ON THE FOREST-TUNDRA AND THE NORTHERN TREE-LINES

A preliminary synthesis

ILMARI HUSTICH

I. TERMINOLOGY

The concepts forest-line or forest-limit, timber-line or tree-line are all somewhat vague and difficult to define, cf. BROCKMAN-JEROSCH (1919), H 1952[1] and others. For this reason, it has not always been easy to plot them accurately on a map. In the sense employed, for instance, by North American writers, the frequently used expression «timber-line« may, thus, mean the northern limit of commercially profitable forest utilization, the polar or altitudinal limit of forest or the tree-line in general.

But, «when is a tree a tree«? According to BROCKMAN-JEROSCH (1919) 5 metres should be the minimum height for a «tree«, whereas HEIKINHEIMO (1921), for the vast northern birch forests, proposes 2 metres. Where cartographic accuracy is needed the concept «tree-line« is too vague an expression. On the other hand, particularly at the polar limit of the forests, the capacity of a tree seedling or a young tree to reach above the snow cover is the crucial point, of course. Thus, when a tree seedling reaches above the snow and grows into a 2 or 5 metres high tree, this fact tells us something concrete, at least about the local climate, the existence of wind shelter, etc.

The same vagueness marks the concept «forest-line«. How many trees are needed on one acre before we can talk of a forest, or «how many logs make a forest«? This simple question is crucial for the paleoecologist, cf. MARTIN (1959, p. 221), but it is also of importance for the evaluation of the concepts used here. HERMES (1955, p. 2) defines a forest in the following words: «Unter Wald verstehen wir eine Vergesellschaftung von 'Stamm'-Bäumen mit Kronenbildung von mindestens 3—5 m Höhe«. But immediately after this the concept is widened considerably: «in der Nähe des polaren Grenzbereichs werden aber schon gute mannshohe Baumgesellschaften as Wald angesprochen.«

[1] The expressions H 1952 etc. refer to the author's earlier papers, see 'References'.

We can hardly operate with just *one* forest or tree-line, because in very few places, in a planted conifer forest in Iceland or near a glacier in Alaska, can we draw a sharp line between the forest and the surrounding treeless heath or moraine. Almost everywhere else we have to operate with many «lines« inside a wide belt where the forest ebbs out to scattered, often small, deformed trees, bushes or low seedlings, cf. KRYLOVA (1964). Sometimes the forest-line or the tree-line is formed by two or three different species.

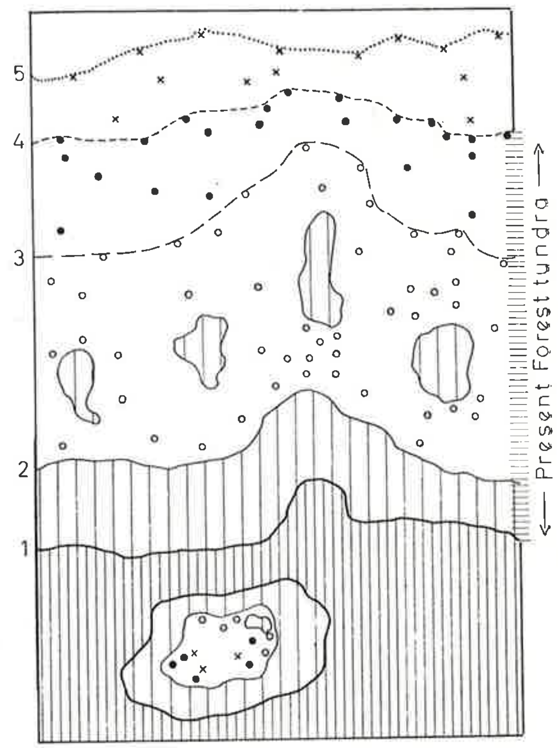


Fig. 1. Idealized forest-limits and tree-lines, see explanation in text.

Fig. 1 shows an idealized arrangement of the different tree and forest-lines. The local pattern of these lines is similar whether we approach the polar, the maritime or the altitudinal line of trees. The principal difference is that as we approach the maritime or the altitudinal line of trees, the distance between the outermost trees and the closed or continuous forest is short, whereas in the continental Sub-Arctic this belt is often very wide.

The expression *economic forest-line* (1) or the timber-line proper as marked on Fig. 1, is here understood to mean the limit beyond which commercial cutting of trees endangers natural regeneration; also the expression *productive forest-line* has been used. At least in part, the expression «economic forest-line« coincides with the *generative forest-line* of KIHLMAN-KAIRAMO (1890) and the *rational forest-line* of HEIKINHEIMO (1921).

The expression *physiognomic forest-line* (2) means the limit of the forest itself regardless of its reproductive capacity. In the belt between the economic forest-line and the physiognomic forest-line the generative reproduction occurs only at intervals of many years (cf. RENVALL 1912, H 1948). Thus the forest is there, but it must be handled carefully. In subsequent discussion this line will be referred to simply as the «forest-line« because without careful investigations we simply do not know where the economic forest-line runs, whereas the physiognomic limit of forest is what we see in the landscape. In «good years« mature seeds develop as far as the forest goes towards the north, to the shore of the ocean or towards the summit of a mountain. In such years the economic and the physiognomic forest-lines coincide. This definition of the physiognomic forest-line corresponds to the evaluation of the concepts *vegetative* and *empirical forest-limits* (KIHLMAN-KAIRAMO 1890).

The expression *tree-line* (3) is here understood to mean the absolute polar, maritime, or altitudinal limit of trees regardless of species; the polar tree-line is in fact formed by different species in different areas. The definition of the concept «tree« varies, however, see above. The marking of the tree-line on a map always assumes a certain degree of subjectivity.

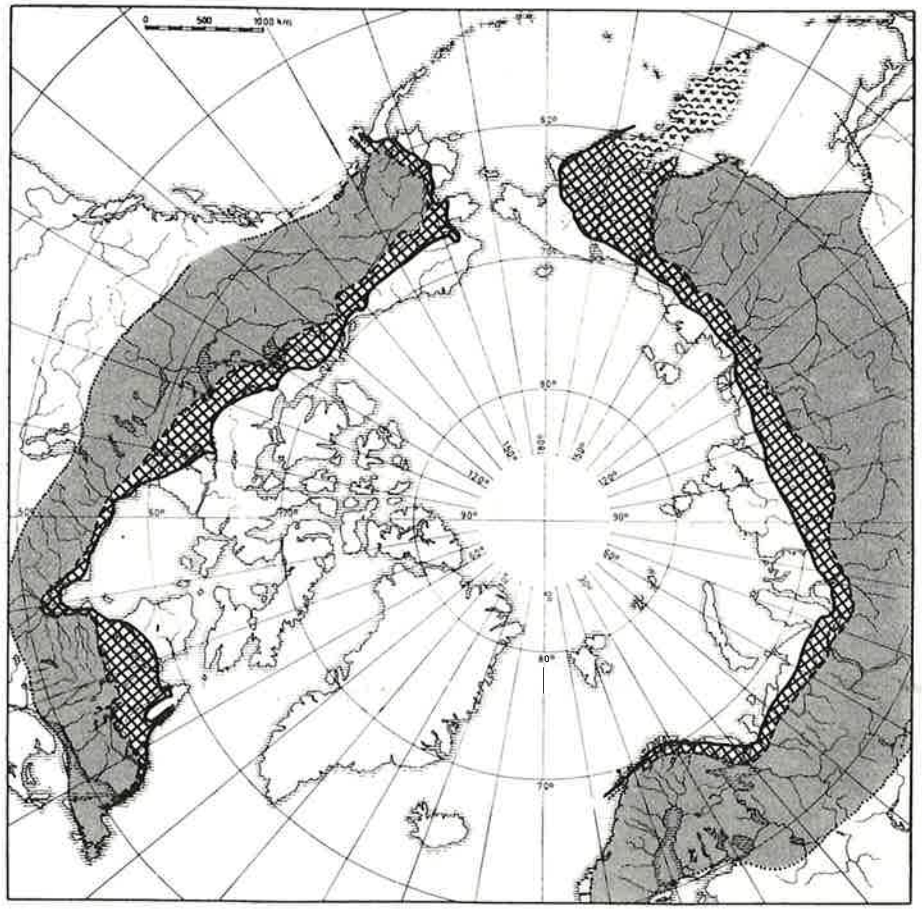
The polar, maritime or altitudinal *species-line* or the northern *limit of a certain tree species* (4) is understood to mean the line of the most advanced outposts attained by a tree-species, irrespective of whether the outermost individual is a seedling, a bush or a tree, or whether the growth is prostrate or tree-like.

To these forest- and tree-lines we could in some areas — still very small — add a «*afforestation-line*«, which marks the efforts of man to expand the forest northwards or towards the summits of mountains.

If necessary — to describe the genesis of a forest-tundra area — the «*historical tree-line*« or the line of former outposts (5) of the forest and tree-line species might be added. Such a historical tree-line is the tree-line during the postglacial thermal maximum (cf. ANDREEV 1954 and TIKHOMIROV 1956). The remnants of these trees are now buried in the peat, sometimes hundreds of miles outside the forest-line of today.

The concept «*Arctic*« belongs to those often used but vague geographical concepts such as «Tropics«, «Savanna«, etc. Different opinions have been advanced regarding the delimitation of the southern limit of the Arctic, cf. the recent compilations by POLUNIN (1951), BRITTON (1957), H 1952, etc.

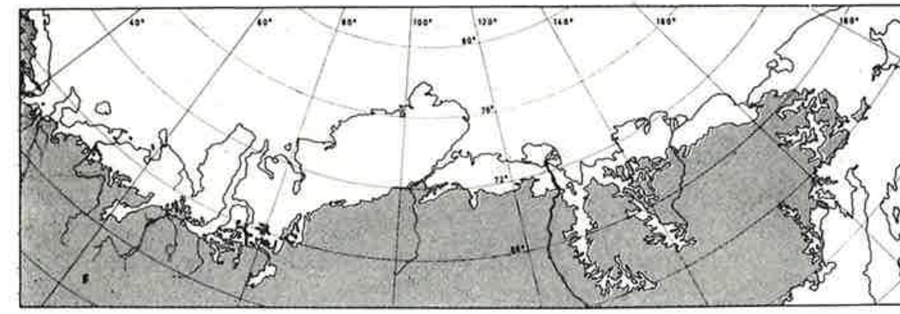
Two definitions have been more used than others, the 50°F (10°C) Isotherm of the warmest month and the «Nordenskiöld-line«, see HARE (1952). *I suggest* (as earlier, in H 1952) *that the polar tree-line should be regarded as the southern limit of the Arctic,* mainly because such a line is more easily mapped. The tree-line is, of course, a concrete thing, whereas isotherms, etc., are interpolated



Map. 2. The forest-tundra zone, roughly approximated using various sources. South of the forest-tundra is marked, very tentatively only, a vast belt wich some prefer to cal the Sub-Arctic, some the Boreal zone. Regarding the subdivision of the Boreal, see Rousseau 1952, Hare 1954, Sjörs 1961, H 1949 and others.

abstractions, which widely fluctuate over hundreds of miles from year to year (see Thomas 1950). Locally, it might be difficult to map the «tree-line« instead of the species-line, but for most purposes the short distance between these lines is of no importance.

Between the outermost limit of a tree-species (regardless of size) and the forest-line proper is a transitional belt of varying breadth in which isolated trees as well as small groves or large «islands« of forests occur, particularly along the rivers. This transitional belt is mostly called *forest-tundra* (Lyesotundra, Waldtundra). The forest-tundra may attain a breadth of hundreds of miles in Canada or Siberia, but in maritime regions such as the Labrador coast,



Map 3. The northernmost forest-tundra stands according to the *Geobotanical Map of the Soviet Union* (Lavrenko and Sochava 1954) This here simplified map, drawn by Mr. *L. Hyttinen,* illustrates, as do maps 5 and 8 how roughly interpolated the phytogeographical lines on such small scale-maps as map 4 etc. really are.

the forest-tundra is replaced by a rather narrow scrub belt («Krummholz«, see H 1939); compare also the extensive descriptions of the forest-tundra ecotone by Andreev (1933, 1935), Blüthgen (1942), Clarke (1940), Drėw and Shanks (1965), H 1950, H 1954, Larsen (1965), Marr (1948), Norin (1958a, 1961), Porsild (1929), Tikhomirov (1956, 1961), etc.

Norin points out that the forest-tundra is not only a region where Arctic and boreal elements intermingle, but an independent phytogeographical region with characteristics of its own. In my opinion the forest-tundra phytogeographically constitutes the phytogeographical *Sub-Arctic* zone proper. Rousseau (1952) uses for the same zone the word *'Hémiarctique',* which has later been adopted by some authors. Regarding the comparison of the forest zonation in northern Eurasia and North America compare, for instance, Kujala 1945, H 1949, Hare 1954, Kalela 1962, Sjörs 1963 and Ahti 1964.

The large region of birch plains («viddas«) and mountain heaths of northern Fennoscandia can also be considered a forest-tundra, a direct continuation of the large forest-tundra of the Kola Peninsula. The word *Sub-Alpine* means, in my opinion, the *vertical* belt between the forest and the altitudinal tree-line. The complicated conditions in northern Scandinavia re the Sub-Arctic region have been much discussed, compare Kalela 1961, Sjörs 1963, Ahti a.o. 1964 and Jalas 1965.

II. THE NORTHERN TREE-LINES

A. Conifer species

Maps 3—4, 6—14 below are mainly drawn according to information contained in a number of published paper or reports, of which the majority is listed in 'References'. My own experience is restricted to the Quebec-Labrador Peninsula, northern Ontario and Fennoscandia. Among the general papers consulted for this purpose must be mentioned *Derevja i kustarniki, Flora Murm. Obl., Flora USSR,* HULTÉN (1950), MUNNS (1938), *Native Trees of Canada,* PETROV (1930), ROWE (1959), SARVAS (1964), SCHMUCKER (1942) and an earlier edition (H 1952) of the Conifer chapter in this paper. Compare also KRYLOV (1961), KÖPPEN (1888—89), SAMBUK and DEDOV (1934), SHELUDYOKOVA (1938), SHIMANJUK (1962) and TOLMACHEV (1954) regarding the Eurasian tree-lines. Unfortunately, the information in the literature regarding the ranges of the tree-species is often confused and confusing and it is difficult to combine the data available. Thus, the maps below represent to a marked degree a rather subjective interpretation only. The excellent geobotanic map of the Soviet Union (LAVRENKO and SOCHAVA 1954, 1956) gives abundant information regarding the main forest types and their distribution, but this map is not easy to use for the mapping of the different tree species. Map 3 above gives an idea of the general forest-line in the Soviet Union based on the northernmost distribution of *Lyesotundra.*

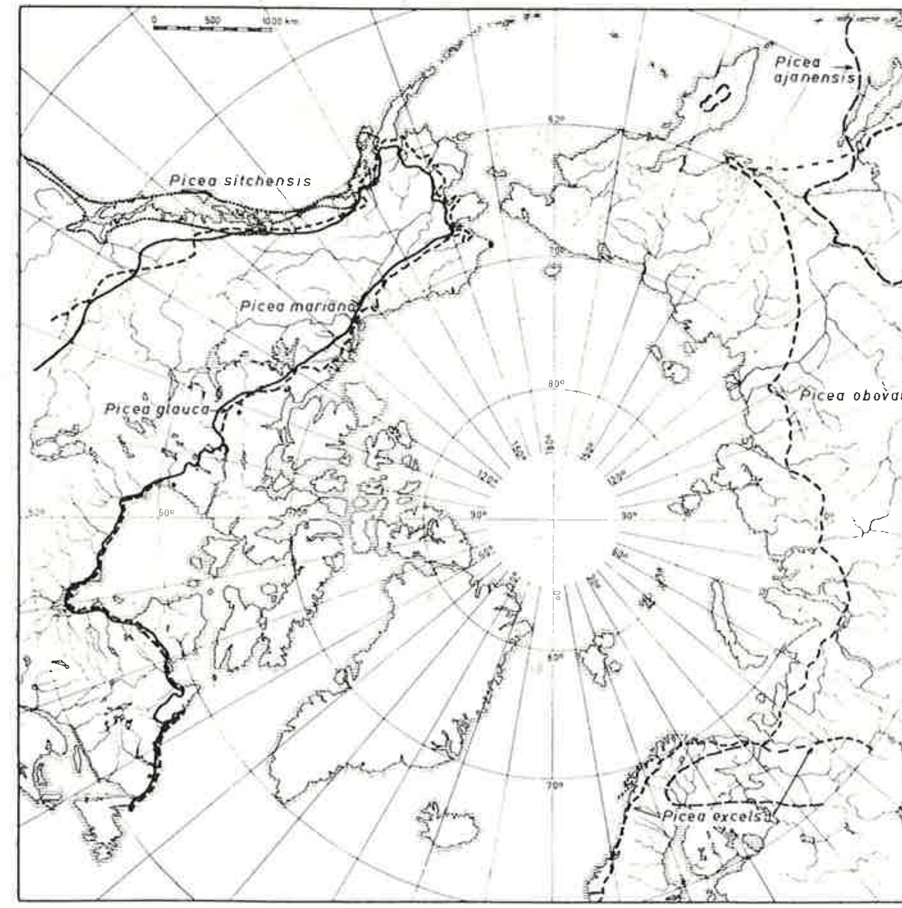
In some parts the forest-line or the tree-lines are not well known. The polar species-lines shown here are, therefore, very tentative and to a high degree rough interpolations only. The Eurasian tree-line is roughly 20.000 km long. The observations are generalized and the scale of the map does not allow many details. To illustrate how the northern range of two wellmapped tree-species, Scotch pine and Norway spruce, look on a larger scale, two more detailed maps are included here.

Theoretically, the lines on the maps are «species-lines« (i.e. line 4 on Fig. 1), but due to the scale of the maps and the information available, the lines might just as well be called tree-lines; in some parts such a line in fact marks the forest-line.

1. Picea. The spruce is, beside *Larix,* the most important tree species in the boreal forest regions and in the forest-tundra. Map 4 shows the polar tree or species-line of the genus *Picea,* including *Picea excelsa* Link (= *P. Abies* (L.) Karst.), *P. obovata* Ledeb., *P. ajanensis* Fisch., *P. glauca* (Moench.) Voss., *P. sitchensis* (Bong.) Carr. and *P. mariana* (Mill.) BSP.

The taxonomic status of the Siberian spruce, *Picea obovata,* has been questioned i.a. by LINDQUIST (1948), who thinks is should be called *P. Abies* var. *obovata* (Ledeb.) Fellm., whereas Russian taxonomists always consider it a distinct species. At any rate, the Norway spruce and the Siberian spruce undoubtedly intergrade between the Kola Peninsula and the Pechora, cf. map. 4, TOLMACHEV (1954, p. 148), REGEL (1940) and others. This question has been discussed very early; SCHÜBELER (1873—75, p. 159) wrote that «*Abies obovata* Ledeb. nur als eine klimatische Form der gewöhnlichen Fichte *(Picea vulgaris* Lb.) zu betrachten ist.«

Map 5 shows the distribution of Norway spruce in north-western Europe



Map 4. The northern range of species of the genus *Picea.* Note the discussion re. *P. obovata* and *P. excelsa* above.

(LINDQUIST l. c., p. 263), note the intricate distribution pattern of spruce in northern Norway.

There is a similarity between the Siberian spruce and the Canadian white spruce *(P. glauca)* in northern stations. Both species have, in the north, short cones, rounded cone-scales, and the young twigs of *P. obovata* (and *P. Abies* var.*arctica* Lindq.) are sometimes glabrous, which is a distinct character of white spruce. (Future forest tree taxonomists might perhaps have to work with a circumpolar collective species «*P. borealis*« of spruce, composed of *P. glauca* as ssp. «*americana*« and *P. Abies* as ssp. «*eurasiatica*«, with var. «*europaea*« and var. «*sibirica*«.)

The Norway spruce forms the polar coniferous tree-line in the Kola Peninsula, cf. TOLMACHEV (l. c., p. 68) and reaches Mesen in the east in the forest-tundra. Its northernmost locality in Norway is near Neiden, at 69° 47° N. Lat. according to *T. Ruden* (in letter); some observers believe that the isolated localities of spruce in the Varanger have developed from seeds of cones which were brought by Lapps. According to LINDQUIST (l. c., p. 263) an isolated outpost occurs on the Rybachi Peninsula.

The ecology of the spruce at the tree-line in the Kola Peninsula is described in a classic work by KIHLMAN-KAIRAMO 1890, cf. also KRYUCHKOV 1962.

Why the spruce tree-line west of the Kola Peninsula runs south of the pine tree line has caused much speculation among the forest scientists (cf. HAGEM 1917 and others). Some believe that the cause may be historical, due i.a. to forest fires, others believe that there is a climatic reason for this discrepancy. However, already SCHÜBELER (1873—75, p. 157) notes that «die Ursache dass die Grenze (der Fichte) nicht höher gegen Norden (an der Nordküste Norwegens) geht, ist kaum in ungünstigen klimatischen Verhältnissen zu suchen. Die mehr oder weniger waldreicher Thäler sind aber durch hohe, weit gedehnte, nackte Felsen von einander getrennt, die im allgemeinen jede Verbreitung durch Selbstsaat geradezu unmöglich machen.«

The Siberian spruce *(P. obovata)* forms the Polar tree-line from about the Kanin Peninsula to Jamal, in an area where the influence of man on the northern forests was devastating in earlier times, see p. 32. According to some authors, the spruce particularly often forms large «forest islands« outside the forest limit proper, see ANDREEV (1956) and LARSEN (1964). Spruce reaches the Barents Sea in the Bay of Haipodorsk (TOLMACHEV l. c., p. 69) and Korotaschka, see map 4. It also grows scattered along the lower Petchora (e.g. near Narjan Mar where it is planted nowadays).

The probably most striking (and most uncertain) locality of isolated tree individuals outside their range of distribution is the spruce-locality reported 1842 by the wellknown Russian explorer *Pachtusov* on the coast of Novaya Zemlya, at about 71° n. Lat. This locality has not been confirmed since and there is no mention of it in TOLMACHEV 1960. MIDDENDORFF noted (1864, p. 543) that «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.« However, as others of *Pachtusov's* observations have later been confirmed, this report of a prostrate spruce on Novaya-Zemlya should be believed according to KÖPPEN (1889, p. 522): «zufällig dort ausgeworfene Fichtensamen konnten keimen und in günstigen Jahren zu kleinen Sträuchern erwachsen, deren Existenz daselbst aber nicht gesichert ist, da die Fichten in diesen hohen Breiten keine Zeit hätte Samen zu bilden.«

Map. 5. The northern and western range of *Picea excelsa* in Fennoscandia, according to LINDQUIST 1948.

In central Siberia spruce grows farther north, a result of the increased continentality. Although spruce reaches 69°30' N. Lat. in the Yenisey region, larch is there northernmost coniferous tree-species; according to SOCHAVA (1930) even in Jamal the larch reaches slightly north of spruce. Spruce reaches its northernmost locality (cf. Flora USSR, 1934) at Chatanga, 71°15' N. Lat. and also grows near the Lena River, scattered up to 70°20' N. Lat. In the big river valleys where the local climate is more suitable (the rivers bring warmer water from inland) and wind-shelter is provided, spruce grows farther north than in the open peatlands between the rivers; this is, of course, true also for other tree species and for other areas.

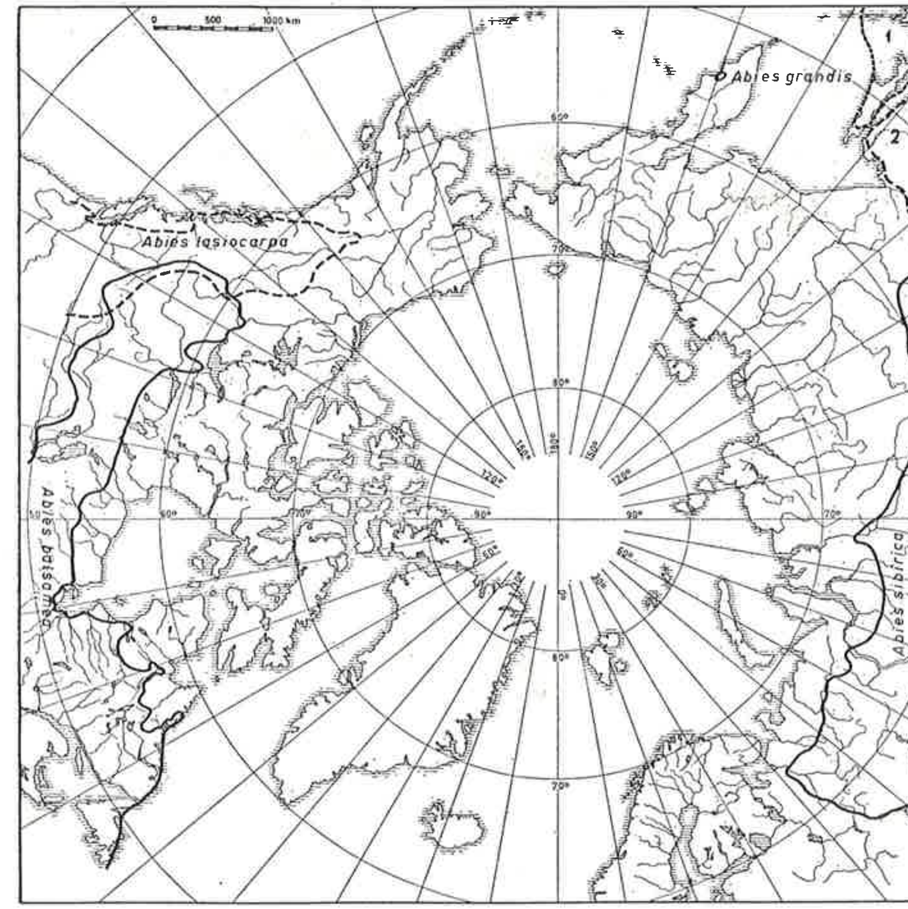
In North America, we have two clear-cut species, white spruce *(Picea glauca)* and black spruce *(P. mariana)*. Although both have approximately the same northern limit, they are well separated taxonomically [1] and partly also ecologically.

It has been customary to designate the black spruce as the «hardier« of the two, but this is erroneous. In exposed situations, where black spruce occurs only as a prostrate shrub with abundant vegetative reproduction, white spruce can grow as a small tree with a straight stem. Farther south black spruce usually grows in bogs or muskegs, whereas white spruce grows in well-drained and generally richer soils. Both species may form extensive, uniform spruce lichen forests, as may also the Siberian spruce near Norilsk (DEDOV 1933, H 1951): lichen woodlands with Norway spruce as the dominant tree seem to be very rare. While black spruce reproduces abundantly by layering, this is seldom the case with white spruce (H 1950).

Towards the north, the ecological differences between the two species prevail. In areas with sedimentary bedrock or in big river valleys where the soil is less acid and the shores loamy, white spruce reaches farther north than black spruce. This is the case, for instance, in Alaska (see SIGAFOOS 1958 p. 172 and SPETZMAN 1959, p. 41), and in the area east of Mackenzie, where white spruce is the dominant conifer in the open woodland as well as in the forest tundra (MACKAY 1958, p. 100—101). The same pattern, i.e. the selective effect of bedrock on the distribution of spruce, appears from TYRRELL's (1895—96) and HANBURY's (1903) descriptions of the area between Coppermine and Hudson Bay; compare also LARSEN's recent papers of 1964 and 1965. In the Hudson Bay Lowland white spruce mostly occupies extreme maritime localities on small dry ridges near the sea (cf. RITCHIE 1957, MOIR 1954, SJÖRS 1961 and H 1957). White spruce forms more commonly the maritime tree-line on the cold islands off Labrador (cf. H 1949). The dominance of white spruce at the polar maritime tree-line on the Hudson Bay east coast is due also to the sedimentary bedrock on the islands (H 1950). White spruce grows higher up on the Brooks Range in Alaska than Norway spruce on mountains in Scandinavia, Kola Peninsula or Ural at the same latitude. White spruce reaches, for instance, 2,700 feet in the Anaktunuk Pass (BRITTON 1957, p. 32); at this latitude the coniferous tree-line reaches about 1200—1500 feet only in Scandinavia; this is a case of the socalled *'Massenerhebung'-effect,* wellknown from the Alps.

Two «races« of white spruce occur in western Canada, namely *P. glauca* var. *albertiana* (Brown) Sarg. and *P. glauca* var. *Porsildii* Raup. Their still unclear northern limits are not shown specifically in Fig. 4.

[1] Note, however, LARSEN's statement from Canada's Northwest Territories: «Apparently intermediate forms between *Picea mariana* and *P. glauca* occur in abundance« (1965, p. 53).



Map 6. The northern range of species of the genus *Abies.* 1= *A. sachalinensis* Mast., 2= *A. nephrolepis* Maxim.

The other spruce species marked on map 4, *P. ajanensis* on Kamtchatka and *P. sitchensis* in westernmost Canada and southern Alaska, are of less importance in this connection. Sitka spruce reaches out to the rugged Kodiak Island, where no white or black spruce occur. *P. sitchensis* is taxonomically near *P. glauca;* they hybridize. The similarity between the two spruce species was observed hundred years ago, cf. MIDDENDORFF (1864, p. 590).

2. Abies. The fir reaches the polar forest and tree-line only in Labrador, extending almost to Ungava Bay near Chimo (see map 6). Otherwise, representatives of this genus are very poorly represented in the northern parts of the conifer forest. It must be noted that firs play an important part in the boreal forests in Canada, particularly in the secondary forests after cutting. The forest industry marches steadily northwards which will fast increase the northern area of fir.

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 (Flora U.R.S.S. 1934). Regarding the remarkable *Abies*-locality at Yenisey at 71°53, n. Lat. (cf. Kjellman's notes and Tolmachev, 1960, p. 67). The locality is situated 100—150 miles from the present range of the fir. It must, however, be kept in mind that isolated conifer trees or bushes are favoured by man as firewood in bad weather and also often destroyed by reindeer.

The Siberian fir is a continental species with a range similar to that of Siberian pine. Ecologically, as well as in its ability to reproduce by layering, the Siberian fir is similar to other fir species.

The Canadian balsam fir, *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.* Balsam fir is found, among other places, on the islands along the Atlantic coast of Labrador (H 1949). The Cordilleran alpine fir, *A. lasiocarpa* (Hook.) Nutt. *(A. balsamea* ssp. *lasiocarpa* (Hook.) Boivin), ascends in the Yukon to 2.000 m. above sea level (Porsild 1951) but does not extend into the forest-tundra proper.

3. Pinus. Map 7 shows the polar tree-line of pine. Only the Scotch pine, *Pinus silvestris* L. (ind. *P. lapponica* Mayr), and the Siberian dwarf pine *P. pumila* (Pall.) Rgl. enter the forest-tundra; cembra pine, *P. sibirica* (Rupr.) Mayr, jack pine, *P. Banksiana* Lam. and lodgepole pine, *P. contorta* Loudon var. *latifolia* Engelm., merely approach the forest-tundra.

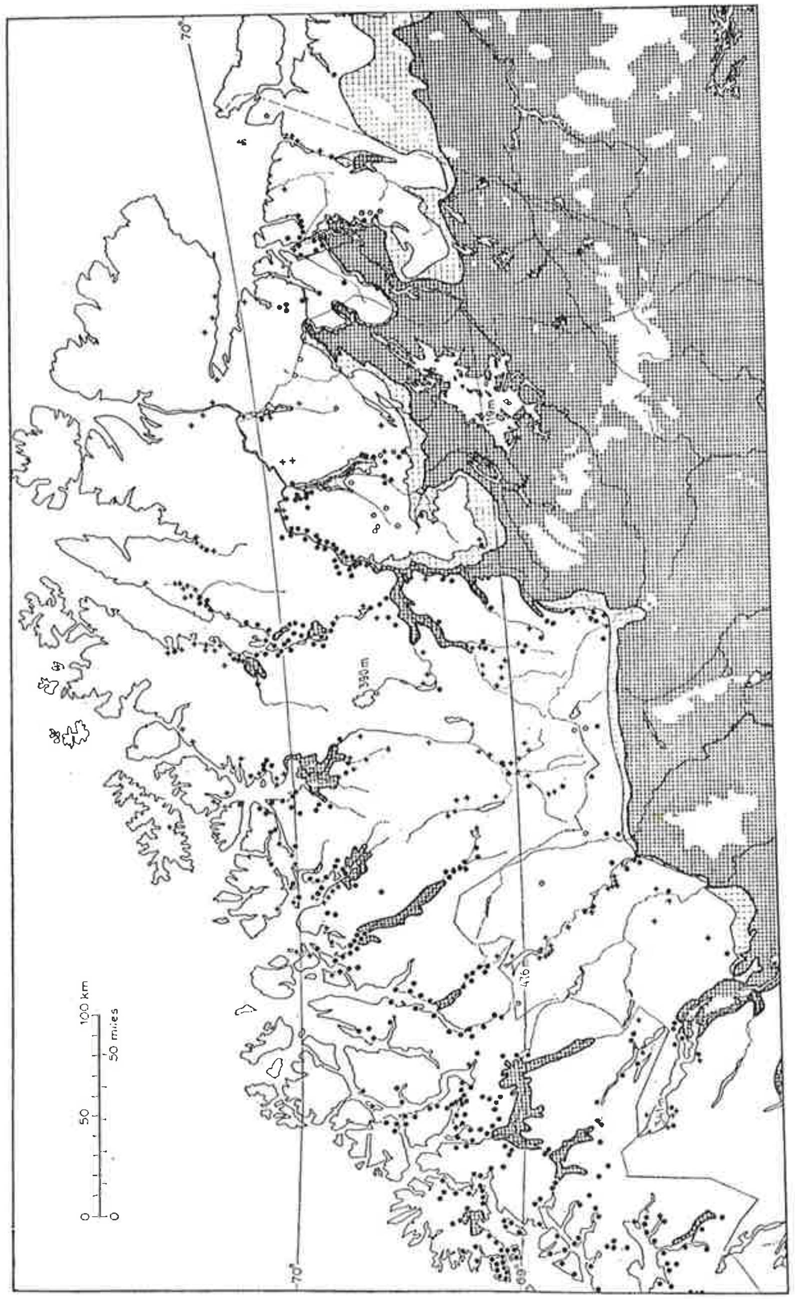
Scotch pine is the dominant conifer at the tree-line in northern Scandinavia. The isolated populations of Scotch pine in the northernmost valleys of Norway are of great interest from a genetical point of view, and should deserve close study (cf. H 1958 and map 8). They are the Scandinavian counterparts of the isolated forest «islands« which occur in the forest-tundra in the north of the Soviet Union or Canada. The northernmost pine forest in the world is situated in Stabursdalen at 70°18' N. Lat. (the northernmost pine tree at 70°29' N. Lat., cf. Ruden 1935, p. 313) and Mikola 1952; the reproduction seems usually to be satisfactory also at this northern latitude. Pine had earlier a wider distribution as Juul (1925) has shown, cf. H 1958. Re. the relation between the pine forest-line and the general flora in such areas, cf. Laine 1964.

Scotch pine 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 Russian authors as *P. silvestris* var. *jakutensis* Suk. from the 'western' pine called *P. silvestris* ssp. *lapponica* Fries; also several other varieties (forms or ecotypes?) have been distinguished.

Scotch pine is not the dominant tree in the forest-tundra east of Petchenga, but it reaches the Arctic circle at Yenisey. Except in the northernmost Urals and on the lower Ob, Scotch pine goes farther north than the Siberian cembra-pine, cf. Sochava (1930).

Map 7. Northern range of species of the genus *Pinus.* Diverging opinions re distribution of *P. silvestris* in central Siberia appear i.a. Neustadt 1957, p. 256 and Tolmachev 1960.

The Siberian pine has, see map 7, a typical continental range, compare *Abies sibirica.* It has been found on the Kola Peninsula near Murmansk and near Zesnoi on the south coast (Fl. Murm. Obl.) far from its ordinary range. *Pinus sibirica* is the only conifer species in the north which was once primarily used for other purpose than wood and fuel; the whole tree was cut to get the seeds ('cedar-nuts'). Parvela (1930, p. 230—31) describes attempts to plant cembra pine in northern Finland during the last century; several crop failures in the last century were partly a reason for this interest. Because the cembra seeds were an important trade article in the north, it is not certain that the cembra pine localities in Kola are spontaneous.



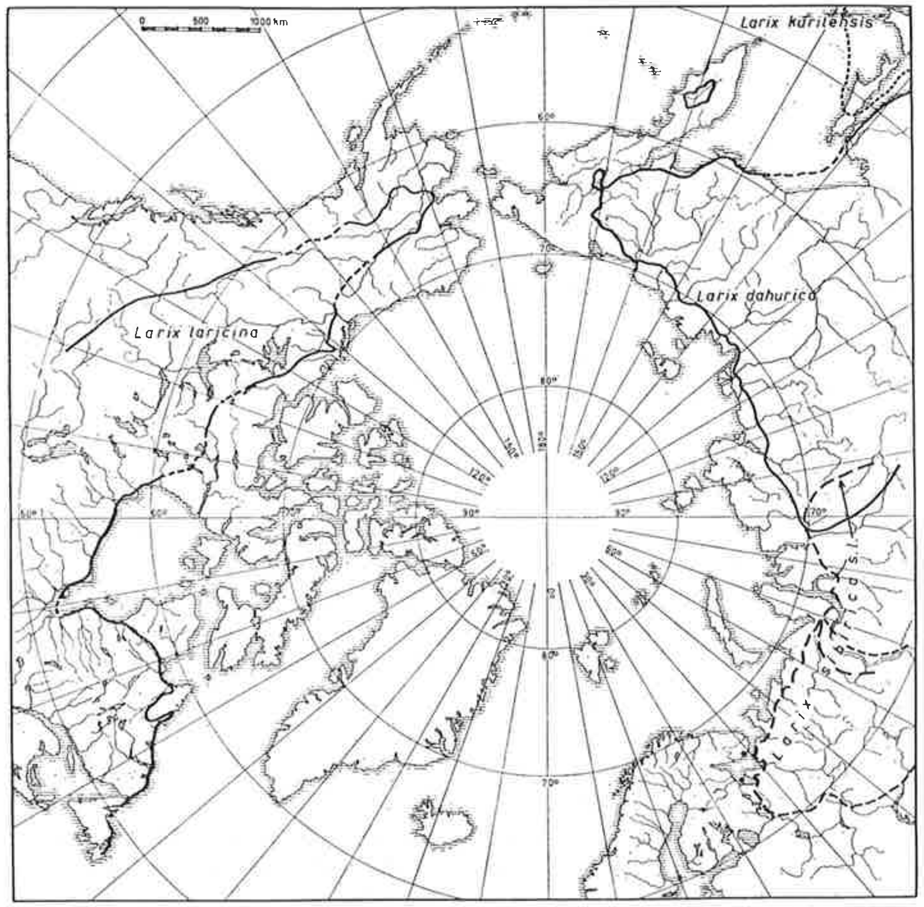
Map 8. The northern extension of pine in Fennoscandia. The darker shading shows more or less closed pine forests, the lighter shaded areas show, very roughly, a belt with pine stands and trees among dominant low birch forest. The white areas inside the shaded area are alpine regions. Dots indicate isolated stands of pine, circles isolated young pines or pine seedlings beyond the pine tree line. Crosses mark fossil remains of pine; compare Fig. 1. The pine tree-line on map 7 is certainly interpolated. After HUSTICH 1958.

The Siberian dwarf pine *(P. pumila* or *P. cembra* var. *pumila)* is a «Krummholz«-species. Thus, it differs ecologically and morphologically considerably from the other conifers in the northern part of the boreal region. In eastern Siberia the dwarf pine grows in a higher latitude and altitude than that reached by pine elsewhere; it often forms a clear belt above the larch forests on the mountains. Ecologically it is similar to *P. mugo (P. montana)* of the European Alps, although *P. pumila* belongs in the section *Pinaster,* whereas *P. mugo* belongs to the section *Strobus.* The Siberian dwarf pine forms the polar limit of conifers in the Kolyma and Anadyr regions, but never reaches tree-size. Its distribution is very similar to the area of *Chosenia macrolepis,* see below. According to TIKHOMIROV (1949) the dwarf pine is phytocenotically very strong. The dwarf pine does not occur east of the Bering Strait (TOLMACHEV 1960, p. 74), although that has been suggested.

Pinus Banksiana or jack pine is the commonest pine species in the boreal Canada. It is a continental species and reaches the coast only along the north shore of the Gulf of St. Lawrence and in Nova Scotia (the pine in Newfoundland is the eastern white pine, *P. Strobus* L.). It seems that FERNALD's view (1919) that jack pine is restricted to Pre-Cambrian bedrock, sandy plains, eskers or moraines is more or less correct, see H 1950. The peculiar range of the jack pine in north-eastern Canada is difficult to explain. One theory is that the species has not reached its climatic limit in the north-east; there are wide areas of suitable localities east and north-east of its present range. It should be noted that the cones of the jack pine usually open after forest fires or during periods of exceptionally hot weather. An interesting feature is that the jack pine near its northern limit in Ontario seems to grow taller than it does near its eastern limit. In western Canada, jack pine reaches the Mackenzie Basin, where it meets the lodgepole pine *(P. contorta* var. *latifolia).* The range of neither species extends into the forest-tundra proper.

4. Larix. Regarding the distribution of the Eurasian species of the genus *Larix,* I have here not followed DYLIS (1948), who divides the Siberian larch into two species, *Larix sibirica* Ledeb. s. str. and. *L. Sukaczewii* Dylis. TOLMACHEV (1960 p. 69) keeps the two «new« larch species together as *L. sibirica,* which, however, is divided into two races: *L. sibirica* ssp. *rossica* (Rgl.) Suk. and *L. sibirica* var. *polaris* Dyl. Regarding *L. sibirica* s. str.; compare, except DYLIS (l.c.), also ARNBORG and EDLUND 1962.

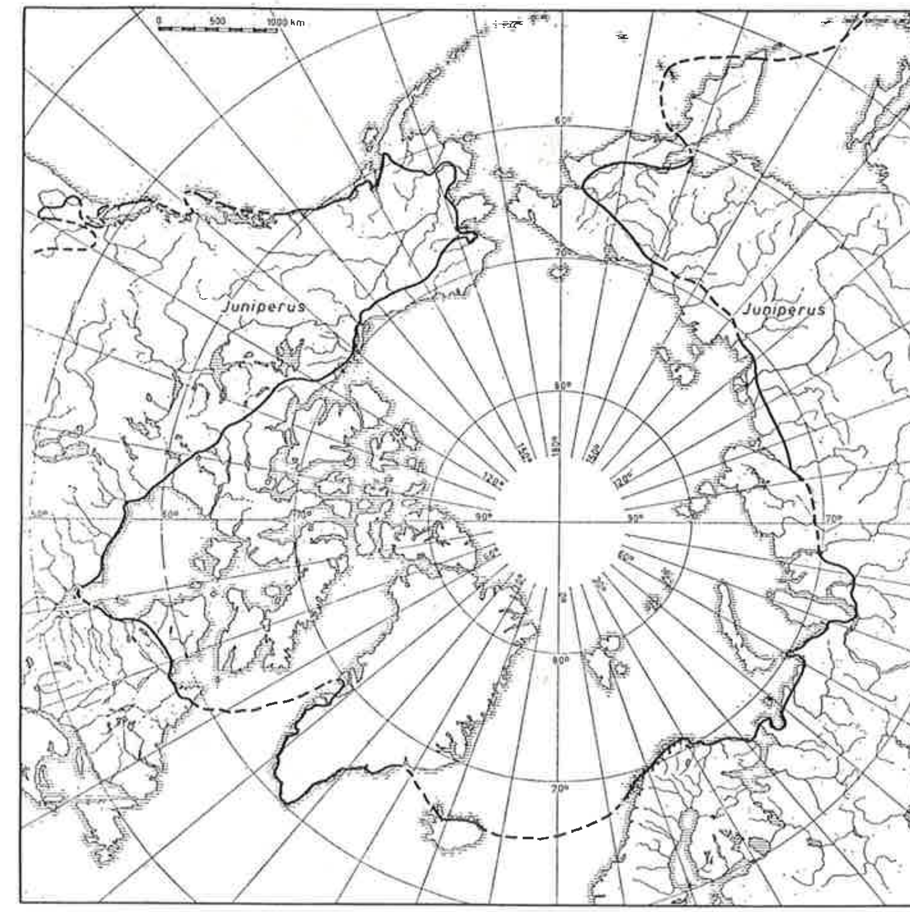
The Siberian larch appears to be a non-aggressive species, restricted to shores of rivers and lakes, mountain slopes, bogs and similar places (cf. SAMBUK 1930) and the same applies to its western species or sub-species. It is interesting to note how closely SAMBUK's description of the behaviour of the larch in the Pechora region parallels that of the tamarack *(L. laricina)* in eastern Canada.



Map 9. Northern range of species of the genus *Larix.* Note the roughly marked 'divide' between *L. Sukachzewii* Dylis and *L. sibirica* s.str., which here are combined to *L. sibirica* s.l. The range of *L. laricina* in northwestern Canada, as marked here, is uncertain. According to E. HULTÉN (verbal inf.) larch has been recently found near the Mackenzie delta.

In the Yenisey valley this species reaches 69°40' n. Lat. and meets in Pjasiva *L. dahurica,* see below. The pattern of the distribution of larch in its northwestern area has been mapped by ZINSERLING (1935); there is only one locality of larch on the Kola Peninsula, see map 9. Another isolated larch locality is reported from Siberia from near 72° N. Lat. (cf. DYLIS 1948, not marked on map 9 above); the same locality is mentioned by TOLMACHEV (1960, p. 70).

Larix dahurica Turcz. forms extensive forests in the eastern Siberian taiga, and entirely dominates the northern forest region east of the Stanovoy Mountains. *(L. Cajanderi* Mayr, likewise credited to eastern Siberia, is according to OSTENFELD and LARSEN (1930) the same species as *L. dahurica* (= *L. Gmelini* (Rupr.) Gordon.)

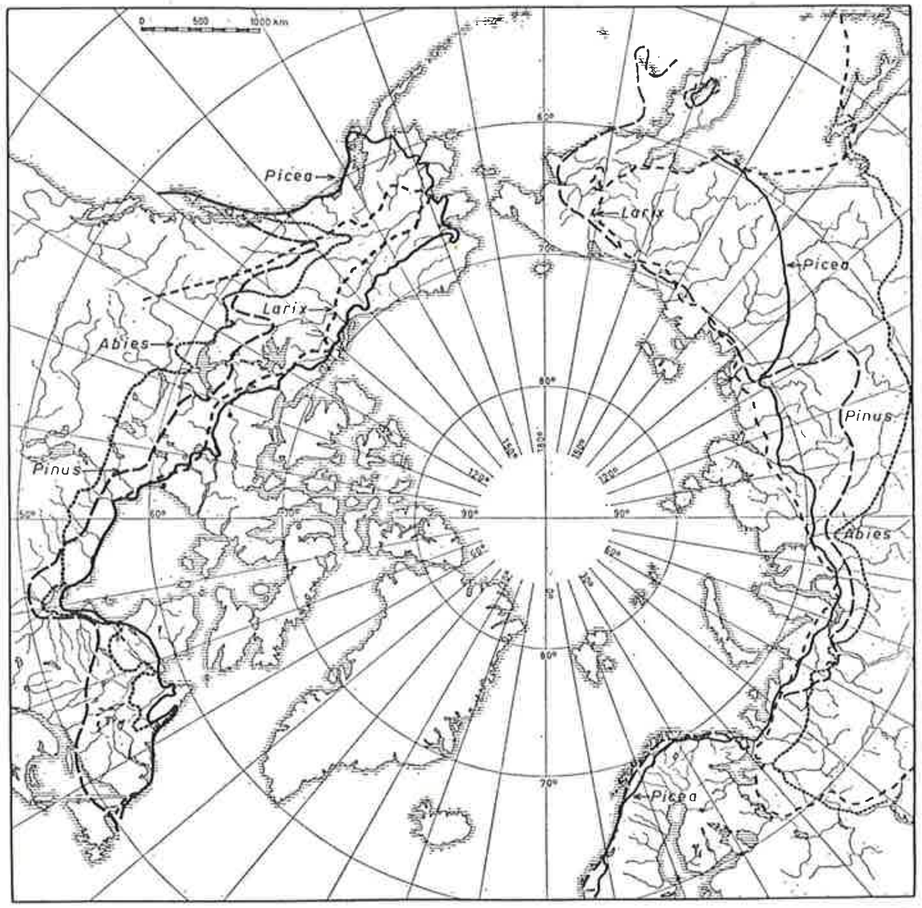


Map 10. Northern range of subspecies of *Juniperus communis* s.l., mainly according to HULTÉN 1962.

The Dahurian larch is the most prominent conifer of the Eurasian polar tree-line, it reaches farther north than any other coniferous species, see map 11. According to TOLMACHEV (1960, p. 72) it grows at Pjasiva at 70°30' N. Lat. and in the valley of Novoy River, north of Chatanga, at 72°37' N. Lat. The larch grove on Tit-Ari-island at 72° N. Lat. in the Lena River (TIKHOMIROV 1957, p. 36) is often described.

In Siberia, larch often forms the polar tree-line, and towards the east also the forest-limit. But the North American larch or tamarack *(L. laricina* (DuRoi) Koch), although widespread in the forest-tunda, rarely forms forests; in Labrador larch may occasionally form lichen woodlands (H 1954).

The large peatlands of the Sub-Arctic Hudson Bay Lowland (H 1957) are covered for miles with low, sparse and pure larch forest; the even age is partly



Map 11. The northern range of species of *Picea, Abies, Pinus* and *Larix,* a combination of information on maps 4, 6, 7 and 9 above. Note here, as on map 15, how different the tree species composition is in the four corners of the forest-tundra.

a result of the attacks by larch-sawfly some decades ago. But towards the cold bay white spruce forms the maritime tree-line proper (cf. Moir 1954), mainly on the sandy ridges, i.e. the only localities with good drainage in the surrounding peatlands.

Across north-western Canada larch, together with white and black spruce, forms the polar tree-line, generally a little behind the spruce.

The Alaskan larch has been distinguished as *L. alaskensis* Wight, a name which has not been accepted generally; Raup (1947) considers it a geographic race (*L. laricina* var. *alaskensis* (Wight) Raup), which extends into north-western Canada.

5. *Juniperus, Tsuga* and *Thuja.* The juniper *(Juniperus communis* L.) is never tree-like in the far north. However, it reaches farther north than other conifers, and for this reason its range (including *J. communis* var. *montana* Ait., var. *nana* Loud. and *J. sibirica* Burgsd.) is shown on map 10. The juniper (s. l.) is also the only almost completely circumpolar conifer, cf. H 1952 and Hultén 1962; it is the only conifer native to Greenland, Iceland, and perhaps Novaya Zemlya (see H 1952, p. 151).

Neither hemlock species *(Tsuga),* nor cedar or arbor-vitae *(Thuja)* species reach the forest-tundra, even though the eastern white cedar *(Thuja occidentalis* L.) does reach southern James Bay, and *Tsuga heterophylla* (Raf.) Sarg. and *T. Mertensiana* (Bong.) Carr. grow in southern Alaska.

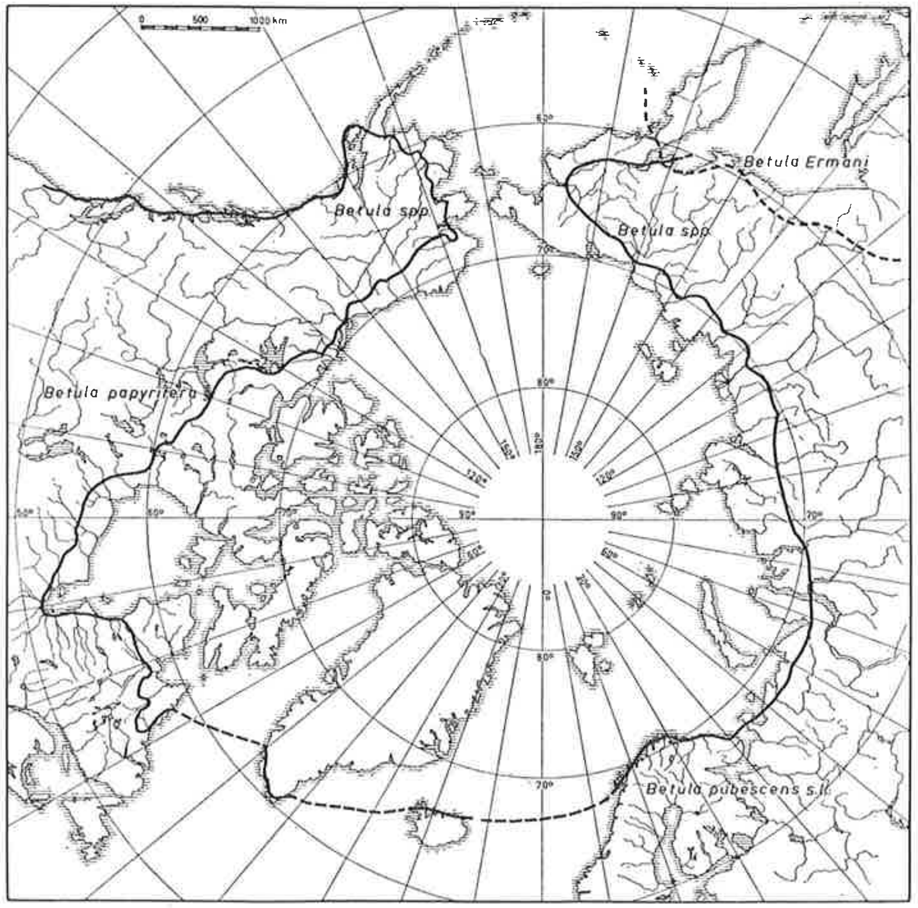
Map 11 combines the maps above of *Picea, Abies, Pinus* and *Larix.* Only the northernmost species of the different conifer genera have been taken into account in this connection. Note *the great difference between the «four corners« of the Arctic and Sub-Arctic, i.e. Alaska, Labrador, Fennoscandia and Anadyr.*

B. Deciduous species

Tree-sized birch, poplar, and aspen reach the polar tree-line in many places. In a few localities some deciduous species reach higher latitudes than the conifers. Species of alder and willows also grow as small trees near or at the polar tree-line and in some cases far beyond it. Particularly from the point of reforestation these small bushes, trees and groves are of importance, because in their shelter conifer seedlings can develop into trees more easily than on the barren tundra. However, the distribution of many of these species is not sufficiently known, and the maps are therefore very tentative. Maps 12—14 include only *Alnus, Betula, Populus, Salix* and *Chosenia* (closely related to *Salix* and of great importance in eastern Siberia). Many birch and particularly willow species never reach tree-size; these species thus form a transition between the arborescent species and the prostrate woody perennials of the Arctic.

1. White birch (Betula spp.). Map 12 shows the polar tree-line (incl. as usual the species-line) of the so-called «white birch«, which in reality includes a number of species (or varieties?). Ecologically and taxonomically these species are so near each other that it is difficult to distinguish the species in areas where the ranges overlap.

In northern Europe the commonest birch at the polar tree-line is usually called *Betula pubescens* Ehrh. However, there are«at least two common, though hardly distinguishable, birch types in the subalpine stand« (Hämet-Ahti 1963, p. 7). Kihlman-Kairamo (1890, p. 163) wrote that «die systematische Trennung der subalpinen Birke von der thalabwärts und weiter gegen Süden waldbildenden Form einer natürlichen Gruppierung nicht entspricht«. Middendorf (1864, p.



Map 12. Northern range of species of the genus *Betula* (excl. dwarf birch species), a preliminary outline.

565) simply uses the name «*B. alba*« for all the white birches of northern Russia, but clearly distinguishes the eastern Siberian *Betula Ermani* Cham. from the ordinary white birch, see below. In Iceland *B. pubescens* is the only tree which forms woods (GRÖNTVED 1942, p. 207). However, it seems very difficult to distinguish with certainty the areas of normal tree-sized white birch in Eurasia and so-called mountain birch, which forms the low scarce woods ('viddas') which are so typical in northern Fennoscandia.

Where pine and birch grow together in the same area as in northern Norway and Finland, the birch usually grows higher up towards the mountains and more northwards on the Arctic coast than pine. The northermost birch forest, probably *B. pubescens,* in the world is situated in Oksevågdalen at 70°57' N. Lat. according to RUDEN (1934, p. 312).

It must be strongly pointed out that the line on map 12 is very tentative only, pending increased knowledge about the taxonomy of *Betulae*.

In North America there seems to be a greater difference between the small-sized birch species *(B. borealis, B.minor,* etc., see below) and tree-sized white birches, at least according to my impressions from north-eastern Canada. *B. papyrifera* Marsh. s. l. is the northern white birch species nearly all over northern Canada. In eastern Canada *B. papyrifera* v. *cordifolia* (Reg.) Fern. goes farthest north. In western Canada and Alaska the main birch in the inland is *B. papyrifera* var. *humilis* Fern. and Raup. (= *B. resinifera* Britton), compare DUGLE (1966).

The white birch is, however, not as common in the northern forests of Canada as in Europe; one reason is the great influence of man in northern Europe; white birch is to a high degree favourably affected by the activities of man, it easily grows after fires. Its proliferous vegetative reproduction allows the birch to fast expand its area. Re. the distribution pattern of white birch in Labrador and the Hudson Bay region, see H 1949 and H 1957, and in Keewatin and Mackenzie, for instance, MACKAY 1958. In Alaska white birch seems to be a little more common than in Canada and together with white spruce it extends more northwards than any other tree species, except balsam poplar (SIGAFOOS 1958).

2. Mountain birch species. It is impossible to map the northern range of the so-called mountain birch species, i. e. *Betula tortuosa* Ledeb. and related species. The mountain birches usually grow as low trees; such forests are often compared to «apple-tree gardens«. The low, twisted, often many-branched mountain birch has no forestry value, except as fuel for the local population. The open mountain birch forests, the 'northern savannas' are, nevertheless, useful in reforestation because pine seedlings grow well in such woods. Particularly in northernmost Europe the area of mountain mirch has increased, due to forest fires and lumbering.

The main mountain birch species in Europe is mostly called *B. tortuosa* Ledeb. According to HYLANDER (1965, p. 299—300) this name should be avoided, the mountain birches in Fennoscandia belong to *B. pubescens* s.l., compare HÄMET-AHTI (1963). HULTÉN wrote recently in desperation that the «taxonomy within the genus *Betula* is today more confused than ever« (1958, p. 66). There are some related 'species' to *B. tortuosa* which ecologically seem to be almost similar, e.g. *B. subarctica* Orl. (Fl. Murm. Obl. III, p. 126) in the Kola Peninsula (probably in northern Scandinavia as well), and *B. callosa* Notö, which occurs in Iceland, in Scandinavia and as far as the Yenisey (LINDQUIST 1945, p. 181).

According to HÄMET-AHTI (l. c.) «*Betula 'tortuosa'* is distributed as far as N. W. Siberia, perhaps even to the Lena River - - - but no continuous, pure subarctic birch forest zone can be distinguished. - - - However, this birch seems to be common in the forest-tundra and may occasionally form pure stands, which east of the Petchora River - - - are probably only present near villages and burnt-over areas«. Leskov regarded the southern limit of the mass occurrence of mountain birch as a good indicator of the boundary between the forest-tundra and the taiga (quoted acc. to Hämet-Ahti l. c.).

In Siberia, *B. Kusmischeffii* (Reg.) Suk., *B. Cajanderi* Suk. and *B. Ermani* Cham. seem to be the vicariant or substitution taxon of *B.tortuosa,* at least ecologically. Dealing with the circumpolar mountain birch forests, Hämet-Ahti writes (l.c., p. 3) that «it is obviously fully correct to interprete all the *B. Ermani* forests as Pacific counterparts to the Atlantic *B. «tortuosa« forests«.* According to Vassiljev (1956, p. 128 etc.) *B. Cajanderi* might be the equivalent of *B. Ermani* in the Anadyr area.

In North America mountain birch is of no importance near or at the conifer tree-line. The effect of man has been smaller in the North American taiga than in similar parts in Eurasia. Re. *Betula minor* (Tuck.) Fern., Fernald wrote that «it closely simulates the Arctic Eurasian and Greenland bush, there passing as *B. alba* var. *tortuosa* (Ledeb.) Schneider - - - « (1945, p. 307). But *B. minor* never forms similar large Sub-Alpine or Sub-Arctic forests as *B. «tortuosa«.* Another Canadian species is *B. borealis* Spach (= *B. microphylla* Bunge?). In western North America the water birch, *B. fontinalis* Sargent, grows scattered up to the polar tree-line, see map in Dugle (1966).

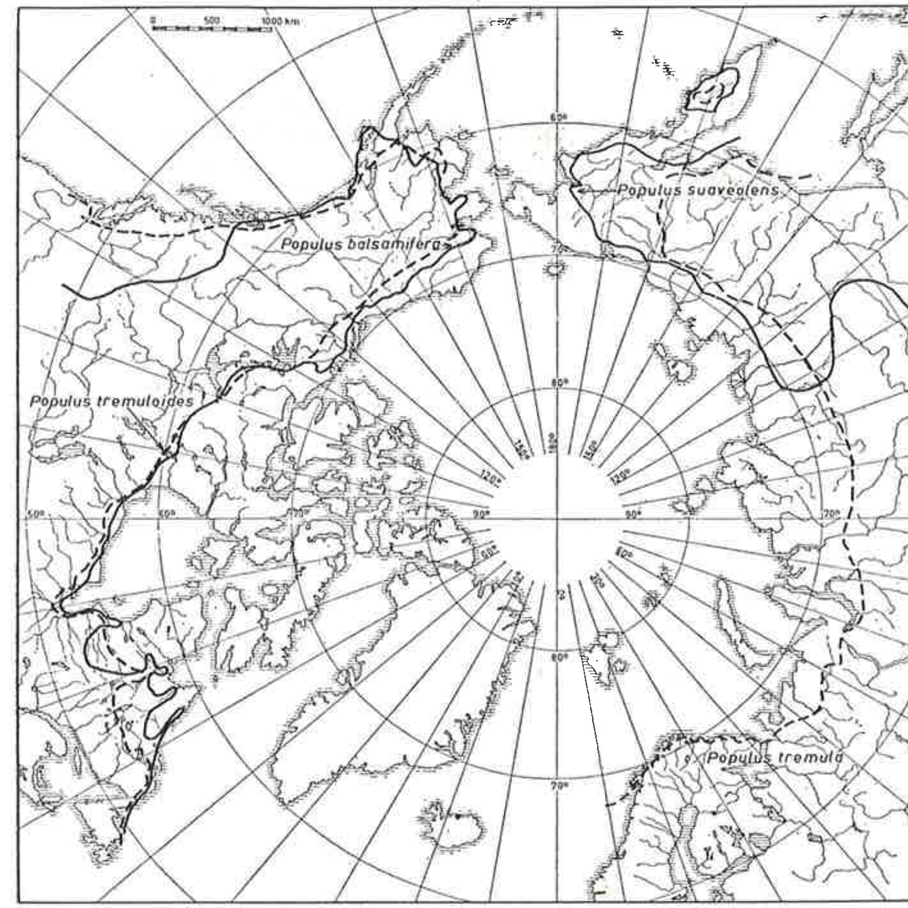
3. Populus. Poplars of the Section *Tacamahaca* reach commonly the conifer tree-line in eastern Siberia, in Alaska and Canada and in a few cases go beyond it.

The balsam poplars have a strong capacity to form vegetative shoots and easily invade recently deposited river shores (cf. H 1957, p. 18—20). Poplars and aspens have male and female inflorescences on different trees, which, of course, considerably restricts their generative reproduction capacity in the margins of their areas. Balsam poplar and aspen often form large clones by vegetative reproduction; they also rot easily.

The Eurasian balsam poplar (*P. suaveolens* Fisch.) has a northern range which is very similar to *Pinus pumila* and *Chosenia macrolepis,* see map 13. It grows scattered and also as a rather high tree on rich alluvial habitats in the far north.

In North America *P. balsamifera* L. (= *P. tacamahaca* Michx.) reaches the forest-tundra (cf. i. a. Dutilly and Lepage 1951) along river banks and southern slopes with good soil and less permafrost than the surroundings, and it goes beyond the coniferous tree-line in westernmost Canada and Alaska.

Map 18 shows the northern limits of the aspen species of interest in this connection, i. e. *P. tremula* L. in Eurasia and Iceland, see below, and *P. tremuloides* in Canada and Alaska. Aspen roots can lie for tens of years in the ground and suddenly grow up, after a fire, for instance. Aspen sometimes forms



Map 13. The northern range of species of the genus ***Populus.*** *P. tremula* in Iceland occurs also on 4 localities in W. Iceland (E. Einarsson, verbal inf.).

large prostrate shrubs on exposed mountain plateaus, but on some suitable southern slopes in the forest-tundra in Utsjoki and Finnmark elegant stands of high aspen grow where pine and birch are more or less twisted and deformed.

The northern aspen and poplar species need more study from several points of view, not least in regard to their importance in reforestation.

Other *Populus*-species, such as *P. trichocharpa* Torr. & Gray, grow in Alaska, but do not reach in the forest-tundra proper.

4. Alnus, Salix, Chosenia and *Sorbus* are represented at or very near the conifer tree-line; in many cases, mainly as bushes, they reach beyond it.

Map 14 roughly illustrates the northern range of alder and willow 'trees'; their distribution is not as well known as the ranges of spruces, larch, etc.

Map 14. A first attempt to mark the northern limit of *Alnus* and more or less tree-sized *Salices.* Re. the northernmost localities of tree-sized *Salix* in northwestern America, compare JOHANSEN 1924, SPETZMAN 1959 a.o. Re. *Salices* in northern Eurasia, see i.a. HULTÉN 1950, HYLANDER 1965, LUNDSTRÖM 1888 a.o. The distribution of *Chosenia macrolepis* is better known, see NORIN 1958.

In Fennoscandia *Alnus incana* Moench. v. *borealis* Norrl. goes far to the north as a small tree up to 70°30' N. Lat. and in the Kola Peninsula to 69°30', here a variety of *Alnus incana* is called *A. kolaënsis* Orl. (Fl. Murm. Obl. III, p. 200). In northern Eurasia and Siberia *A. fruticosa* Rupr. reaches in Chatanga 71°45' N. Lat. and in Taimyr 70°45' N. Lat., often as a small tree.

In northwestern Canada *A. tenuifolia* Nutt. commonly reaches tree-size. In Eastern Canada *A. crispa* (Ait.) Pursh. grows in the far north, but does not attain tree-size. *A. crispa* is an important species on lake shores and near the summits of the coastal mountains of Labrador, for instance. According to FERNALD

(1945) the vicarious species of the European *A. incana* in Canada is *A. rugosa* (DuRoi) Spreng. v. *americana* (Reg.) Fern., which however does not reach into the forest-tundra.

The alders are important as «soil makers« and as shelter for conifers near the tree-line. From the reforestation point of view, the distribution of alder is of great importance and should be much more studied, particularly its ecology in the north.

Willows grow as small trees in the forest-tundra; in very few cases tree-sized *Salices* reach beyond the conifer tree-line. However, the taxonomy of the circumpolar willows is not clear. On map 14 I have tried to outline the distribution of such *Salix*-species which are known to reach tree-size even in the far north. Willows can often play the same pioneer role as mountain birch and alder in the forest-tundra. At the tree-line on the west coast of Hudson Bay, for instance, the best developed young white spruce trees grow in high willow thickets (H 1957).

In northern Scandinavia tree-like *Salix caprea* L. goes up to Varanger. In parts of Siberia at the polar tree-line the tree-sized *S. viminalis L.* and *S. speciosa* Hook. are of some importance. *S. speciosa* also grows in Alaska, here called *S. alaxensis* (Anderss.) Cow. (RAUP 1943, p. 115). *S. alaxensis* grows 25 feet high on the Arctic slope (SPETZMAN 1959, p. 45) and is there the main source of firewood, cf JOHANSEN 1924. *S. jenisseiensis,* a similar species, grows as a 5—6 metres high tree at Lena up to 70°45' N. Lat. (NORIN 1958, p. 848). In Canada *S. Bebbiana* Sarg. (which also grows in Anadyr, see VASSILIEV 1956) reaches tree-size but does not extend near the tree-line.

Chosenia macrolepis (Turcz.) Kom. is an anemochore 'willow'-species, which usually grows as a high tree in north-eastern Siberia, see map 14, where in places, together with *Populus suaveolens,* it is the only tree species, cf. also the map of *Pinus pumila.* NORIN, see above, mentions the species from Lena River at about 70°45' N. Lat., where it grows as a 8—10 m high tree.

Sorbus aucuparia L. occurs scattered as a small tree in the forest-tundra. In northern Scandinavia the mountain ash (usually its var. *glabrata* (W. & G.) Hedl.) grows as far north as the white birch (RUDEN 1934, p. 312); it also is sometimes seen high up in the Sub-Alpine region on the northern mountains in Scandinavia as in the Kola Peninsula (KIHLMAN-KAIRAMO 1890, p. 75) and in Iceland (GRÖNTVED 1942, p. 217). Greenland's mountain ash is another species, *S. decora* (Sarg.) Schneid. v. *groenlandica* (Schneid.) Jones, which also grows in Labrador, but rarely in the forest-tundra. Because of the scarce information available the distribution of the *Sorbus*-species is not mapped here.

The deciduous species are not easy to map; some genera are still taxonomically unclear. But all over the circumpolar forest-tundra there are at least some deciduous species which reach tree-size and, thus, are of importance for the understanding of the effect of the climate on tree growth.

III. COMPARISON OF THE TREE-LINES OF CONIFEROUS AND DECIDUOUS SPECIES

The similarity of the ecology of tree-line trees has often been stressed. The description above and the maps show how different the *species* composition is in different parts of the circumpolar tree-line.

I have below (see map 15) tried to illustrate the possible difference in distribution of different tree species and 'tree-types' by dividing tthe species concerned into three categories: evergreen conifers, larch and broad-leaved species. The main difference between these tree-types is their different response to winter climate. The following collective tree-lines (incl. the relevant species-lines) are compared:

a. a combination of the tree-lines of all evergreen conifers mapped above, except *Pinus pumila* and *Juniperus* spp.

b. the tree-line of larch.

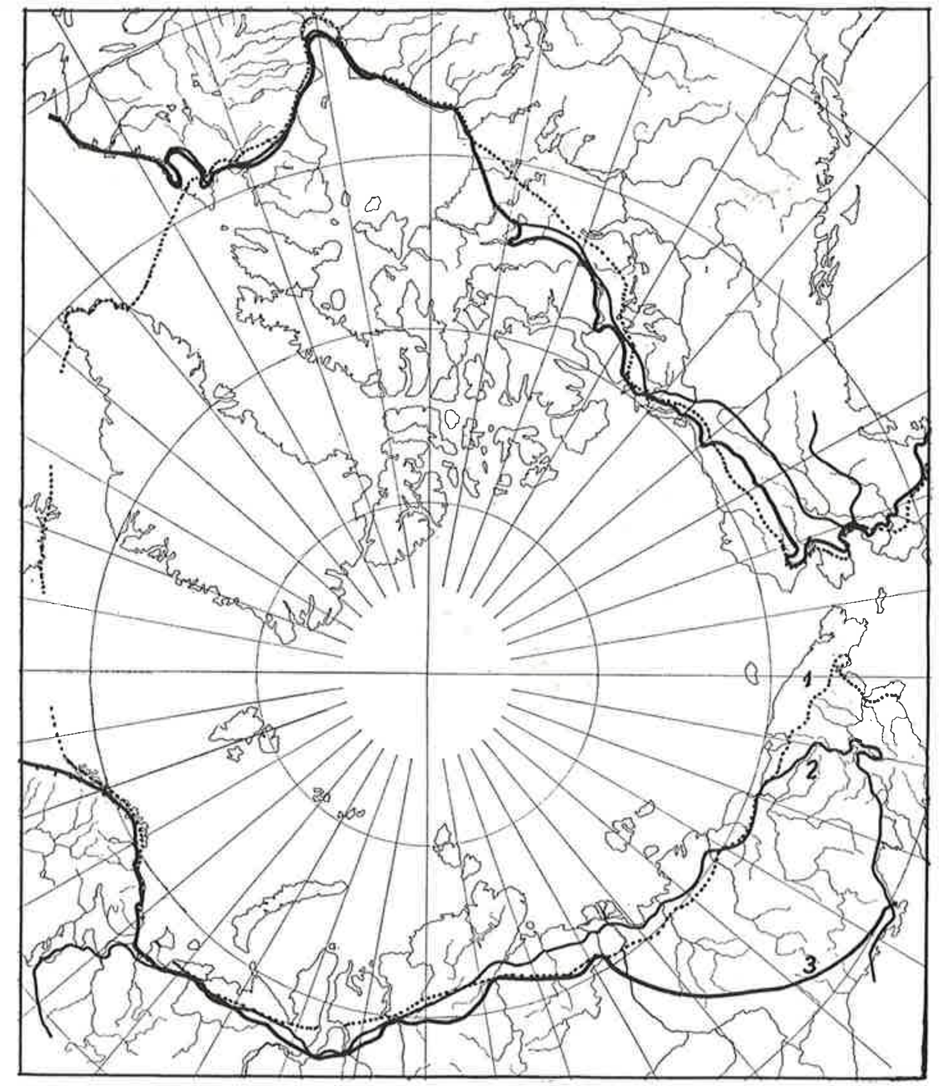
c. a combination of the tree-lines of deciduous species which reach tree-size. Owing to our unsatisfactory knowledge of the willow, mountain birch and alder species, the line 1 on map 15 is, however, in fact a combination of the ranges of white birch (coll.), poplar, aspen and Chosenia, which can all attain tree-size even at their northernmost localities.

If we compare these different tree-lines on map 15, we note that there is not a particularly great degree of difference, except in eastern Siberia.

The pattern of these three physiologically and ecologically different tree-lines should be analyzed according to their response to the climate. It might also be of interest from the point of view of the possibility of reforestation in the future. However, this problem will be dealt with in an other connection.

The occurrence of tree-sized broad-leaved species but no spontaneous conifer species in Iceland and Greenland must be noted. Which is the real reason for this great anomaly from the usual pattern of the tree line? Another anomaly on the map 15 is the absence of larch in northern Scandinavia, for which it is hard to assume a climatic factor; perhaps the Fennoscandian Pre-Cambrian shield forms a barrier, compare KASHIN and KOZOBRODOV (1966) and ZINSERLING (1935).

One point in this connection is stressed by KRYUCHKOV (1961, p. 4): «If spruce in winter loose more moisture than birches, this is due to the fact that the transpiration surface of spruce in winter is hundreds of times larger than that of birch trees. In spruce the water balance is disturbed more violently and more frequently in winter and spring than in birch trees and this often leads to their ruin. For this reason the forest tundra of the Kola peninsula is composed primarily of birch trees, which, in turn, occur in low-lying and sheltered places. Spruce begins to appear somewhat farther south, in the shelter of the birch belt.« Although this statement is only partly correct (note man's influence in creating



Map 15. A. comparison of (1) the northern range of broad-leaved trees (combined of more or less tree-sized *Betula, Populus* and *Chosenia*), (2) the northern range of *Larix* and of (3) evergreen conifers.

the birch forests in European Russia, for instance) there is certainly some truth in it. Is the absence of suitable hardy mountain birch species one reason why the distribution of conifers is so restricted west of Hudson Bay?

IV. GENERAL REMARKS ON THE FOREST-TUNDRA

The circumpolar forest-tundra, or the Sub-Arctic s. str., is different from place to place in its topography, its bedrock and quaternary history.

Sedimentary and Archaean bedrock alternate over the forest-tundra zone as limited on map 2 above. The influence of the bedrock on the floristic composition of the vegetation is wellknown (compare the serpentine-discussion) as also the fact that a certain content of lime is often found in the habitats of the northernmost outposts of certain species. A welldrained southern exposition is in itself a positive factor in this connection, particularly if associated with positive soil factors, compare the extensive literature concerning the *'sydbergs'* in northern Sweden (SJÖRS 1956, etc.).

Norway spruce seems to grow well i.a. on Cambro-Silurian sedimentary bedrock or on till of such material. Scotch pine, as jack pine a.o., is on the other hand more prominent in areas dominated by more acid bedrock. Siberian larch on its western border 'prefers' sedimentary bedrock or limestone and dolomite outcrops, but avoids the Pre-Cambrian bedrock. The important components of the Canadian taiga and forest-tundra, white and black spruce, differ in this respect, as the wellknown explorer LOW (1895) pointed out long ago. Black spruce occurs generally on more acid bedrock and on soil with low pH-values, whereas white spruce grows on rich clayey and alluvial soils in river valleys; large areas in Labrador lack white spruce because of this edaphic difference between the two species. The mosaic of white spruce and black spruce groves at the tree-line in northwestern Canada can partly be explained by the bedrock pattern.

White spruce, Siberian larch, cedar and balsam poplar seem to prefer or at least not to avoid basic sedimentary bedrock. Tree-line species which seem to prefer acid bedrock are jack pine, black spruce and aspen.

In many parts of the forest-tundra zone there are large peatland areas, where tree growth is restricted. However in some areas trees grow well on peat. The accumulation of peat slowly changes the influence of the underlying bedrock. In the Hudson Bay Lowlands (cf. H 1957, RITCHIE 1958, SJÖRS 1961, etc.) black spruce grows on old peat soils, probably at earlier times covered with larch or white spruce. The conditions are probably in many ways similar in northern Russia and western Siberia. Generally, however, peatlands restrict tree growth and the polar tree-line reaches northwards not on peatlands but in river valleys and on south-exposed low mountain slopes.

A problem which has often been discussed is the relation between permafrost and tree growth. If we try to compare only large scale maps of the southern limit of permafrost and the northern limit of trees it is difficult to find a correlation. This is because permafrost in fact does not restrict the growth of all tree species to the same degree.

Recently HOPKINS and others (1955) have made a study of the relation between permafrost and tree growth in Alaska. They point out (p. 137) that «tall willow shrubs and isolated pure stands of balsam poplar on river flood plains generally indicate the presence of unfrozen ground«; the minimum depths of permafrost beneath tall willows on flood plains is about 8 feet, under pure stands of mature aspen or white birch 4 feet and under mixed white spruce and balsam poplar 3 feet, whereas black spruce can grow in wet tundra or muskeg with permafrost only 1 foot under the ground. «On the lower reaches of the river Kolyma larch grows almost in moss alone, for under the mosses in the forest there is pure ice« (SHVETSOV 1963, p. 774). The wellknown «black spruce islands« in the north (cf. ANDREEV 1956, H 1957, SJÖRS 1961), which are a common feature of large peatlands near the tree-line, are favorable sites for the preservation of permafrost. The occurrence of palsa bogs at the southern line of permafrost correlates well with the northern tree-line (AUER 1927, H 1939 and others).

The only conifers which seem to 'avoid' permafrost and even 'semipermafrost' are Scotch and jack pine. Their root systems generally go deep, whereas black spruce (cf., for instance, HORTON and LEES 1961) and also larch have a rather shallow root system.

The destructive effect of a fire is very strong in the forest-tundra (H 1954), because i.a. of the insufficient supply of seeds for regeneration. Usually conifers in such localities are followed by birch; the effective sprouting of the birch stumps left over by the fire is an important factor. This succession accounts to a high degree for the character of the Utsjoki «pseudo-tundra« in northernmost Finland and is, of course, seen all over the circumpolar forest-tundra. The effect of fires on the species composition of the forest-tundra cannot be underestimated. LUTZ writes re conditions in Alaska that as a result of repeated fires, «areas formerly in white spruce may become essentially treeless, supporting herbaceous or shrub communities. Fireweed-grass and dwarf birch-willow may become so firmly established that it is difficult for forest-tree seedlings to become established. Natural reconversion of such lands to forest may require 100 to 200 years. Fires are most likely to result in replacement of white spruce forest by relatively permanent treeless communities at the upper altitudinal and latitudinal limit of forest growth« (1955, p. 92). The areas of lichen woodlands which occur scattered in the forest-tundra zone are plainly the most susceptible. The fires also account for a certain paludification of the forests, etc. (cf. H 1957, p. 36—37). SIRÉN (1961) describes the effects of forest fires in the forest-tundra zone in northern Finland and mentions cases of char coal, stumps, etc. of pine far away from the present trees and stands in the forest-tundra. The farther north we go, the more destructive is the effect of forest fires, particularly on spruce. In Labrador the effect of forest fires is wellknown and causes the emergence of «tundra« on formerly wooded slopes.

Thus, the succession of tree species in the forest-tundra and the predominance or scarceness of deciduous tree species in places can be attributed not only to the effects of the climate or of bedrock, permafrost and other edaphic factors, but also to the effect of fires in earlier times. It is probable that fires in the forest-tundra have been largely caused by man. There is already an extensive literature on this subject.

In some parts of the forest-tundra land rises continuously because of the isostatic movement as a result of the glaciation. At least along the west coast of Hudson Bay it seems as if the species have advanced in accordance with the speed of the rising of the land. In areas with low shores and peatlands, there are restrictive edaphic conditions for some tree species, such as pine, balsam fir, aspen and white birch (see H 1957), but for some other tree species we don't know if the reasons for their absence along the shores of Hudson Bay and James Bay is due to edaphic conditions or to a too slow expansion in postglacial time; in this area the macroclimate itself is no restrictive factor. BELL (1897) points out that balsam poplar generally avoids the sea. RITCHIE has illustrated how the white spruce forest invades the younger shrub-dominated plains near Hudson Bay and is ultimately replaced by a black spruce community on large peat mounds (1957, p. 432), compare also MOIR 1954 and H 1957.

The supposed vegetation during the last glaciation is of interest. The forest tree-line existed at that time near the Charpatians and in the Ukraine, but in eastern Siberia forest occurred north of the Arctic Circle at Lena and Chatanga. In the area of the Lena mountains the composition of the forest was about the same during the whole Quaternary period as today (FRENZEL 1960). This certainly had a great effect on the tree species composition in that area today, cf. BOJARSKAJA 1965.

In North America only Alaska was free of ice during the last glaciation as well as earlier. According to BENNINGHOFF (1954) the fossil flora in the unglaciated Fairbanks district from about 22,000 years ago revealed no contrast to the present vegetation. During the last 15,000 years glacial advances and retreats in the Cook Inlet region have been accompanied by shifts in the distribution of the coastal Sitka-spruce forest, the spruce-birch interior forest, and tundra bog vegetation, but apparently without changes in the distribution of the species in the region. BENNINGHOFF concludes that some facts «suggest partition of floras by the Bering Strait in pre-Pleistocene time, with no subsequent exchange of forest species« (1954, p. 246), cf. COLINVAUX 1963. This is an important fact when dealing with the historical distribution of tree-line forming species.

Only one conifer species is in present time circumpolar in the forest-tundra, *Juniperus communis* s.l. Not even among deciduous trees, there seems to be any species (except *Salix alaxensis (S. speciosa)* which sometimes reaches tree-size) which occurs on both sides of the Bering Strait. Whether this is a result of different history or of the deep-felt respect of the taxonomists for the Bering Strait is difficult to know. However, according to YURTSEV (1963) white spruce has been found in interglacial deposits in eastern Siberia.

In North America spruce and larch were according to HULTÉN among the species which during the interglacial extended their area beyond the southern boundary of the maximal glaciation. Thus, these species survived south of the ice and were able to fill out their area from there. HALLIDAY and BROWN (1949) supported this theory regarding the common Canadian tree species.

It is believed, according to a much discussed theory, cf. LÖVE and LÖVE (1963), that on so-called «refuges« several plants and animals «overwintered« the last glaciation. Regarding the existence of such refuges the biologists (but not the geologists) seem to agree, only the number of species that could have lived there is discussed. The location of the supposed refuges during the glaciation in North America is more doubtful, particularly the existence of refuges in north-eastern Canada is an unsolved problem so far. Most authors seem to agree that no tree species could qualify as «overwinterers«. Nevertheless, LINDQUIST (1948) believed that *Picea excelsa* v. *arctica* had existed during the glaciation on the North Scandinavian refuges.

I have above compiled a few facts regarding the history of the tree species in the forest tundra. As maps marking the maximal glaciation and the last glaciation show, nearly the whole forest-tundra zone was covered by ice with the exception of central Alaska and parts of central Siberia. But, omitting perhaps the attempts to describe some Alaskan tree species as separate varieties of generally distributed species, there is at least no easily understood correlation between the distribution of the tree species today and their supposed glacial history.

As regards the prospects of reforestation, it might be easier to operate with a species still in expansion than with a species which reached its present range several thousand years ago. But the essence of this can be judged only by studying the genetics of the tree species in question.

Since Pre-historic time man has moved across and along the northern tree-lines. In the forest-tundra zone the sparsely and slowly growing trees have been much in demand for fuel or building material. In some areas as in northern Europe, where the nomads and settlers were more numerous, this had a locally disastrous effect. In the forest-tundra zone mature seeds are formed only occasionally, depending on the climate of the summers, see RENVALL 1912 HAGEM 1917, KUJALA 1927, H 1948, a.o.

There are nowadays few areas near or at the polar tree-line which have not been at least to some degree affected by man or his herds of reindeer. The activity of man has periodically accentuated or neutralized the effect of the climatic fluctuations.

There is also in this respect a marked difference between the different tree species. Some tree species have a rapid vegetative reproduction through layering or other means, some are easily eliminated after cutting or fire, etc. The spruces and larches as also the deciduous tree species have generally a good vegetative reproduction. The pines, on the other hand, hardly ever (exept the Siberian dwarf pine) have any layering or similar means of vegetative reproduction.

The influence of man has, thus, also been *selective* in regard to the species structure of the forest-tundra and the tree-lines.

Earlier Russian authors describe vividly the effect of mans activity along the important trade route from Mesen to Obdorsk. The forest-tundra in European Russia was more densely populated in the 16. and 17. century than in the beginning of this century (MIDDENDORFF 1864, SHITKOV 1911 and POHLE 1917). On the other hand, the Polyarnij Ural, for instance, was until recently little affected by man (GORODKOV 1926). Omitting a large number of references re man's activity at the forest-line, I, however, here only quote NAUMENKO (1966, p. 49) on *Larix dahurica* in the Kolyma basin (see map 9): «The natural and anthropogenous factors, among which the fires are of major importance, contribute to the decrease of the forest protective potential of the area in question. It is an urgent necessity to establish a forest shelter-belt about 150—200 km wide and to accomplish in it a special complex of measures of forest-protection and reforestation.« Exactly the same was said about the northernmost forests in Finnish Lapland in the 1910's and 1920's. How many decades will it take before the same urgent need suddenly is felt in Alaska and Canada?

The Lapps in Scandinavia and Finland have changed large parts of the northernmost forests and created a forest tundra or «pseudo-tundra« (SIRÉN 1961). According to HEIKINHEIMO (1921) one Finnish settler-family in the forest tundra used annually 120—130 m^3 wood for fuel only, i.e. roughly the annual growth of about 600 hectars, if we assume that the annual increment in the northernmost pine forest is about 0,2 m^3 per hectare (EIDE 1924).

The fire-wood problem in the North American Arctic was in many places on the coast easily solved by driftwood from the great rivers. The Eskimos moving in the barren grounds in northwestern Canada had, however, difficulties, cf. TYRRELL 1896—7. It is difficult to know how much man has been responsible for the present irregularity of the tree-line in the Northwest Territories, but seemingly, however, less than in Eurasia.

The role of reindeer in the forest-tundra has been much discussed. Reindeer and caribou destroy young seedlings and also older trees during the hornfelling time in the autumn. RENVALL (1919) extensively studied the subject in Finnish Lapland. He recommended several measures against the damage done by the reindeer in the northern Scotch pine forests where the reproduction from seed is uncertain. ANDREEV (1954) observed that at least 75 % of all dead trees at or near the tree-line were destroyed by reindeer; he advocated strong control measures against reindeer grazing in the forest-tundra.

The effect of the reindeer is not always negative. Reindeers move around with tree seeds in their cloves and skin, a 'zoo-chore' dispersal of seeds which should be more thoroughly investigated. With the «parcels« of *Cladina* lichens used for reindeer travelling in winter, pine and spruce seeds have occasionally been brought long distances (cf. H 1958).

In North America the destructive effect of the large caribou herds on tree growth have not been studied as intensively as the damage done by reindeers in northern Europe; the caribous do not to any high degree move in commercially exploited forests. RITCHIE (1959) describes the effect caused by caribou in grazing areas in northern Manitoba which has changed the structure of the lichen vegetation, compare also CLARKE (1940), HARPER (1955) and H 1951.

In recent years the way of life has changed strongly also in the Sub-Arctic. The nomads are not moving any more. Lapps, Samojeds, Jakutes and Chukchis a.o. Arctic and Sub-Arctic peoples live normally in huts. Thus, the direct destructive effect of man in vast areas of the forest tundra has considerably decreased during the recent decades. Isolated farms have been left in the far north in Finland and Scandinavia when people move southwards or into the nearest villages and towns. The urbanisation has increased all over. The Kola Peninsula was formerly inhabited mainly by Reindeer Lapps or by Lapps living of fishing in coastal waters. This area has now one of the highest urbanisation percentages (85 %) anywhere. In Canada and Alaska, Indians and Eskimos in the forest-tundra have moved into large government-planned or -sponsored settlements and only partly make their living out of game and fish.

The forest-tundra itself is, therefore, less densely populated nowadays than in the last centuries. On the other hand, the need of raw materials for an increased forest industry brings also the hitherto inaccessible resources into consideration. This means increased movement of the forest industry into the forest-tundra. It also means an increased understanding of the need for reforestation wherever possible. These problems of the foresters in Scandinavia and Finland will soon be the problems of USSR, Canada and Alaska.

Many and various opinions have been expressed in recent decades regarding the possibility of reforestation of the forest-tundra. There is a clear correlation between the views of the forest scientists in this respect and the «quality« of climate at the time when they expressed their views, see H 1948. Scientists working at the beginning of the century in northern Europe were rather pessimistic about the possibilities of «moving« the economic forest-limit to the north. The forest-limit concept was also earlier considered a rather static one, but now we know that this phytogeographical border certainly is a very dynamic one. The tree-line moves north when the climate improves and stagnates again when the summer climate gets colder for longer periods. The pessimistic view still prevailing in the twenties regarding tree planting in the north has however gradually changed into a more optimistic view, particularly often expressed during and immediately after the well verified climatic improvement in the thirties, cf. H 1948, MIKOLA 1950, 1959, ERKAMO 1956 and SIRÉN 1961.

We can move towards active reforestation by preserving the outposts of the forest and by increasing the possibilities of natural regeneration at the present polar tree-line. Man can also create completely new forests using the same species as those which make up the nearest natural forests or by introducing entirely new species which in other places with similar conditions have done well. Nowadays, tree planting has been done successfully in Iceland and northernmost Norway and it has been tried in Greenland of all places, thus, preventing further political disturbances by eliminating the need to look for timber in «Vinland«.

Finally a short survey re. the correlation between climatic factors and tree-growth at the tree-line. Such a correlation can be established by using two different approaches:

a) we can compare the present tree-line with isotherms of the warmest months, a much used method, and, thus, visually get an idea of the correlation between climate and tree-line. We can also use in this context temperature sums of the summer or of the growth season or more elaborate indices composed of temperature, precipitation, radiation, etc.

b) we can correlate the annual tree growth (easiest to use and measure is growth in thickness) of trees in the north with temperature series and with combined climatic indicators using, for instance, multiple regression analysis.

In many connections I have pointed out that climate in the north changes from year to year and that this «climatic hazard coefficient« as I have called it (H 1948, etc.), is particularly great in the north. Thus, when using isotherms and other climatic devices it must be clearly understood which period they represent.

Isotherms are only crude measurements for illustrating the climate — still more crude than the tree-line approximations on the maps above. But to the north the July isotherm, however, gives a still rough but yet an increasingly accurate correlation with the tree growth. The duration of different growth processes of the forest-tundra pine are concentrated to July. The July Isotherm at the tree-line itself must, therefore, be a better indicator of tree growth than in more southern parts of the boreal forest region, where precipitation comes in as an added influence.

A new approach was introduced by THORNTWAITE in the thirties and used for instance by HARE (1950) to delineate the boreal forest formation in eastern

Canada. THORNTWAITE's annual evapotranspiration function is an accumulating logarithmic function of monthly mean temperatures and the tree-line in eastern Canada seems rather nicely to follow HARE's advice.

ENQUIST's «climatic constant« (1933) for the tree-lines in Sweden is methodologically of a certain interest. Meteorological stations at, outside and inside the tree-line in question were placed in a coordinate system based on number of days and the maximum temperature during these days. According to ENQUIST spruce at its tree-line needed at least 65 days with a maximum temperature of at least 12.5°C to survive. The result is, of course, too exact to be true. The idea was later adopted in a modified way, for instance, by HOPKINS (1959), who tried to evaluate some characteristics of the forest and tundra regions in Alaska.

Of interest in this connection is also an important paper by JEFFREE (1960) on the climatic pattern between 40° and 70°N. lat. and its influence on the distribution of species. JEFFREE operated with the January and July mean temperatures and the logarithm of winter precipitation. HINTIKKA (1963) has used an approach similar to JEFFREE's.

An other method to illustrate the correlation of climate/tree-line is to apply mathematical analysis to define the correlation between the growth of the trees in the north and the climate at the nearest meteorological station. ERLANDSSON (1936), pioneer in this field, showed adequately that the mean temperature in July is a good indicator, a fact previously, of course, recognised but not so well illustrated as in his classic paper. Later HUSTICH and ELFVING (1944) tried a multiple regression analysis using radial growth series of pine from northernmost Finland compared with a differentiated series of climatic indicators. Here, too, the simple July-temperature emerged as the best single indicator. Our paper also demonstrated the important «lag« effect, i.e. the belated effect of a very favourable or a very bad summer on the growth of the tree-line pine in the following years. A similar approach with a greater material and with much longer series was worked out by SIRÉN in 1961.

The annual variations in the growth processes at the tree-line are very prominent and are, of course, not restricted only to growth in thickness. All the vegetative and generative processes of the northernmost trees are interlocked with each other and concentrated to an extremely short growth season at the tree-line. Years with good cone production affect other growth processes of the trees, an interesting subject, which is not yet sufficiently studied. The maximum of female flowering coincides, for instance, with maximum growth of length of the shoots, and this maximum again occurs one year after a good summer in which radial growth reaches its maximum.

We have to understand the physiology of the forest-tundra tree-species to understand in a deeper sense the ecology of the tree-line.

ACKNOWLEDGEMENTS

This paper was originally prepared as an aid to the participants in the UNESCO -sponsored Symposium on Sub-Arctic Egology in Helsinki 1966. I thank Professor P. KALLIO for much encouragement and inclusion of the paper in the Third Report of the Kevo Sub-Arctic Station.

Grateful thanks are tendered to i.a. following participants in the Sub-Arctic Symposium: Dr. T. AHTI, Mr. E. EINARSSON, Professor E. HULTÉN, Professor P. MIKOLA, Professor N. POLUNIN and particularly Dr. IAN SIMMONS for addenda and corrections re both facts and language. Unfortunately, because of the fact that the printing was already in a very advanced stage during the Symposium, only a part of the corrections etc. suggested could be taken into account in this connection.

REFERENCES

The literature mentioned below covers only partly the vast field of research which has gone into the forest-tundra and tree-line question, cf. the comprehensive *Arctic Bibliography*.

AHTI, T. 1964. Macrolichens and their zonal distribution in boreal and arctic Ontario. Ann. Bot. Fenn. 1, 1. Helsinki.

„ , HÄMET-AHTI, L. and JALAS, J. 1964. Luoteis-Euroopan kasvullisuusvyöhykkeistä ja kasvullisuusalueista. Luonnon. Tutk. 68. Helsinki.

ANDREEV, V. N. 1933. Geobotanical Expedition Inst. f. Reindeer Industry to the Yamal Peninsula. Orig. Russ. Bull. Arct. Inst. 1933, 12. Leningrad.

„ 1935. Rastiteljnost i rajoni vostotsnoi tsasti Bolsjezemelskoj tundri. Tr. Polyarn. Kommissii 22. Moskva.

„ 1954. Extension of arboreous plants into the tundra. Orig. Russ. Botan. Journ. Moscow.

„ 1956. The Contemporary Afforestation of the Tundra. Orig. Russ. In TIKHOMIROV 1956, see below.

ARNBORG, T. and EDLUND, E. 1962. Lärkskogar i Sibirien. Norrl. Skogsvårdsförb. Tidskr. Stockholm.

AUER, V. 1927. Untersuchungen über die Waldgrenze und Torfböden in Lappland. Comm. Inst. Quaest. For. Finl. 12.

BELL, R. 1897. The Geographical Distribution of Forest Trees in Canada. The Scott. Geogr. Mag. XIII. 6. Edinburgh.

BENNINGHOFF, W. S. 1952. Interaction of vegetation and soil frost phenomena. Arctic, vol. 5, 1. Montreal.

„ 1954. Quaternary Vegetation of Central-Alaska. VIII Congrés Int. Botan. Paris.

BLÜTHGEN, J. 1942. Die polare Baumgrenze in Lappland. Veröff. Deutsch. Wiss. Inst. zur Kopenhagen, I, 10. Berlin.

BOJARSKAJA, T. D. 1965. Der Grad der Veränderlichkeit der Planzendecke im Pleistocän. Peterm. Mitt. 102. Jena.

BRITTON, M. E. 1957. Vegetation of the Arctic Tundra. 18th. Biol. Coll. Corvallis.

BROCKMANN-JEROSCH, H. 1919. Baumgrenze und Klimacharacter. Pflanzengeogr. Komm. der Schweiz. Naturf. Gesellsch. Zürich.

CAJANDER, A. K. 1903. Beiträge z. Kenntniss der Vegetation der Alluvionen des nördlichen Eurasiens. I. Acta Soc. Scient. Fenn. XXXII, 1. Helsinki.

CLARKE, C. H. D. 1940. A biological investigation of the Thelon Game Sanctuary. Nat. Mus. Canada Bull. 96. Ottawa.

COLINVAUX, P. A. 1963. A Pollen Record from Arctic Alaska. Nature. Vol. 198. London.

DEDOV, A. 1933. Character of the natural feeding ground of the Taimyr circuit. Orig. Russ. Reindeer Industry. Vol. 4. Leningrad.

Derevja i kustarniki SSSR I, II. Acad. Sci. U.S.S.R. Moscow 1949, 1951.

DREW, J. V. and SHANKS, R. E. 1965. Landscape Relationships of Soils and Vegetation in the Forest-Tundra Ecotone. Ecol. Monogr. 35,3. Durham.

DUGLE, J. R. 1966. A taxonomic study of western Canadian species in the genus *Betula*. Can. J. Bot. 44. Ottawa.

DUTILLY, A. et LEPAGE, E. 1951. La traversée de l'Ungava en 1945. Contr. Arct. Inst. Cath. Univ. Amer. 2, F. Washington.

DYLIS, N. V. 1948. Siberian larch. Orig. Russ. Contr. à la Conn. Faune et Flore de l' U.R.S.S. Nouv. Sér., Sect. Bot. 2, 10. Moskva.

EIDE, E. 1934. Furuens vekst og foryngelse i Finnmark. Medd. fr. det Norske Skogforsøksvesen 3. Oslo.

ENQUIST, F. 1933. Trädgränsundersökningar. Sv. Skogsv. för. tidskr. Stockholm.

ERKAMO, V. 1956. Untersuchungen über die pflanzenbiologischen Folgeerscheinungen der neuzeitlichen Klimaschwankung in Finnland. Ann. Bot. Soc. Vanamo 28,3. Helsinki.

ERLANDSSON, S. 1936. Dendrochronological Studies. Data 23. Uppsala.

FERNALD, M. L. 1919. Lithological factors limiting the ranges of Pinus Banksiana and Thuja occidentalis. Rhodora 21. Boston, Mass.

„ 1945. Some North American Corylaceae (Betulaceae). Ibid 47.

Flora Murmanskoy Oblasti I—III. Acad. Sci. U.S.S.R. Moscow 1953—1956.

Flora U.S.S.R. I—V. Orig Russ. Acad. Sci. U.S.S.R. Moscow 1934—1936.

FRENZEL, B. 1960. Die Vegetations- und Landschaftszonen Nord-Eurasiens während der letzten Eiszeit. Abh. Math.-Naturv. Akad. Wiss. und Lit. 6. Mainz.

GORODKOW, B. N. 1926. Der polare Ural im oberen Laufe des Flusses Ob. Orig. Russ. Trav. Mus. Bot. Acad. Sci. U.S.S.R. 19. Moscow—Leningrad.

GRÖNTVED, J. 1942. The Botany of Iceland. IV, 1. Copenhagen.

HAGEM, O. 1917. Furuens og granens frøsaetning i Norge. Medd. Vestl. Forstl. Førs. anst. I, 2. Bergen.

HALLIDAY, W. E. and BROWN, A. W. A. 1943. The distribution of some important forest trees in Canada. Ecology 24. New York.

HANBURY, D. T. 1903. Through the Barren Ground of North-Eastern Canada to the Arctic Coast. Geogr. Journ. 22. London.

HARE, F. K. 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. Geogr. Review 40,4. New York.

„ 1952. Some climatological problems of the Arctic and Subarctic. Compendium of Meteorology. Boston, Mass.

„ 1954. The Boreal Conifer Zone. Geogr. Studies 1,1. London.

HARPER, Fr. 1955. The Barren Ground Caribou of Keewatin. Univ. of Kansas, Misc. Publ. 6. Lawrence.

HEIKINHEIMO, O. 1921. Die Waldgrenzwälder Finnlands und ihre künftige Nutzung. (Ref.) Comm. Inst. Quaest. For. Finl. 4. Helsinki.

HERMES, K. 1955. Die Lage der oberen Waldgrenze in den Gebirgen der Erde. Kölner Geogr. Arb. 5. Köln.

HINTIKKA, V. 1963. Über das Grossklima einiger Pflanzenareale in zwei Klimakoordinatensystemen dargestellt. Ann. Bot. Soc. Vanamo 34,5. Helsinki.
HOPKINS, D., KARLSTROM, T. and others 1955. Permafrost and Ground Water in Alaska. U.S. Geol. Surv. Prof. Paper 264-F. Washington.
„ 1959. Some characteristics of the climate in forest and tundra regions in Alaska. 'Arctic', 12,4. Montreal.
HORTON, W. and LEES, J. C. 1961. Black spruce in the foothills of Alberta. Dept. of For. Techn. Note 110. Ottawa.
HVOSLEF, O. 1956. Skogene nordenfor polarcirkelen. Tidskr. f. Skogsbruk 64. Oslo.
HULTÉN, E. 1950. Atlas över växternas utbredning i Norden. Stockholm.
„ 1962. The circumpolar plants I. Kungl. Sv. Vet. Akad. Handl. IV, 8,5. Stockholm.
HUSTICH, I. 1939. Notes on the coniferous forest and tree limit on the East Coast of Newfoundland-Labrador. Acta Geogr. 7,1. Helsinki.
„ and ELFVING, G. 1944. Die Radialzuwachsvariationen der Waldgrenzkiefer. Soc. Scient. Fenn. Comm. Biol. IX, 11. Helsingfors.
„ 1948. The Scotch Pine in northernmost Finland. Acta Bot. Fenn. 42. Helsinki.
„ 1949. On the Forest-Geography of the Labrador Peninsula. Acta Geogr. 10,2. Helsinki.
„ 1950. Notes on the Forests of the East Coast of Hudson Bay and James Bay. Ibid. 11,1.
„ 1951. The Lichen Woodlands in Labrador. Ibid. 12,1.
„ 1952. The boreal limits of Conifers. Arctic 6,2. Montreal.
„ 1954. On forests and tree growth in the Knob Lake area, Quebec—Labrador Peninsula. Ibid. 13,1.
„ 1957. On the phytogeography of the Subarctic Hudson Bay Lowland. Ibid. 16,1.
„ 1958. On the recent expansion of the Scotch pine in Northern Europe. Fennia 82,3. Helsinki.
HYLANDER, N. 1965. Nordisk Kärlväxtflora II. Stockholm.
HÄMET-AHTI, L. 1963. Zonation of the mountain birch forests in northernmost Fennoscandia. Ann. Bot. Soc. Vanamo 34,4. Helsinki.
JALAS, J. 1965. Die zonale and regionale Gliederung der Fennosskandischen Vegetation. Rev. Biol. Roum. Ser. Bot. 10. Bucarest.
JOHANSEN, Fr. 1924. General observations on the vegetation. Can. Arctic Exped. V, C. Ottawa.
JEFFREE, E. P. 1960. A Climatic Pattern between Latitudes 40° and 70° N. and its probable Influence on Biological Distribution. Proc. Linn. Society 171. London.
JUUL, J. G. 1925. Furuens utbredelse i Finnmark og Troms. Tidskr. f. Skogsbruk 33. Oslo.
KALELA, A. 1961. Waldvegetationszonen Finnlands und ihre klimatischen Parallelltypen. Arch. Soc. Vanamo 16. Suppl. Helsinki.
„ 1962. Notes on the forest and peatland vegetation in the Canadian Clay Belt region. I. Comm. Inst. Forest. Fenn. 55, 53, Helsinki.
KASHIN, U. I. and KOZOBRODOV, A. S. 1966. On the northern distribution limit of the larch (Larix) in the forests of the Archangelsk region. Orig. Russ. Botan. Journ. 51,3. Moscow.
KIHLMAN (Kairamo), A. O. 1890. Pflanzenbiologische Studien aus Russisch Lappland. Acta Soc. F. Fl. Fenn. 6.
KRYLOV, G. V. 1961. Lesa Zapadnoj Sibiri. Acad. Sci. Sib. Sect. Biol. Inst. Moscow.

KRYLOVA, I. L. 1964. On the principles of the distribution of some life forms of arboreous plants. Orig. Russ. Botan. Journ. 49,9. Moscow.
KRYUCHKOV, U. V. 1961. Factors giving rise to a forest-tundra. Acad. Sci. USSR, Ser. Geogr. (Mimeogr. Transl.).
KUJALA, V. 1927. Untersuchungen über den Bau und die Keimfähigkeit von Kiefern- und Fichtensamen. Comm. Inst. Quaest. For. Finl. 2. Helsinki.
„ 1945. Waldvegetationsuntersuchungen in Kanada. Acad. Scient. Fenn. A. IV. Helsinki.
KÖPPEN, Fr. 1888—89. Geographische Verbreitung der Holzgewächse. Beitr. Kenntn. d. Russ. Reich. 3. St. Petersburg.
LAINE, U. 1964. Über die floristischen Waldgrenze der Kiefer in Westteil von Inari—Lappland. Ann. Univ. Turk. A, II, 32. Turku.
LARSEN, J. A. 1964. An outline of materials for a postglacial bioclimatic history of Keewatin, Northwest Territories, Canada. Univ. Wisconsin Dept. of Meteor. Techn. Rep. 15. Madison.
„ 1965. The Vegetation of the Ennadai Lake Area, N.W.T. Ibid. 18.
LAVRENKO, E. M. and SOCHAVA, V. B. (Edit.) 1954. Geobotanicheskoy karte SSSR. Moscow.
„ 1956. Rastitelny pokrov SSSR. (Explan. text to the Geobotanical map, see above). Acad. Sci. USSR. Moscow.
LINDQUIST, B. 1945. Betula callosa Notö, a neglected species in the Scandinavian subalpine forests. Sv. Bot. Tidskr. 39, 2. Uppsala.
„ 1948. The main varieties of Picea Abies (L.) Karst. in Europe. Acta Horti Berg. 14,7. Stockholm.
LOW, A. P. 1895. Explorations through the Interior of the Labrador Peninsula. Geogr. Journ. V, 6. London.
LUNDSTRÖM, A. N. 1888. Om Jenissej-strändernas Salix-flora. Botan. Not. 41. Lund.
LUTZ, H. J. 1955. Ecological Effects of Forest Fires in the interior of Alaska. U.S. Dept. Agricult. Techn. Bull. 1133. Washington, DC.
„ 1959. Aboriginal Man and White Man as Historical Causes of Fires in the Boreal Forest. Yale Univ., School of For. Bull. 65. New Haven.
LÖVE, A. and Löve, D. (Edit.) 1963. North Atlantic Biota and their history. Pergamon Press. Oxford.
MACKAY, J. R. 1958. The Anderson River Map-Area, N.W.T. Dept. of Mines and Techn. Survey. Geogr. Br. Memoirs 5. Ottawa.
MARR, J. W. 1948. Ecology of the forest-tundra ecotone on the east coast of Hudson Bay. Ecol. Monogr. 18. Durham.
MARTIN, S. P. 1959. How many logs make a forest? Ohio Journ. of Science 59, 4.
MIDDENDORFF, A. 1864. Sibirische Reise. Band IV, 1: Die Gewächse Sibiriens. Kais. Akad. d. Wiss. St. Petersburg.
MIKOLA, P. 1950. On variations in tree growth and their significance to growth studies. Comm. Inst. Forest. Fenn. 38. Helsinki.
„ 1952. On the recent development of coniferous forests in the timber-line region of northern Finland. Ibid. 40.
„ Metsänviljelyn mahdollisuuksista pohjoisella metsärajalla. Metsätal. Aik. 11. Helsinki.
MOIR, D. R. 1954. Beach ridges and vegetation in the Hudson Bay Region. Proc. North. Dakota Acad.
MUNNS, E. N. 1938. The Distribution of Important Forest Trees of the United States. U.S. Dept. of Agricult. Misc. Publ. 287. Washington.

Native Trees of Canada. Dept. of Int. For. Serv. Bull. 61. Ottawa 1950.
Naumenko, Z. M. 1964. Picea obovata Led. at the north-eastern extremity of its distribution area. Orig. Russ. Botan. Journ. 49,7. Moscow.
„ 1966. The northern limit of the distribution of Dahurian larch. Orig. Russ. Ibid. 51, 1.
Neustadt, M. I. 1957. Istorija lesov i paleogeografija SSSR. Acad. Sci. USSR. Geogr. Inst. Moscow.
Norin, B. N. 1958 a. On the generative and vegetative reproduction of trees in Subarctic conditions. Orig. Russ. The Vegetation of the Far North, 3. Moscow.
„ 1958 b. On the characterization of Chosenia macrolepis Kom. communities. Orig. Russ. Botan. Journ. 43. Moscow.
„ 1961. What is the «Forest-tundra«? Orig. Russ. Ibid. 46, 1.
Ostenfeld, C. H. and Syrach-Larsen, C. 1930. The species of the Genus Larix and their geographical distribution. Det Kgl. Danske Vid. Selskab. Biol. Medd. IX, 2. Köpenhamn.
Parvela, A. A. 1930. Oulun läänin viljelyskasvit. Ann. Zool. Bot. Vanamo 13. Helsinki.
Petrov, V. 1930. Flora Jakutiae I. Acad. Sci. U.S.S.R. Leningrad.
Pohle, R. 1917. Wald- und Baumgrenze in Nordrussland. Zeitschr. d. Gesellsch. f. Erdkunde zu Berlin.
Polunin, N. 1951. The real Arctic. Journ. of Ecology. Vol. 39, 2. London.
Porsild, A. E. 1929. Reindeer Grazing in Northwest Canada. Dept. of Int. Report. Ottawa.
„ 1951. Botany of southeastern Yukon adjacent to the Canol Road. Nat. Mus. Can. Bull. No. 121. Ottawa.
Raup, H. M. 1947. The Botany of Southern Mackenzie. Sargentia VI. Jamaica Plains. Mass.
Regel, C. 1940. Die Vegetationsverhältnisse der Halbinsel Kola, 4. Spec. Nov. Regni Veget. Beih. 82, 4. Berlin.
Renvall, A. 1912. Die periodischen Erscheinungen der Reproduktion der Kiefer an der polaren Waldgrenze. Acta For. Fenn. 1. Helsinki.
„ 1919. Suojametsäkysymyksestä. Ibid. 11.
Ritchie, J. C. 1957. The Vegetation of Northern Manitoba II. Ecology 38. New York.
„ 1959. The Vegetation of Northern Manitoba III. Arctic Inst. North America, Techn. Paper 3. Montreal.
Robinson, J. M. 1960. Forest Resources of the Northwest Territories Portion of the Mackenzie River Basin. The Polar Record 10. London.
Rousseau, J. 1952. Les zones biologiques de la Péninsule Québec-Labrador et l'Hémiarctique. Can. J. Bot. 30. Ottawa.
Rowe, J. S. 1959. Forest Regions of Canada. Dept. of North. Aff., For. Br. Bull. 123. Ottawa.
Ruden, T. 1934. Fra våre nordligste skoger. Tidsskr. f. Skogsbruk 42. Oslo.
Sambuk, F. 1930. Botaniko-geografichesky ocherk loding reki Pechory. Trav. Mus. Bot. Acad. Sci. USSR 22. Leningrad.
„ and Dedov, A. W. 1934. Die Unterzonen der Petschora Tundren. Acta Inst. Bot. Acad. Sci. USSR. Geobotanica I. Leningrad.
Sarvas, R. 1964. Havupuut. WSOY. Porvoo.
Schmucker, T. 1942. Distribution des espèces arborescentes. Silvae Orbis 4. Berlin.
Schübeler, F. C. 1873—75. Die Pflanzenwelt Norwegens, Christiania.
Sheludyakova, V. A. 1938. Rastitelnost bassin reki Indigirki. Sov. Botan. 4—5. Moskva.

Shimanjuk, A. P. 1962. Sosnovie lesa Sibiri i Daljnevo Vostoka. Acad. Sci. Sib. Sect. For. Inst. Moscow.
Shitkov, A. 1911. Der Erforschung der Samojeden Halbinsel. Peterm. Mitt. 57. Jena.
Shvetsov, P. 1963. Living and working on the frozen ground of the Arctic. New Scientist No. 371. London.
Sigafoos, R. S. 1958. Vegetation of Northwestern North America, as an Aid in Interpretation of Geologic Data. U.S. Geol. Surv. Bull. 1961 — F. Washington.
Sirén, G. 1961 a. Skogsgränstallen som indikator för klimatfluktuationerna i norra Fennoskandien under historisk tid. Helsingfors.
„ 1961 b. Taka-Lapin metsien historiasta ja ilmastosta historiallisena aikana. Lapin Tutk. Seuran Julk. II. Rovaniemi.
Sjörs, H. 1956. Nordisk växtgeografi. Scand. Univ. Books. Stockholm.
" 1961. Surface patterns in Boreal peatland. Endeavour, Vol. XX. London.
„ 1963. Amphi-Atlantic Zonation, Nemoral to Arctic. In 'North Atlantic Biota'. Pergamon Press. Oxford.
Sochava, V. 1930. La limite extrêmes des forêts dans la région de la rivière Liapine. Orig. Russ. Trav. Mus. Acad. Sci. U.S.S.R. XXII. Leningrad.
Spetzman, L. A. 1959. Vegetation of the Arctic Slope of Alaska. U.S. Geol. Surv. Prof. Papers 302. Washington.
Tanfiljev, G. I. 1911. Die polare Grenze des Waldes in Nordrussland. Odessa.
Thomas, M. K. 1960. Canadian Arctic Temperatures. Dept. of Tranport, Meteor. Branch., Mimeogr. report. Ottawa.
Tikhomirov, V. A. 1946. On the origin of the dwarf pine (Pinus pumila Rgl.) associations. Orig. Russ. Mat. on the Flora and Vegetation USSR II. Moskva.
„ (Edit.) 1956. The Vegetation of the Far North and its Utilization I. Acad. Sci. USSR. Moscow.
„ 1957. Ov ohrane lesov Krainevo Severa. Priroda 3, 12. Moskva.
„ 1961. The changes in biogeographical boundaries in the north of USSR. Bot. Tidsskr. 56. Copenhagen.
Tolmachev, A. I. 1954. K istorii vozniknovenija i razvitija temnohvoynoy taygi. Acad. Sci. USSR. Sahal. Sect. Moscow.
„ 1960. Flora Arctica URSS. I. Orig. Russ. Acad. Sci. USSR. Moscow.
Tyulina, L. 1936. On the forest vegetation of Anadyr Land and its correlation with the tundra. Orig Russ. Trans. Arctic Inst. Acad. Sci. USSR. 60. Leningrad.
Tyrrell, J. B. 1896. Report on the country between Athabasca Lake and Churchill River. Geol. Surv. Can. Ann. Rept. 8, D. Ottawa.
„ 1897. Report on the Doobaunt, Kazan and Ferguson Rivers. Ibid. 9, F.
Yurtsev, B. A. 1963. Floristic relations between steppes and prairies. Botan. Not. Lund.
Vassiljev, V. N. 1956. Rastiteljnost Anadyrskovo Kraya. Acad. Aci. USSR. Moscow.
Zinserling, D. A. 1935. Über die Nordwestgrenze der sibirischen Lärche (Larix sibirica Ledb.). Orig. Russ. Acta Inst. Bot. Acad. Sci. USSR. Leningrad.