difficulties in the delimitation of associations, the definition of what constitutes equilibrium in a region where associations are so poorly defined, and the reconstruction of seral development. Added to these troubles is the disturbing failure to adjust the distribution of many species to any climatic values that have yet been set up, and the evidence that northern plant communities may not actually be adjusted to known climatic features. Griggs goes so far as to suggest that some entirely new basis may have to be established before we can form a rational organization of arctic vegetation.

Floristic plant geographers have raised concepts of "conservative" and "aggressive," or "rigid" and "plastic" species; but we do not yet know how significant these categories will be when applied to the organization of plant communities. It has already been proposed that criteria of "species potentiality" will have to be used in this organization before common ground can be found between modern floristic and physiological plant geography. Ecologists have attempted to deal with the situation in the physiological terms of "ecological amplitude," but Cain ('39, p. 161) thinks that this may be conditioned by the age of the species and its relative "capacity for extending its range despite the availability of apparently suitable habitats." In a later paper ('40) he suggests that the biotype depauperation of a species by isolation is more significant than age in determining its capacity to extend its range. The existence of conservatism in species has been sadly lacking of proof, but the recent findings of geneticists (see pp. 61–62*a*) have set it up firmly as at least a good working hypothesis.

It is not impossible that if we are ever to understand the structure and development of boreal plant communities, with their complicated distribution of species and dominance, we will first have to learn where the species lived during the Wisconsin glaciation. Did they survive on large areas where they formed large populations in which their inherent variability could be maintained; or were they parts of limited populations which were depauperated of biotypes and reduced to a "rigid" condition? It is possible that the rôle of a species in the formation of a young boreal community may be determined as much by these inherent limitations as by the interaction of the multitude of external environmental factors.

Two phases of this matter must be borne in mind. First, if such a rating of potentiality for species is set up, we have to deal, not only with extremes, but also with a series of intermediate conditions depending upon the amount of depauperation that has occurred. Further, some populations that were reduced to uniformity under the influence of isolation during the Wisconsin may subsequently have managed to fuse with others and so to regain their potentialities. Second, the ordinarily accepted species set up by taxonomic criteria may not show the same abilities in migration, establishment, and dominance at different points. Races which show little or no structural peculiarity, isolated from their kind by the ice, may be conservative while larger populations have remained aggressive.

In connection with their studies of speciation, Clausen, Keck and Heisey ('40) make a comment which is significant here, although they do not go into the matter of conservatism vs. aggressiveness: "That modifications and heritable variations have been confused by many botanists is evident in the literature. There has been a paucity of evidence showing to what extent plants may be modified in different types of environment, and how modifications compare with heritable variations. These comparisons have been emphasized . . ., for such a study is fundamental to an understanding of plant interrelationships, and of plants in relation to their environment."

Concepts of conservatism, aggressiveness, and the history of the development of plant communities over long periods of time are to be applied not only in the classic approaches to boreal plant geography, but also in studies based upon the hypothesis of continental drift. It will be noted that the phytogeographic applications of the theory of continental drift are not discussed in the present paper. American students have done very little in this field, but recent papers by Steffen ('37, '38) in Germany serve to outline the current thought and research that touch upon it. E. V. Wulff's paper on an "Introduction to the historical geography of plants" ('32) should also be consulted.

With regard to recent changes of climate and their probable effects upon vegetation boundaries, there are some ecological aspects that need elucidation. As previously stated, Griggs believes that the present tree line in Alaska is not to be correlated directly with contemporary climatic factors, but rather that the forest has lagged behind the change in its favor, and is but slowly advancing to a position of actual adjustment. This idea of "lag" in development is not a new one in phytogeography. Cowles ('01, pp. 79 and 179) utilized it in his analysis of vegetation in the Chicago region, and Clements ('34) uses it in discussing the "Relict Method in Dynamic Ecology." Rübel ('35; see also Faegri, '37*b*, p. 430) has tried to reduce it to a factoral interpretation in his paper on "The Replaceability of Ecological Factors and the Law of Minimum." Hutchinson ('18) has suggested that the deciduous forests of Ontario have lagged behind climatic changes in their movement northward, and await the further development of soils suitable to them. The present writer has postulated somewhat similar conditions in the central part of the Mackenzie basin ('30), and has suggested also that the forest boundaries in southern New England have shown a tendency to persist after climatic changes have occurred ('37).

The fundamental issue has been stated by Deevey ('39, p. 719), in his discussion of the writer's studies in southern New England: "The concept of widespread and long-continued persistence of forests not adjusted to the prevailing climate logically leads to a negation of ecological theory, and Raup's hypothesis must be construed to include only local areas of relic vegetation." If ecological theory postulates the continued adjustment of vegetation to climate, then Deevey is right; but if the interpretations set forth in the preceding paragraphs are correct, we must postulate conditions wherein vegetation is very often *in process* of adjustment, and actually existing with only partial adjustment. That such conditions need not be local is shown by the large-scale fluctuations of the tree line.

It should be noted in this connection that Hultén arrived at similar conclusions on climatic adjustment in his study of the boreal distribution of species ('37*b*). In fact the idea is inherent in the persistence hypothesis which has been discussed elsewhere in this paper.

Vegetation Mapping. The mapping of vegetation from aerial photographs should yield more useful results than it has to date. Large sections of northern Canada have now been photographed, and maps made showing the general topographic features. The pictures have been made at oblique angles, and from comparatively low altitudes. The writer has demonstrated that vegetation can be mapped in considerable detail from these photographs provided adequate ground studies have been made in selected places (Raup

'35). The maps prepared by the Topographical Survey of Canada, while remarkably accurate, do not have enough detail to serve as bases upon which to put all the vegetational information that can be gained from the photographs. The writer found it necessary, therefore, to construct his own maps from the photographs, with a scale of 4 inches to the mile. A minimum of ground work consists of a series of transects selected so as to cut most of the recognizable types of vegetation. The sites of transects can be located with great accuracy on a photograph and become the "base-lines" or standards from which the whole photograph is analyzed. It is essential to know the time of year in which the pictures were made, since the aspects of the various plant associations change materially during the growing season.

Life-form Classification. Life-form classifications, either on biological or physiognomic bases, have never been made for the boreal American floras except in the arctic. Raunkiaer ('08) published "biological spectra" for many parts of arctic America and Greenland in his classic paper on "The Statistics of Life-forms as a Basis for Biological Plant Geography." His figures were derived from such published lists as were available at the time, and consequently many of them are open to criticism on account of their incompleteness. The only local flora in arctic America that could then be considered well known was that of Ellesmereland (Simmons, '06). It has already been noted that the floras of most of the other regions of the arctic had been only partially collected and studied; and due to the circumstances under which the pioneer work was done the resulting lists very often failed to give a balanced representation of the plant life. If the Raunkiaer system of classification is to be tested thoroughly for boreal America, therefore, much more detailed work is needed in the light of recent floristic studies. This has been well begun by Gelting ('34), and Böcher ('33) in Greenland. So far as the writer is aware, no purely physiognomic system has been applied in our region.

As previously stated, Jones ('36, '38) has made some useful correlations, in western Washington, between the Raunkiaer system and the Merriam life-zone classification. The application of some system of life-form studies to such plant communities as are recognized in boreal America has not yet been tried. The same complicating historical factors that have conditioned the development of the flora and its arrangement into communities must also be taken into consideration when life-forms are analyzed for their geographic significance. No one has tried to correlate life-form with relative conservatism or aggressiveness.

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