THE BOREAL LIMITS OF CONIFERS*

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THE expressions "forest-limit", "timber-line", or "tree-line" are all somewhat vague and difficult to define, and for the same reason it is not always easy to plot them accurately on a map. In the sense employed by North American writers, "timber-line" may mean the limit of commercially profitable forest utilization, the limit of forest in a biological sense, or simply the limit of trees. Sometimes it is not even easy to determine "when a tree is a tree".

Figure 1 shows the idealized trend of the different tree- and forest-limits. The local trend of these lines is similar whether near the polar, maritime, or altitudinal limit of trees. The principal difference being that as we approach the subarctic sea, or the vertical limit of trees, the lag between the vanguard of trees and the actual limit of continuous forest is slight, whereas in continental regions it is often very great. To understand the diagram, the following definitions may be helpful.

By "economic limit of forest"(I) is meant the limit beyond which commercial cutting of trees endangers natural afforestation. It is more or less what the past generation of Finnish foresters meant by the "*suojametsärajä*" or "*skyddsskogs*"-limit and also, at least in part, the "generative" forest-limit of Kihlman-Kairamo (1890) and the "effective" forest-limit of Sernander (1900) or Heikinheimo (1921).

By "biological limit of forest"(II) is meant the limit of continuous forest. In subsequent discussion this will be referred to simply as the "forest-limit". It corresponds to the "vegetative" and "empirical" forest-limits of Kihlman-Kairamo and Sernander.

By "tree-line"(III) is meant the absolute polar, maritime, or vertical limit of a given species in tree-form. The definition of what is meant by "tree" varies with different authors. According to some European writers a tree must be at least 5 metres high, whereas for subarctic regions Heikinheimo (1921) suggests 2 metres, providing that its trunk projects above the maximum snow cover of the locality.

The expression "polar tree-line" combines the most northerly limit of the

*This article is based on a paper which was published in Swedish in *Communicationes Instituti Forestalis Fenniae*, Vol. 40 (1952) pp. 1–20. Because this information was not readily available in English Dr. Hustich undertook to rewrite his paper for *Arctic*. Minor differences between the present maps and those published in 1952 are due to changes kindly suggested by E. Hultén (in a letter) [*Larix laricina* and *Abies lasiocarpa* in Alaska–Yukon; *Larix dahurica* on the lower Lena, and *Abies gracilis* in Kamchatka]. The writer also wishes to thank his friend, A. E. Porsild, Chief Botanist of the National Museum of Canada, who kindly edited the present paper, and suggested minor corrections to the maps.

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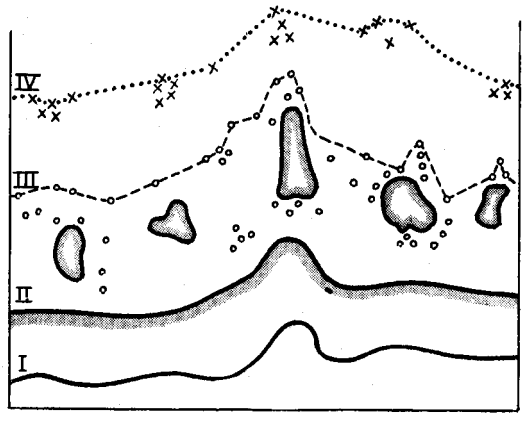

Fig. 1. Idealized trend of tree- and forest-limits: (I) Economic limit of forest; (II) Biological limit of forest; (III) Tree-line; (IV) Limit of species.

tree-like species of any forested area; it follows, therefore, that the polar tree-line in different areas may be formed by different species of trees.

By "limit of species"(IV) is meant the line of most advanced outposts attained by a species northward, seaward, or in a vertical direction, irrespective of whether growth is prostrate, ascending, or tree-like. Not infrequently the "tree-line" or "*Baumgrenze*" in the written accounts of explorers proves to be identical with the "limit of species", rather than with the "tree-line" in the sense given above.

Between the limit of species and the forest-limit is a transitional zone of varying breadth in which isolated trees as well as clumps of trees, or even small or large "islands" of trees, may occur. This transitional zone has been called "forest-tundra" and is the "*lyesotundra*" of the Russians. It may attain a breadth of over 100 kilometres but, especially in maritime regions such as for example the Atlantic coast of Labrador, may be replaced by scrub forest (Hustich, 1939). In my opinion the forest-tundra zone (ecotone, *sensu* Marr, 1948) phytogeographically constitutes the Subarctic proper, and the polar tree-line therefore represents the southern limit of the Arctic. In Rousseau's (1952) terminology, the forest-tundra is called "*zone hémiarctique*", whereas the northern spruce forests which were called "open boreal woodland" by Hare (1950) or taiga by Hustich (1949), according to Rousseau form the "*zone subarctique*".

The so-called "subalpine regions" or plains of northern Finland, Norway, and Sweden, which are dominated by alpine birch forest, should really be considered forest-tundra, being a direct continuation of the forest-tundra of the Kol'ski Poluostrov (Kola Peninsula). The word "subalpine" should, at any rate, be restricted to mean the vertical zone between the continuous evergreen forest and the alpine limit of trees, whereas the largely unforested Fennoscandian plateau is, in fact, a subarctic region in which scattered "islands" of forest and isolated trees occur.

Among the different "limits" discussed here, the "limit of species" is the one most easily mapped because most phytogeographers and foresters, who have visited the arctic and subarctic regions, have noted the outposts of tree species.

Figures 2–5 are mainly drawn from information contained in a number of published papers of which the more important are given in the list of references, and only in the Labrador-Ungava Peninsula, Hudson Bay region, and northern Fennoscandia has my own experience been incorporated (Hustich, 1939; 1948–50). It should be noted, however, that in some parts of the Arctic the northern limit of forest is not well known, and the lines shown are sometimes tentative. I wish to express my gratitude to Dr. Eric Hultén, who some years ago gave me sketch-maps showing the trend of the polar forest-limits in Eurasia. In the course of preparation of the present paper these sketch-maps have been brought up-to-date where needed. The polar limits for conifers in Fennoscandia are based on Hultén's atlas (1950).

Figure 2 shows the polar limit of the genus *Picea* (spruce) including *Picea Abies* (L.) Karst. (=*P. excelsa* Link), *P. obovata* Ledeb., *P. glauca* (Moench.) Voss., and *P. mariana* (Mill.) BSP.; the northernmost outposts in Alaska for *P. sitchensis* (Bong.) Carr are shown also. The genus *Picea* is, next to that of *Larix* (larch), the most important in the polar forest regions, although in Fennoscandia, this is not the case except in the Kol'ski Poluostrov.[1]

The specific status of the Siberian spruce, *Picea obovata*, has been questioned by Lindquist (1948) who thinks it should be called *P. Abies* var. *obovata* (Ledeb.) Fellman, whereas Russian taxonomists always consider it distinct. At any rate, the two species undoubtedly intergrade between the Kol'ski Poluostrov and the Pechora. I wish to call attention here to the striking similarity between *Picea obovata* and *P. glauca* in northern stations, where both species have short cones, rounded cone scales, and where the young twigs of *P. obovata* and *P. Abies* are sometimes glabrous.

Possibly future forest taxonomists will have to work with a circumpolar collective species of spruce, composed of *P. glauca* as ssp. "*americana*" and *P. Abies* as ssp. "*eurasiatica*" with the races var. "*europaea*" and var. "*obovata*"!

In North America, on the other hand, we have two clear-cut species, namely white spruce (*Picea glauca*) and black spruce (*P. mariana*). Although both have approximately the same northern limit, they are well separated taxonomically as well as ecologically. In forestry publications it is customary to designate the black spruce as the hardier of the two, but this is erroneous, at least in the Labrador-Ungava Peninsula. White spruce definitely ranges beyond black spruce near the maritime subarctic forest-limit in the Hudson Bay region, along the Atlantic seaboard, and in the interior of Ungava (Hustich, 1949; 1950). Where the two species occur together under extreme conditions, they may superficially be alike, although the annual shoot of the white spruce is always glabrous, while that of the black spruce is hairy. In exposed situations where black spruce occurs only as a prostrate shrub with abundant

[1]Although I have not been able to check Pachtusov's original record, it is of interest here to revive Middendorff's observation (1864, p. 543) that spruce was reported on Novaya Zemlya by the Russian navigator Pachtusov in 1842, who also recorded *Juniperus*, stating that the prostrate spruces he saw were even smaller than the dwarf birches growing on the island. "Wäre der Gewährsmann nicht von so erprobter Zuverlässigkeit, so hätten wir das Recht an dieser kaum glaublichen Mittheilung zu zweifeln, weil Nowaja-Semlja für baumlos gilt".

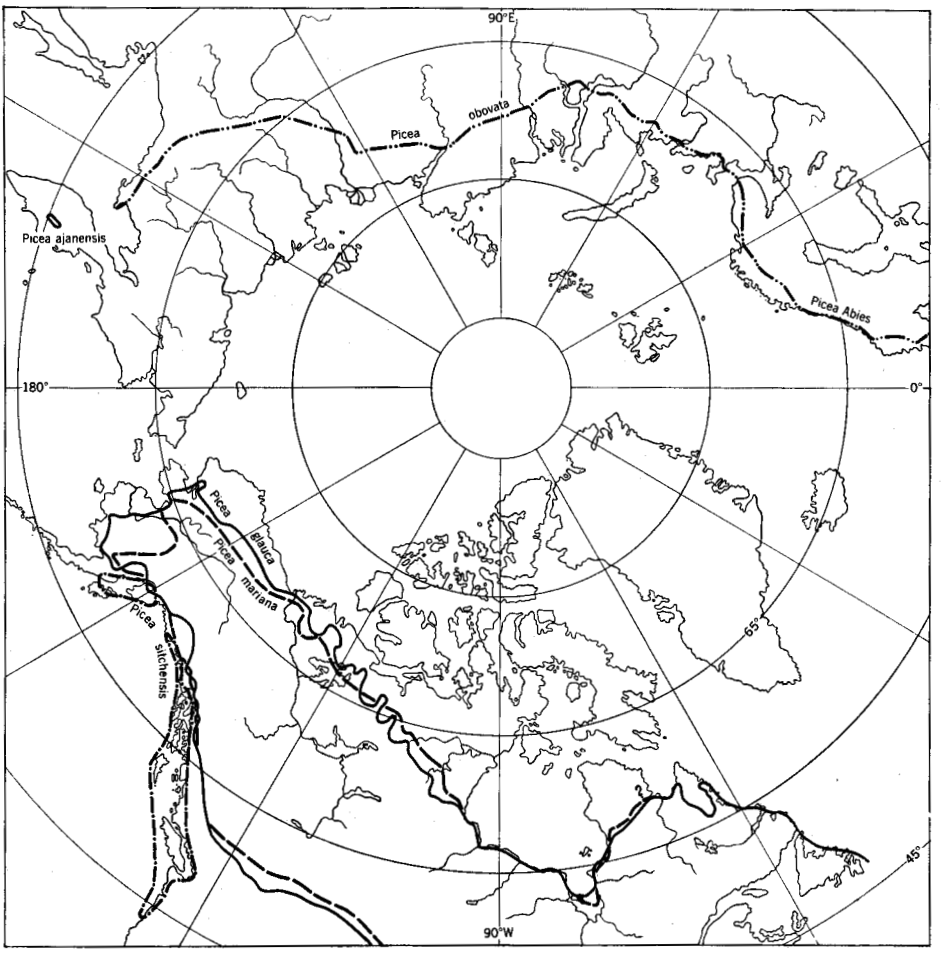

Fig. 2. The polar limits of the northern species of the genus *Picea*.

vegetative reproduction, the white spruce is tree-like. Farther south black spruce usually grows in acid bogs or muskegs, whereas white spruce grows on well-drained and generally richer soils. Both species may form extensive, uniform spruce–lichen forest, as may also the Siberian spruce near Noril'sk (Dedov, 1933; Hustich, 1951). While black spruce reproduces abundantly by layering, this is almost never the case with white spruce.

In *Picea glauca* two races occur in western Canada, namely *P. glauca* var. *albertiana* (Brown) Sarg. and *P. glauca* var. *Porsildii* Raup. In the area adjacent to Great Slave Lake and Mackenzie, Raup (1946) reported that *P. glauca* var. *albertiana* meets with a main species. Judging from the description, var. *albertiana* is not limited to western Canada and may prove to be a northern race of *P. glauca*. For this reason its northern limit has not been shown specifically in Fig. 2. *P. glauca* var. *Porsildii* (Raup, 1947) is the dominant spruce on alluvial soils in the Mackenzie Valley where it extends north to the Delta (Porsild, 1951).

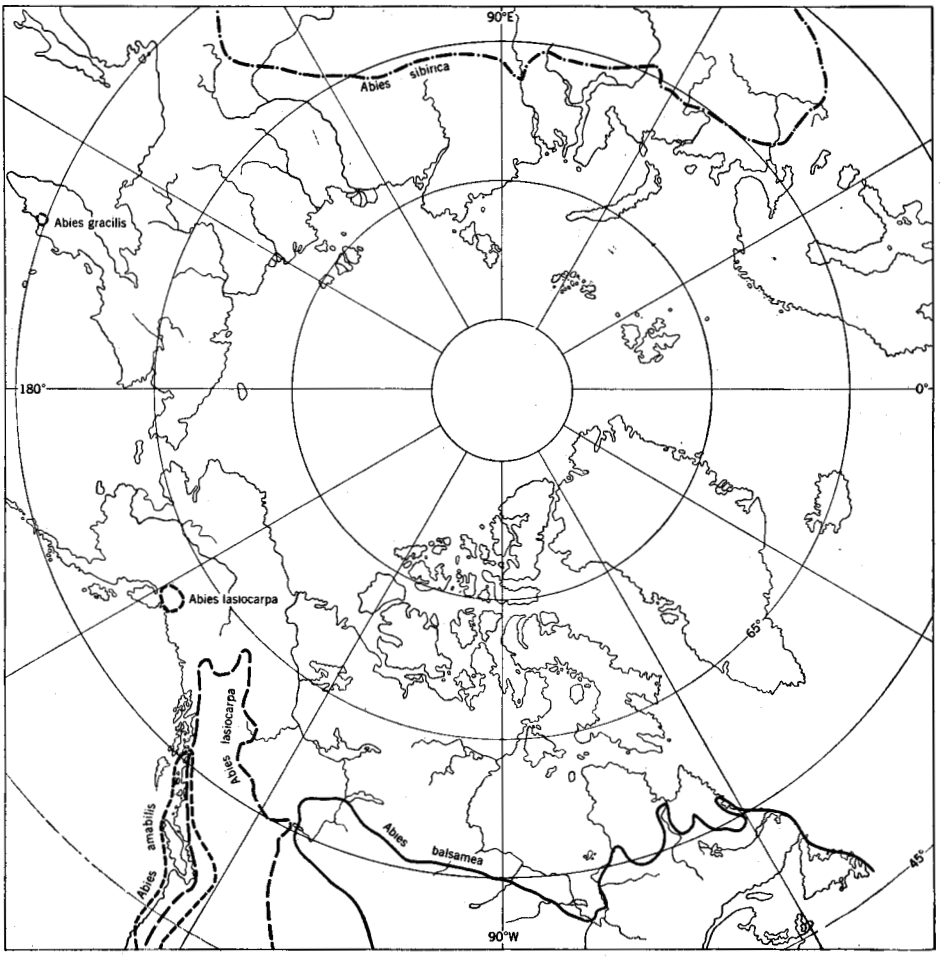

Fig. 3. The polar limits of the northern species of the genus *Abies*.

The genus *Abies* (fir) reaches the polar forest-limit only in Labrador along the Atlantic coast, extending almost to Ungava Bay (Fig. 3). Alaska, too, has a species of *Abies* but, otherwise, representatives of this genus reach only into the middle part of the taiga and are poorly represented in the northern parts of the evergreen forest.

The Siberian fir (*Abies sibirica* Ledeb.) is widely distributed in the Siberian taiga and in the valley of the Yenisey where it extends well beyond the Arctic Circle (Middendorff, 1864; 'Flora U.R.S.S.', 1934). It is a pronouncedly continental species with a range similar to that of *Pinus sibirica* (see Fig. 4). Ecologically, as well as in its ability to reproduce by layering, the Siberian fir simulates the balsam fir of Canada.

In Canada, *Abies balsamea* (L.) Miller ranges from the eastern slope of the Rocky Mountains to the Atlantic coast but is not as continental as *A. sibirica*, and is found on the islands along the Atlantic coast of Labrador where it enters the forest-tundra zone, without, however, reaching the polar tree-line.

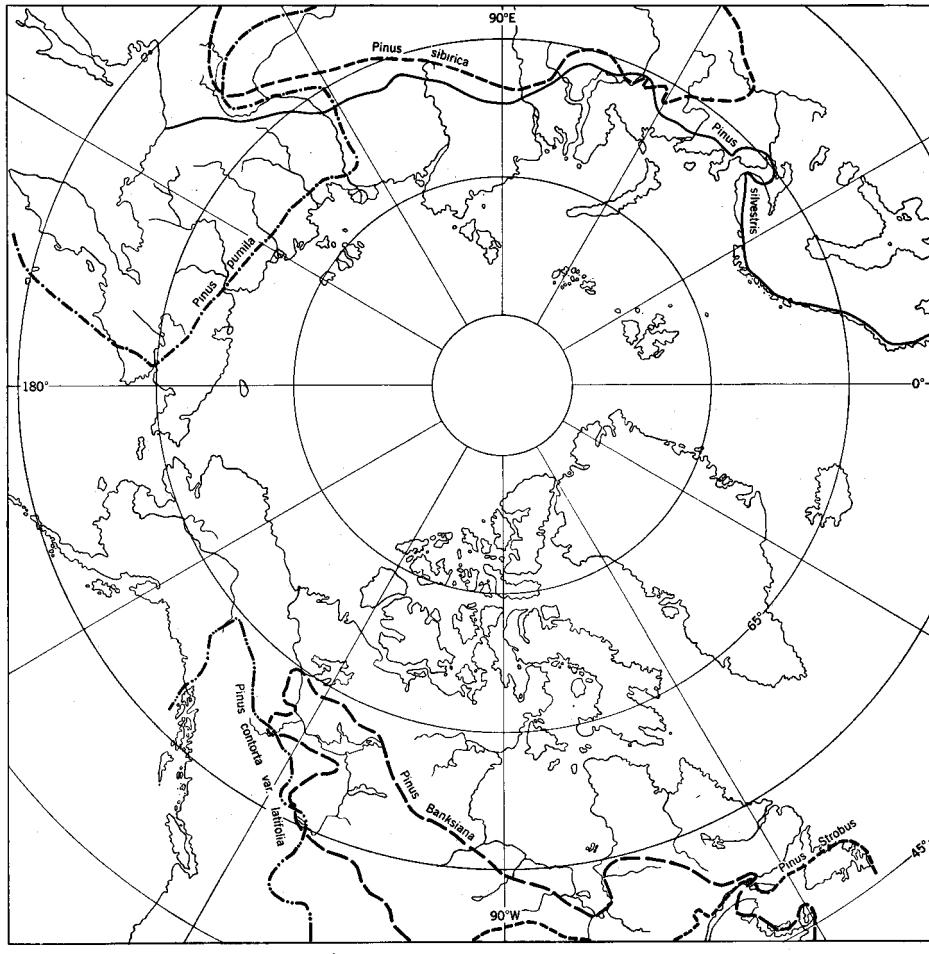

Fig. 4. The polar limits of the northern species of the genus *Pinus*.

The Cordilleran alpine fir, *A. lasiocarpa* (Hook.) Nutt., in the Yukon, ascends to 2,000 metres above sea level (Porsild, 1951) but does not extend into the polar forest-tundra.

Figure 4 shows the polar limit of the genus *Pinus* (pine) of which only *P. silvestris* L. and *P. pumila* (Pall.) Regel enter the forest-tundra region, while *P. sibirica* (Rupr.) Mayr, *P. Banksiana* Lam., and *P. contorta* Loudon var. *latifolia* Engelm. merely approach the polar forest-limit.

A remarkable feature of the Scandinavian polar tree-line is that the pine is the dominant conifer. Why spruce appears south of the pine west of the Kol'ski Poluostrov has caused much speculation among Scandinavian and Finnish forest-scientists. Some believe that the cause may be historical, i.e., due to ancient forest fires, others that it may be climatic. In North America the pine does not reach the subarctic seaboard either in Labrador or in Alaska.

Scotch pine (*Pinus silvestris*) occupies a large area, reaching from the Atlantic to the Sea of Okhotsk, although the pine which occurs in the eastern

part of this area is distinguished by Sukatschev as *P. silvestris* var. *jakutensis* Suk. The isolated populations of Scotch pine in the northernmost valleys of Norway are of great interest from a forest-genetical point of view, and deserve close study. They are the Scandinavian counterparts of the isolated "islands" of forest which occur elsewhere in the Subarctic.

P. sibirica, the Siberian cembra pine, is of continental range although recently two isolated stations (not shown in Fig. 4) have been discovered in the Kol'ski Poluostrov (Hultén, 1950; Nekrasova, 1951). At present it is not possible to determine whether these isolated occurrences are spontaneous. According to the reports of early travellers the seeds of cembra pine were formerly an important trade article and so much in demand that this pine was almost exterminated.

The Siberian dwarf pine (*P. pumila*) has a remarkable distribution. In eastern Siberia it attains a higher latitude than that reached by pines elsewhere. Its ecology is very similar to that of *P. mugo* (*P. montana*) of the European Alps, although *P. pumila* belongs in the section *Pinaster* whereas *P. mugo* belongs in the section *Strobus*. *P. pumila* forms the polar limit of conifers in the Kolyma and Anadyr regions, but never reaches tree-size. Its distribution is included in Fig. 4. Its history and ecology have recently been investigated by Tikhomirov (1946) who points out that the species is "phytocenotically extremely strong", and a primary species wherever it occurs. According to Porsild (1939) *P. pumila* does not occur east of Bering Strait.

Jackpine (*P. Banksiana* Lam.) is the commonest pine of the boreal zone in Canada. It is a continental species reaching the sea coast only along the north shore of the Gulf of St. Lawrence and in Nova Scotia whereas the pine occurring in Newfoundland is the eastern white pine, *P. Strobus* L. The peculiar range of the jackpine in the Labrador-Ungava Peninsula is difficult to explain. One theory is that the species has not reached its climatic limit in the northeast. It should be noted that the cones of the jackpine open only after forest fires or during periods of exceptionally hot weather. Another interesting feature is that the jackpine, near its northern limit in Ontario near the Mattagami River (Smoky Falls), seems to grow taller than it does near its eastern and northeastern limit. In western Canada, jackpine reaches the Mackenzie Basin where it meets the lodgepole pine, *P. contorta* var. *latifolia*; but the range of neither extends into the forest-tundra.

Figure 5 illustrates the polar limit of the genus *Larix* (larch). For the Eurasian species I have followed Dylis (1948) who divides the Siberian larch into two species, *Larix sibirica* Ledeb. *s. str.* and *L. Sukatschewii* Dylis of which only the latter reaches the Kol'ski Poluostrov (Zinserling, 1935). Judging from the description, *L. sibirica* appears to be a non-aggressive species, restricted to shores of rivers and lakes, mountain slopes, bogs, and similar places (compare Sambuk, 1930), and the same may be true of *L. Sukatschewii*. It is interesting to note how closely Sambuk's description of the behaviour of the larch in the Pechora region parallels that of *L. laricina* in eastern Canada.

Larix dahurica Turcz., on the other hand, is an aggressive species which forms extensive forests in the eastern Siberian taiga, and entirely dominates

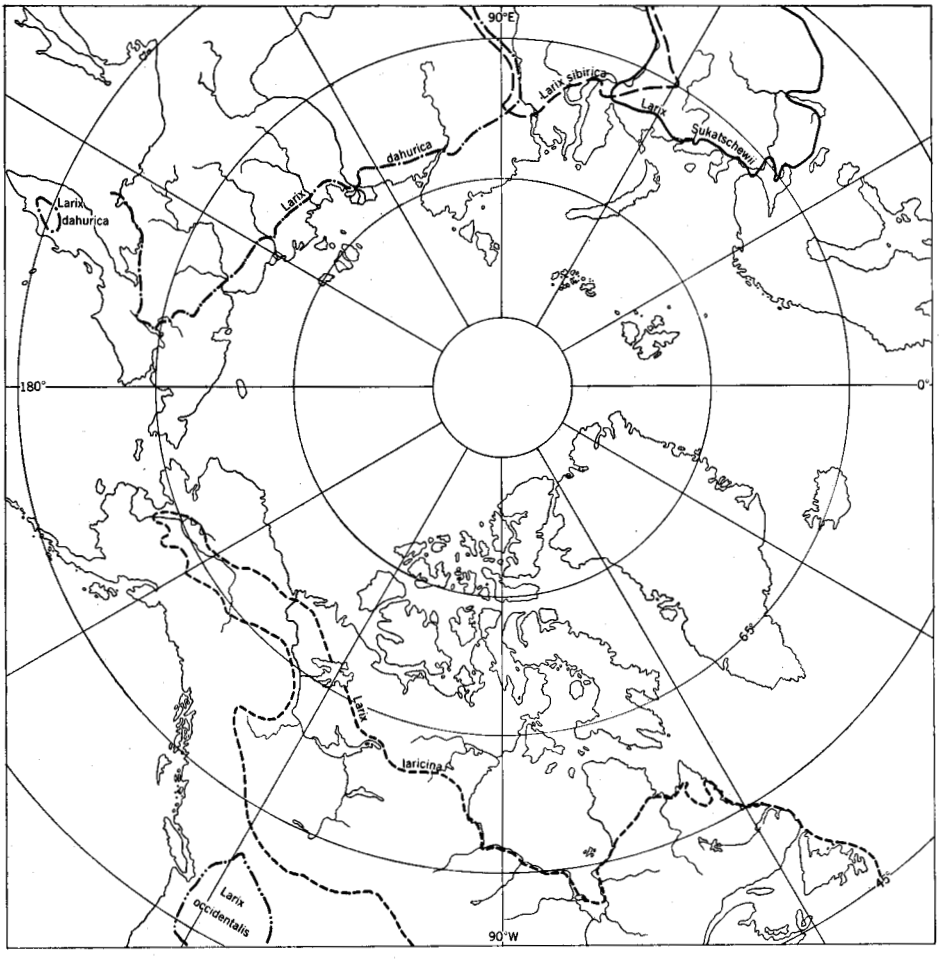

Fig. 5. The polar limits of the northern species of the genus *Larix*.

the region northeast of the Stanovoy Krebet (Stanovoy Mountains). *L. Cajanderi* Mayr, likewise credited to eastern Siberia, has been reported by Russian authors from the Yakutsk region and from northeastern Siberia. According to Ostenfeld and Larsen (1930) *L. Cajanderi* is synonymous with *L. Gmelini* (Rupr.) Gordon, which again is the same as *L. dahurica* Turcz. The range of *L. Cajanderi*, therefore, is not shown specifically in Fig. 5.

In Siberia, larches most often form the polar tree-line. In North America, *L. laricina* (DuRoi) Koch, although widespread in the forest-tundra, very rarely forms forests. In large bogs and fens in Labrador it may occasionally be the dominating species, and elsewhere may even form lichen forest; but across northern Canada *L. laricina*, together with white and black spruce, forms the polar tree-line. The Alaskan larch has been separated as *L. alaskensis* Wight, a name which has not been accepted generally, although Raup (1947) considers it a good geographic race, *L. laricina* var. *alaskensis* (Wight) Raup, and shows that it extends into northwestern Canada. Ostenfeld and Larsen

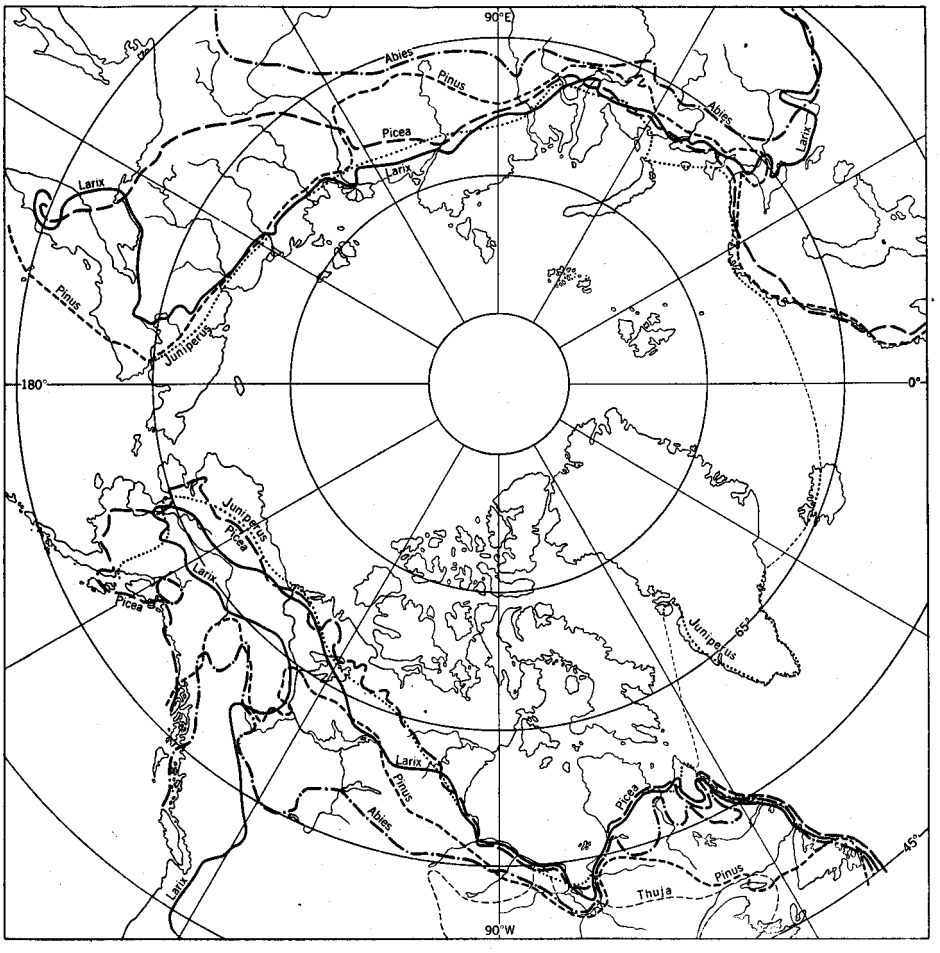

Fig. 6. The polar limits of *Picea, Abies, Pinus,* and *Larix* as shown on Figs. 2–5, and of *Juniperus communis* L. and *Thuja occidentalis.*

(1930), on the other hand, considered it only a trivial variation of *L. laricina.*

Larch generally avoids the sea coast. This is very noticeable in the Hudson Bay region where it is never found on the smaller islands. On the mainland, too, it is invariably found "behind" the black and white spruce. The same is true on the Labrador coast, in Alaska, in the Mackenzie Delta (Porsild, in letter), and in northern Europe.

In Fig. 6, showing the polar limits of spruce, fir, pine, and larch, I have added that of the juniper[1] (*Juniperus communis* L.), although it is never tree-like and occurs only as a dwarf shrub within the forest-tundra. It does, however, belong with the conifers, and for this reason I have shown its range in Fig. 6, but not in Fig. 7 which shows the polar tree-line. The common northern juniper is the only almost completely circumpolar conifer; it is the only conifer native to Greenland, Iceland, and Novaya Zemlya (see p. 151) and

[1] *Juniperus communis s. lat.* here includes var. *montana* Ait. as well as *J. sibirica* Burgsd. and *J. communis* var. *nana* Loud.

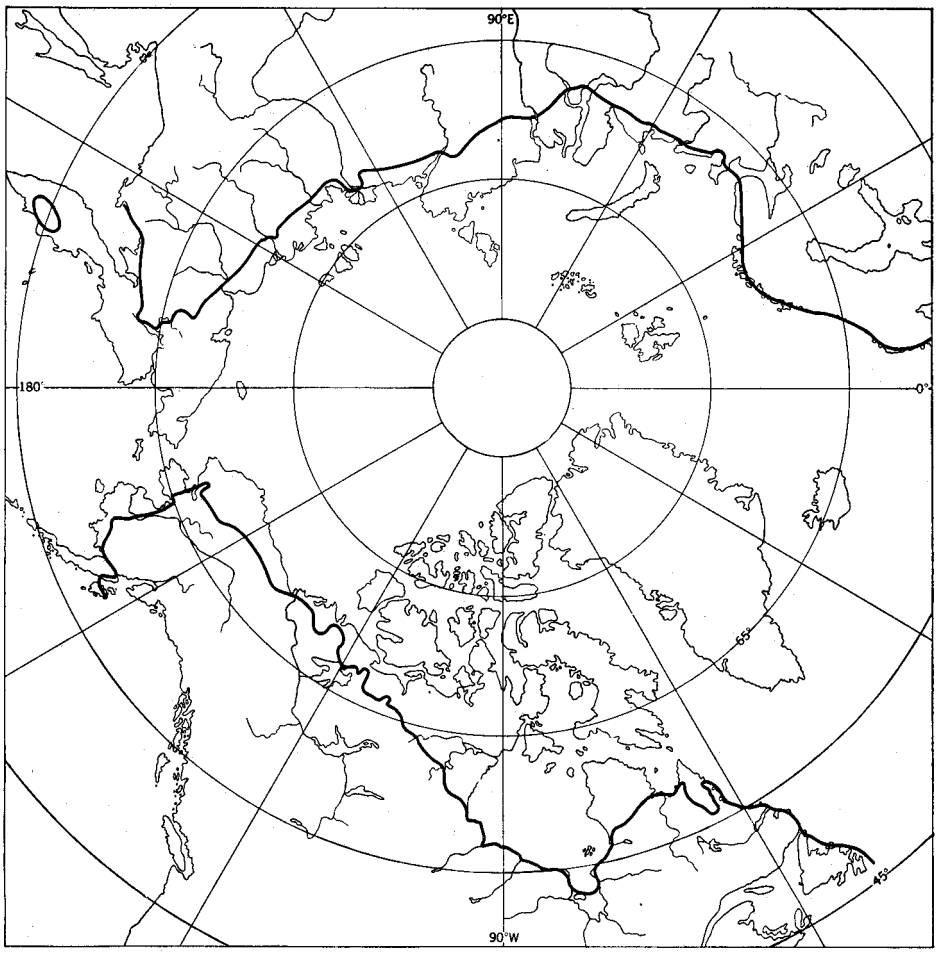

Fig. 7. The polar limit of tree-like conifers, irrespective of species.

the only one found in the Torngat region of Labrador and near North Cape in Norway.

Neither hemlock (*Tsuga*) or arbor vitae (*Thuja*) reach the polar limit of conifers, even though the eastern white cedar, *Thuja occidentalis* L., does reach southern James Bay, and *Tsuga heterophylla* (Raf.) Sarg. and *T. Mertensiana* (Bong.) Carr., southern Alaska. But nowhere do they extend into the forest-tundra region. The range of *Thuja occidentalis* is given in Fig. 6.

Figure 7 combines the information given in Figs. 2–6, showing the polar limit of tree-like conifers, irrespective of species, omitting the not truly arborescent *Juniperus communis s. lat.* and *Pinus pumila.*

This paper deals only with conifers. If birch, alder, aspen, balsam, poplar, and tree-like willows were mapped, we would, however, obtain about the same picture, only the line would include Iceland and southernmost Greenland and extend farther north in Alaska and in easternmost Siberia.

For practical purposes, the line in Fig. 7 could, I believe, be called the southern limit of the Arctic, at least phytogeographically. Plant life is conditioned by climatic and edaphic factors, and the species itself is of little consequence because everywhere the northernmost individuals of coniferous tree species show almost the same characteristics. It is natural, therefore, that phytogeographers and climatologists (e.g., Miller, 1950) have tried to evolve a common equation or formula embodying the climatic requirements of all tree species at their polar limit. Hare (1952) has brought together the published information dealing with this problem, and in his map (p. 956) has synthesized the pertinent information. I have tried here to assemble the fundamental, although very approximate, phytogeographical data for the climatologists, and it may be helpful to add some remarks on the ecological character of the polar limits of conifers.

The polar limit of conifers is a phytogeographic boundary which is determined by the same general conditions that determines the boundaries of other species. As we approach it, we find a marked decrease in the edaphic amplitude of all species. That is, species are restricted to certain habitats. Thus, those that in the centre of their area are not pronounced calciphiles, near their northern limit are often restricted to habitats with calcareous soil. The distinct selectivity with regard to edaphic conditions of a given species near its northern limit is very noticeable in the forest-tundra where trees grow only on south-facing and well-drained slopes, in the valleys of rivers, in sheltered depressions, or on calcareous soil. In some parts of the forest-tundra this is not always so evident because fires and human activities may have disturbed the original distribution of trees. It is often possible, however, from the accounts of earlier travellers to reconstruct the original pattern of forest and forest islands in the forest-tundra.

Conditions favouring the formation of forest-tundra, and the occurrence of isolated islands of forest may vary in different parts in the forest-tundra; but the microclimatic factors are probably the most important. The human factor, however, in some places may have played an active part, as, for example, in the cutting of trees for fuel by arctic nomadic tribes. This is certainly the case in parts of northern Russia where the Samoyedy have caused great changes in the forest-tundra.

Isolated stands of trees in the northern part of the forest-tundra may possibly be relics from a warmer postglacial period, when continuous forest extended farther north than it does today. Thus, the present forest-tundra region of northern Scandinavia, Finland, and the Kol'ski Poluostrov may once have been occupied by continuous forest. Fossil evidence of former conifer forest is known to occur at elevations above and beyond the present polar limit of forest.

With regard to the probable migration of tree species in postglacial time Hultén (1937) stresses the importance of a former land connection across the Bering Sea. The different extent of glaciation in the southern parts of the Arctic and the northern parts of the Subarctic, as well as in the taiga region, must also be taken into consideration, as for example in Russia where the eastern

limit of larch more or less coincides with the eastern limit of the last glacial advance in northeastern Europe. During the last glaciation the most northern outpost of the Siberian taiga was in the region of Indigirka, well beyond the Arctic Circle (see Frenzel and Troll, 1952). This, and the fact that two ice sheets converged in the Stanovoy Krebet, certainly must have had a great deal to do with the present peculiar distribution of conifers in northeastern Siberia.

There have been several oscillations of the polar limit of forest in post-glacial time; some have lasted hundreds, some even thousands of years, while others have been of much shorter duration. Phytogeographical boundaries are notoriously unstable, and many species near their northern limits are most susceptible to climatic changes, even if of short duration, and particularly to changes in temperature. During the last decades there has been a fairly well marked amelioration of the climate of the forest-tundra region of northern Europe, and in northern Finland there has been a higher incidence of good pine seed-years during the nineteen 'twenties and 'thirties when the radial growth of trees likewise showed a marked increase (compare Mikola, 1952; and Hustich, 1948). A similar amelioration has taken place in the far north of Russia and Siberia (Ahlmann, 1948; Regel, 1950; *et al.*). But I am not so sure that this has been the case in subarctic Canada, where, at any rate, the amelioration has been less pronounced. Marr (1948) reported an advance of the tree-line in the Richmond Gulf area on the east coast of Hudson Bay, but my own measurements of the radial growth of the white and black spruce (Hustich, 1950) do not indicate a very distinct increase. Lysgaard's climatic map (1949) showing the latest world fluctuations likewise suggests that greater increases in temperature have taken place in northern Europe than in eastern Canada. Nissen (1951) has given a most interesting account of how this fluctuation has affected the reproduction of pine in northern Norway.

Although the coniferous forest, near its northern limit, is composed of different species having different ecological requirements, most of them react in a similar manner to the climatic conditions which characterize the southern boundary of the Arctic. The effect of wind and snow blast is similar and produces the same pattern of stunted growth in *Larix laricina* as in *Picea glauca* and *P. mariana*, or in *Pinus silvestris*. Reproduction, too, follows the same pattern in larch, spruce, and pine. In favourable years the incidence of florescence is by no means impaired, and may even be more intense than in places of more favourable climate. But there is a marked decrease in the production of viable seeds as we approach the polar limit of forest, and the conclusion reached by Renvall (1912), as well as by other Scandinavian and Finnish investigators, that viable seed is produced only in favourable years near the polar limit of forest, probably applies to all regions.

It is remarkable, on the other hand, that the ability to reproduce by vegetative means (adventitious root-formation, layering, and by vegetative shoots) is not universal among all species near the polar limit of trees. Thus, in Scotch pine and white spruce vegetative reproduction is rare, whereas in black spruce, balsam fir, alpine fir, and Siberian fir, it is the rule. The North American larch, likewise, readily reproduces vegetatively although dense scrub forest (*Krummholz*) is formed only by *Pinus pumila*, *Abies lasiocarpa*, *A.*

balsamea, and *Picea mariana*. Along the Labrador coast the scrub forest formed by black spruce and balsam fir may be as impassable as the "*Krummholz*" zone formed by the mountain dwarf pine of the central European Alps. Porsild (1951) has described similar *Abies lasiocarpa* scrub forest at timber-line in southeastern Yukon.

The composition of the forest-tundra of northern Europe differs in many respects from that of other parts of the Subarctic. In northern Scandinavia birch (*Betula tortuosa s. lat.*) is forest-forming whereas the birches of North America and Russia are not. In North America, on the other hand, especially in the Mackenzie District, in the Yukon, and in Alaska, alder (*Alnus crispa*) may form dense scrub forest even beyond the northern limit of spruce (Porsild, 1939). The same is the case on mountains along the Labrador coast. Various deciduous species occur in the forest-tundra but they are not forest-forming, except in the Anadyr region where *Populus suaveolens*, *P. tremula*, and some arborescent willow and birch species form a deciduous forest beyond the *Larix dahurica* forest. A comparison of the birches of the Old and New worlds is difficult because the nomenclature of the genus *Betula* in different parts of the Arctic and Subarctic is in urgent need of clarification.

The farther north one travels, whether in America or Eurasia, the greater becomes the percentage of circumpolar species in the flora; likewise, the similarity of the dominant vegetation types becomes more pronounced. It is surprising, therefore, that not a single arborescent species is circumpolar, even though several birches of the forest-tundra may be closely related. Not even the dwarf birch, *Betula nana*, is circumpolar, for in some parts of the Subarctic it is replaced by species of similar growth habit and ecology (*B. exilis* and *B. glandulosa*). Only *Juniperus communis* (incl. var. *montana*) is almost completely circumpolar, except for a gap in the Bering Sea region.

Considering the great similarity between the boreal forests of the Old and New worlds it is equally remarkable that none of the Eurasian conifers occur in eastern North America and that white spruce has not reached eastern Asia. Perhaps taxonomists and phytogeographers dealing with the taxonomy of boreal tree species have been unduly impressed by the importance of the Atlantic Ocean and Bering Strait as phytogeographic barriers. At any rate, it is fairly well agreed that, with the exception of the quite distinct black spruce, the Eurasian and American spruce and larch species, which form the polar limit of conifers, must be rather closely related.

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[1]A more complete list of papers dealing with the polar tree- and forest-limits will be found in Hustich (1952).

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