

## Research Activities on the Forest Line in Northern Finland

PAAVO KALLIO,<sup>1</sup> HELI HURME,<sup>1</sup> SEPPO EUROLA,<sup>2</sup> YRJÖ NOROKORPI<sup>3</sup> and PENTTI SEPPONEN<sup>3</sup>

(Received 9 November 1983; accepted in revised form 22 May 1985)

**ABSTRACT.** Forest line research is one of the main areas of study open to the northern research stations, especially numerous in Fennoscandia. High latitude environmental conditions make considerable demands on the adaptability of plants growing in the subarctic. Besides low temperatures, low light intensity and low energy yield are a challenge to autotrophs: the light rhythm is quite different from that farther south.

Detailed mapping of the forest line is now undertaken every 10 years in northern Finland to study the climatic changes causing shifts in the limit. All 12 monitoring areas are situated north of the Arctic Circle. Similar monitoring may be started in other Fennoscandian countries in the near future and might prove useful for studying the effect of the general pollution of the forests.

One of Finland's many northern research stations is at Kevo and belongs to the University of Turku. It is the site of the Circumpolar Forest Line Arboretum, where material is collected from all the circumpolar areas. There are three gardens altogether: one close to the station and the others at a distance of some 10 km (Fig. 3). They are managed jointly by the Kevo Station, the National Board of Forestry and the Forest Research Institute.

Cooperation in northern research has a long history in Fennoscandia; for example, the project started during the IBP period for studying the northern birch zone continued the work begun by Wahlenberg at the start of the 19th century. The project deals mainly with the variation of the birch and other components of this northern ecosystem. Attention is also paid to the stimulating question of the co-evolution of the different organisms.

**Key words:** arboretum, circumpolar, monitoring, mountain birch, treeline, tree provenances

**RÉSUMÉ.** La recherche sur la limite forestière est un des principaux domaines de recherche accessibles aux stations de recherche nordique, particulièrement nombreuses en Fennoscandie. Les conditions environnementales rencontrées dans les latitudes élevées exigent une capacité d'adaptation considérable des plantes trouvées dans les régions subarctiques. Non seulement la basse température mais aussi le niveau peu élevé de la lumière et le faible rendement énergétique présentent un véritable défi aux autotrophes. Le rythme de la lumière diffère de façon considérable de celui des régions plus au sud.

Le dressage de cartes détaillées de la limite forestière est maintenant entrepris tous les dix ans dans le nord de la Finlande afin de permettre l'étude des changements climatiques affectant la limite. Les douze postes de surveillance sont situés au nord du cercle polaire. Une surveillance semblable sera peut-être bientôt entreprise dans d'autres pays et pourrait servir à étudier l'effet de la pollution générale sur les forêts.

L'une des nombreuses stations de recherche nordique en Finlande se trouve à Kevo et est sous la direction de l'Université de Turku. Elle est le site du Jardin de la limite forestière circonfolaire où on collectionne du matériel de toutes les régions circonfolaires. Il existe trois jardins dont l'un se trouve près de la station, tandis que les deux autres sont à quelque 10 km de cette dernière (fig. 3). Ils sont dirigés conjointement par la Station Kevo, la Commission nationale des forêts et l'Institut de recherche forestière.

Il existe depuis longtemps en Fennoscandie une coopération en recherche nordique. Le projet lancé durant la période IBP visant l'étude de la zone nordique de bouleau, par exemple, continue le travail entrepris par Wahlenberg au début du 19<sup>e</sup> siècle. Le projet porte aussi attention à la question stimulante de la co-évolution des différents organismes.

**Mots clés:** arboretum, circonfolaire, surveillance, bouleau des montagnes, limite forestière, provenance des arbres

Traduit pour le journal par Maurice Guibord.

### INTRODUCTION

The forest line forms an important limit for many other living organisms besides the relevant tree species. It is an indicator of ecological factors such as the past and present climatological changes influencing species distribution. These sensitive forest line areas need special study, for example, for forestry demands. This has led to heightened international interest and the organization of the first two forest line conferences, held at Kevo-Abisko (Finland-Sweden) in 1977 and Kuujuarapik (Poste-de-la-Baleine, Canada) in 1981.

The Fennoscandian sector of the subarctic (*cf.* Hustich, 1979) deviates clearly from the average circumpolar subarctic zone. Due to the Gulf Stream, thermal conditions in northernmost Fennoscandia are almost northern boreal while light conditions are arctic. Thus agriculture as an important livelihood extends here as far as 70°N, while in northern Quebec and Labrador, for example, it is possible only below 54°N. In Fennoscandia the forest line is formed of birch, and this zone was described already by Wahlenberg (1812) after his journey to Lapland in 1800. In addition to Fennoscandia, this zone extends

to the Kola Peninsula, Iceland and southern Greenland. It is an indicator of relatively high oceanicity (see Hämet-Ahti, 1963). There are also other special features of Fennoscandian forest line areas: pine grows here farther north than spruce, and larch, which is a typical forest line species in Eurasia, does not reach Fennoscandia due to its distributional history.

Although the Fennoscandian forest line area is a special case circumpolarly, it nonetheless presents a good object of study even for more general interests in forest line ecology. It is an area easy to reach, with long traditions in northern studies generally and forest research specifically (*cf.* Kihlman, 1884, 1890; Renvall, 1912; Hagem, 1917; Ruden, 1949; Sjörs, 1963). It also has a very good and dense network of field stations offering their services to scientists representing different interests as well as countries.

This paper deals with research projects recently started in Finnish Lapland, partly as common Nordic projects to study forest line problems, the Fennoscandian birch ecosystem being of special interest. A more international task is the circumpolar forest line arboretum in Finnish Lapland for different species, which also serves research aimed at introducing new species into northern areas.

<sup>1</sup>Kevo Subarctic Research Institute, University of Turku, SF-20500 Turku, Finland

<sup>2</sup>Department of Botany, University of Oulu, SF-90570 Oulu, Finland

<sup>3</sup>Forest Research Institute, Rovaniemi Research Station, SF-96300 Rovaniemi, Finland

## MONITORING FOREST LINE DYNAMICS IN NORTHERN FINLAND

*Background*

The tundra formed by the receding ice was replaced by birch forests in Fennoscandia about 10 000 years B.P. The invasion of Scots pine forests occurred between 8500 and 7500 B.P., and they remained in the same area some 3000 years (Hyvärinen, 1975). Pine had advanced well outside its present limits and grew within most of the present mountain birch region. Shortly after 5000 B.P. a climatic deterioration set in, causing a general retreat in forest limits of both birch and pine. About 3000 B.P. the forest lines had retreated to their approximate present locations, and at the same time the Norway spruce had reached its northern limits. Variations, however, have taken place after this period due to climatic fluctuations and during the last few centuries also to human influence. Hustich (1945, 1948, 1958), Mikola (1952) and Sirén (1961) have stressed the ecological significance of climatic fluctuations on forest line dynamics. Hustich (1975) introduced the concept of a climatic hazard coefficient to indicate northerness in the stress to which the forest line is subjected. Seed years in pine were rare early this century (Renvall, 1912) but the climatic improvement and good seed years in the thirties caused a certain optimism in forestry economics (Mikola, 1970). The history of the forest line is much the same in other parts of Fennoscandia (Kullman, 1981a,b) and circumpolarly (Gorchakovskiy and Shiyatov, 1978). So far no exact data on the actual procedures of change in forest lines are available. Such knowledge could, however, be very important when deciding about the future exploitation of these sensitive areas.

The good network of field stations in northern Finland and the

active interest in forest research north of the Arctic Circle offer a unique possibility for obtaining more detailed data about the development of the forest line in the future. The mapping of 12 selected areas, each representing a different type of forest line, is planned every ten years in northernmost Finland (Fig. 1). The responsibility for fulfilling this work lies with the field stations, the Finnish Forest Research Institute being the main organizer.

*Monitoring Methods*

The first mapping was performed in 1983 and 1984, and the next measurements on the same plots will be taken in 1990 and thereafter every ten years. Each of the 12 areas include 1-3 sites, which represent local variability concerning tree species, edaphic factors such as soil, exposition, etc. Each site is composed of 3-5 clusters of three circular monitoring plots. The plots are generally 300 m<sup>2</sup> in area, but in cases where there are only a few trees 500 m<sup>2</sup> is used. One of the clusters is placed in stands of average density, one as near the estimated forest line as possible and one close to the treeline. Because the latitudinal (horizontal) forest line is very gradual, the location of the clusters there is generally more difficult than in the altitudinal (vertical) forest line. The distance may therefore be even 2-3 km between them, the average being only a few hundred m in the altitudinal forest line.

The centres of the plots are permanently marked. A very general description of the sites has been made, covering such information as on slope direction, steepness, macrotopography, the type of forest line (climatic, edaphic or caused by snow conditions), height above sea level, thermal sum (+5° d.d.) and average height of trees. All the trees (height >2 m) are mapped within the plot, and their diameter at chest height, height, propagation (number of cones and catkins) as well health condition is estimated; seedlings are also mapped with the same accuracy. The different parameters that possibly affect the forest line will be monitored during this research program, and consequently the ground vegetation, soil condition and herbivores of the trees are analyzed carefully. This material can certainly serve other interests in the future also, as is already planned at some of the sites.

## FOREST LINE ARBORETUM AS A TOOL FOR RESEARCH

The forest line is one of the most important vegetation limits in the world, especially in studies of the effect of the macroclimate (Hustich, 1966; Tikhomirov, 1970). Although there are many thousands of tree species, the number forming the polar forest limit is below 20. These trees must have some specific qualities for their ecological adaptation.

The species of the polar forest line differ between Eurasia and North America, but they mostly belong to the coniferous genera *Picea* and *Larix*, and only occasionally to *Pinus* and *Abies*. Among deciduous species, the genus *Betula* is prevalent, but in some areas other species are found as well (e.g., *Populus*, *Salix*, *Alnus*, *Chosenia*).

The north is young (Dunbar, 1968) and the trees have had little time for adaptation. Accordingly, the present distribution of forest line trees does not indicate the total area of their potential distribution or explain the limiting ecological factors; neither are the competition processes between the species yet known. The ability of subantarctic trees, e.g., *Nothofagus*, to thrive on the Faroe Islands (Ødum, 1979), and the successful

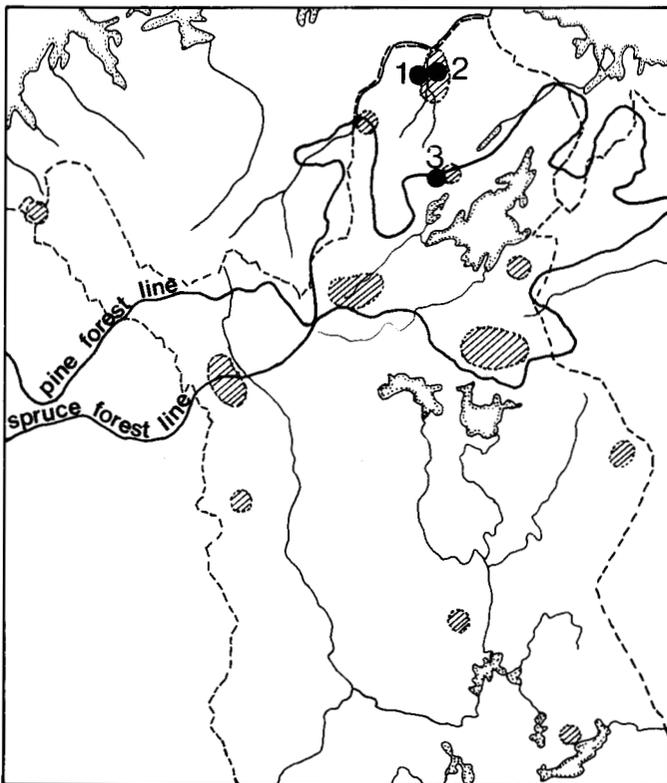


FIG. 1. Forest line monitoring areas in northernmost Finland (hatched). 1 = Kevo Station, 1-3 = forest line arboreta. The northern limits of Norway spruce and Scots pine forests are shown.

transplantations of *Larix sibirica*, *Picea sitchensis* and *Populus trichocarpa* in Iceland (Bjarnason, 1968) and Greenland (Böcher, 1979) indicate that not all the species have been able to realize their potential distribution. So man has become a factor in the distribution of organisms, creating a totally new situation in animal and plant evolution.

### *The Concept of a Forest Line Arboretum*

Many forest line species have large ranges with widely varying environmental conditions. The treeline of the black spruce (*Picea mariana*) extends in North America from Kuujuarapik on Hudson Bay (ca. 55°N) to the Mackenzie River delta (ca. 70°N). This means that not only light conditions differ but also oceanity/continentality differences may be large. So, although there is only a small number of species, the number of provenances is large.

To study the genetic variation and evolution of forest line trees, it is necessary to keep the environmental factors as constant as possible. This can be done by having all the species and their different provenances in the same place for comparative eco-physiological research. The circumstances vary then, however, differently from the optimum for each species. The Kevo Subarctic Research Institute of the University of Turku decided to start this international task and to establish an arboretum at its research station in the northernmost part of Finland (Fig. 1). Forest line research goes back a long way in Finland (see, e.g., Kihlman, 1890; Renvall, 1912; and the papers by Hustich in the review article by Fogelberg, 1981), and practical experience of cultivating foreign trees at northern latitudes has been accumulated at the Forest Research Institute.

### *Three Sites for Research*

From the Kevo Subarctic Research Station it is easy to reach all the different latitudinal and vertical forest lines to be found in northern Fennoscandia and to study the differences in the ecological demands of the species. The forest line arboretum was established in three different areas in Finnish Lapland (Fig. 1). All the plots are ca. 4 hectares in size and are fenced to keep out reindeer and hares (Fig. 2). In each of them all the native trees were removed and the humus layer was mixed with sand and gravel by ploughing with a chain rototiller. At the southernmost site part of the area was left untouched for comparison. The areas will be under constant study, records being made of the changes in the vegetation, insects and other pests, the diseases affecting the planted trees and also the soil structure and decomposition rates. No fertilizer has been applied.

### *Project Responsibilities*

The Kevo Subarctic Research Institute cooperates with the National Board of Forestry and the Forest Research Institute in Finland. Each of the three organizations has its own duties. Kevo's task is to obtain the seed material from different localities on the circumpolar northern treeline, to supervise the planting of 3-4-year-old trees, and to coordinate research. The National Board of Forestry, which owns the land, took charge of the big nurseries in northern Finland (Imari in Rovaniemi and Pakatti in Kittilä), where the seeds are germinated and the seedlings raised before being transplanted to the arboretum. The first material for the arboretum was provided by the Forest Research Institute, and their long experience of transplantation and soil preparation has been important.

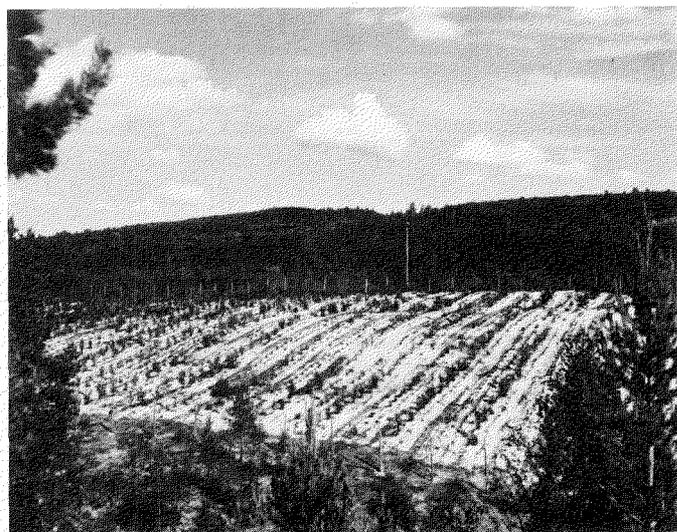


FIG. 2. Forest line arboretum site no. 1 close to Kevo Station. The soil is sand and locally there are large boulders. The first trees were planted in summer 1977. Photo M. Sulkinoja, 1981.

### *International Cooperation in Collecting Forest Line Material*

Years yielding seed with good germinability occur very seldom in the forest line region (cf. Renvall, 1912). For pine, for example, the thermal sum (+5° d.d.) must be 50% higher than average before germinability reaches 50% (Pohtila, 1980). This is possible because of the wide climatic fluctuations in the forest line region. The international forestry organizations collecting seed cannot help much in providing material, as their interest is mostly in economic forestry far south of the forest line, and so far these northern areas are not covered by gene banks either. Thus the best way of getting material for the arboretum has been to organize excursions to collect cones or cuttings from certain areas. Some material has already been collected on trips to northern Canada, Alaska and the Chukchi peninsula in eastern Siberia. Some help in this work has also been given by scientists and research institutes outside Finland. However, as germinability is almost always very low, much work must be done before the whole circumpolar forest line region is represented by a sufficient number of ecotypes of each species (Fig. 3). International regulations limit the transport of live trees or cuttings, which would speed up the task. So the only way seems to be to find scientists and institutes interested in collaborating in providing the material still needed. We therefore request such collaboration and would be grateful to receive material from treeline or near-treeline sources. Table 1 gives a list of the coniferous species that have either been planted or are in the nursery at the moment (winter 1984-85).

It will take a long time before the entire area of the three arboreta is needed for planting treeline species. The sites have therefore temporarily been used for studies on the evolution of the mountain birch (*Betula pubescens* ssp. *tortuosa*). There are some 185 origins of *Betula* species and their hybrids from different parts of northern Fennoscandia, Iceland and Greenland, making a total of ca. 13 600 trees, planted at the three sites. This material offers excellent opportunities for study not only for plant taxonomists and ecologists (Kallio *et al.*, 1983), but also for people interested in such subjects as plant-animal interaction, nutrient cycling and photosynthetic adaptation.

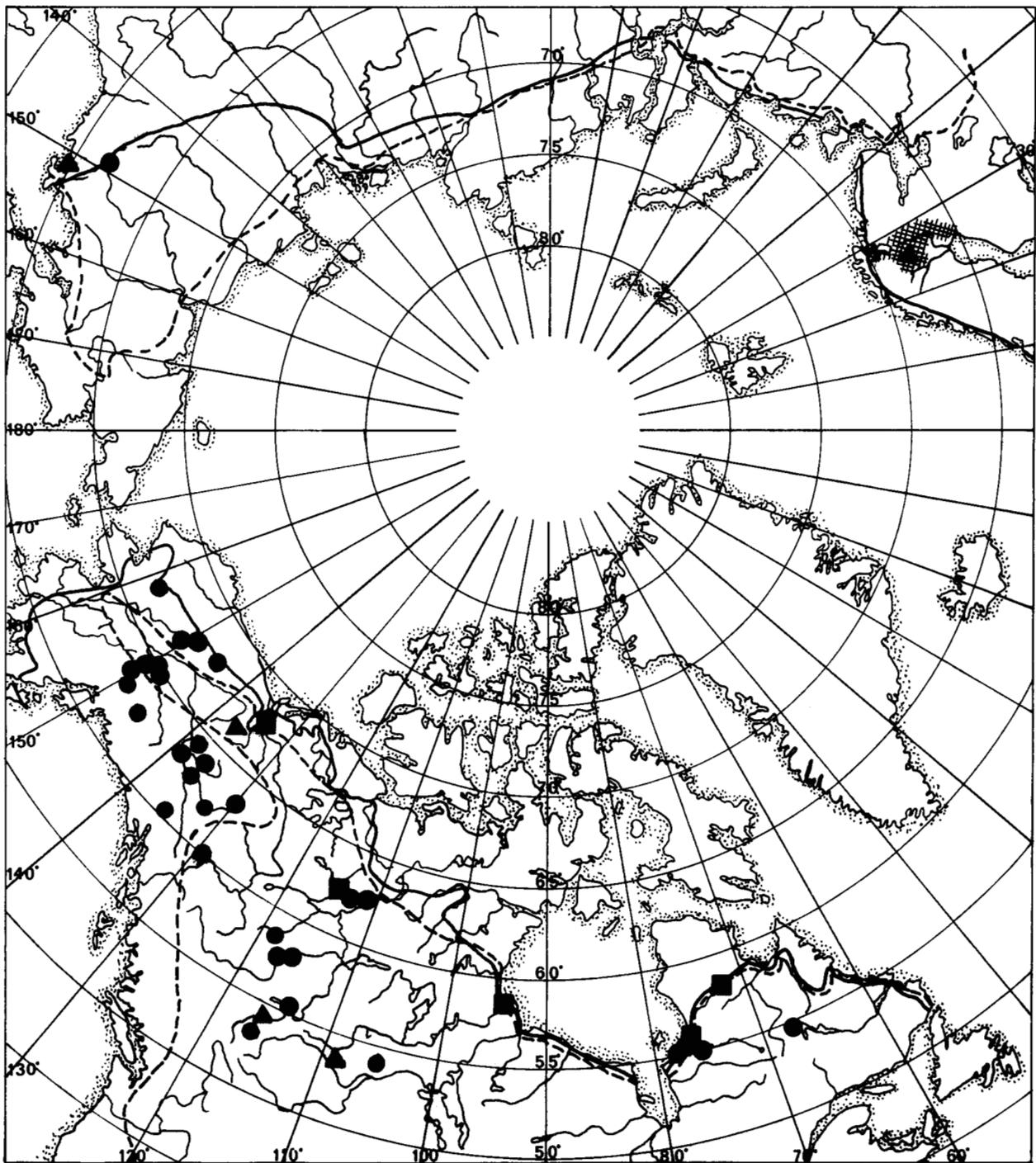


FIG. 3. Localities of the material received for the forest line arboretum and the main forest lines in the circumpolar region. Evergreen conifers = circles/solid line; larch = triangles/broken line; both = squares; hatched area in northern Finland = Norway spruce and several provenances of Scots pine. See also Table 1.

Besides offering a valuable starting-point for international research on the above subjects, these birch trees will also provide protective shade for young forest line trees in the future.

#### INTERNORDIC BIRCH ECOSYSTEM PROJECT

##### Background

Mountain birch (*Betula pubescens* ssp. *tortuosa*) is the main component of the northwest European subarctic ecosystem

(Treter, 1984). It is the most important primary producer (600 kg d. wt.·ha·yr; Kjelvik and Kärenlampi, 1975) in the area, which may be regarded as a part of the boreal/oroboreal zone (e.g., Ahti *et al.*, 1968) or as a typical subarctic forest tundra (Hustich, 1970). This quite unique ecosystem (Fig. 4) was a natural choice for Nordic research cooperation, which had already been successful in the past (see Wielgolaski, 1975a,b). The details of the project have been discussed by more than 20 scientists from all Nordic countries at several meetings since 1981, and the research program was started in 1983. One aim of this study is to amass

useful information for land planning and development decisions concerning the sensitive subarctic area of Fennoscandia.

TABLE 1. The coniferous tree line species represented in the forest line arboretum from Alaska, northern Canada, Far-Eastern USSR and northern Finland, winter 1984-85<sup>1</sup>

Species	Area of origin	Number of			Total number
		provenances	planted trees	young seedl.	
<i>Abies balsamea</i>	Yukon	2	7	—	117
	Alberta	1	96	—	
	Quebec	1	—	14	
<i>Larix dahurica</i>	Magadan Obl.	1	1091	—	1091
<i>Larix laricina</i>	Yukon	1	198	—	414
	N.W.T.	1	—	6	
	Alberta	1	144	—	
	Saskatchewan	1	63	—	
	Manitoba	1	—	1	
<i>Larix sibirica</i>	'Archangel-origin' mother tree from N. Finland	1	389	—	389
<i>Picea abies</i>	N. Finland	1	407	—	407
<i>Picea glauca</i>	Alaska	5	909	—	2994
	Yukon	5	990	—	
	N.W.T.	2	—	55	
	Alberta	2	179	—	
	Manitoba	1	288	472	
	Quebec	4	12	89	
<i>Picea mariana</i>	Alaska	6	1004	37	2927
	Yukon	1	365	—	
	N.W.T.	2	—	226	
	Alberta	2	213	—	
	Saskatchewan	1	100	—	
	Manitoba	1	—	166	
<i>Pinus banksiana</i>	N.W.T.	1	—	214	573
Quebec	1	—	359		
<i>Pinus contorta</i>	Yukon	1	473	—	473
<i>Pinus pumila</i>	Magadan Obl.	1	—	1	1
<i>Pinus sylvestris</i>	N. Finland	16	2678	—	2678
			9808	2256	12064

<sup>1</sup>For more exact location of the origins, see Figure 3.

The background units in the organization are the universities of Helsinki, Turku and Oulu in Finland, the Royal Swedish Academy of Sciences and the universities of Lund, Uppsala and Umeå in Sweden, and the universities of Oslo, Bergen and Tromsø in Norway. In Iceland the Mogilsá Forest Research Station is the centre for the project, and in Greenland the research is carried out by Hørsholm Arboretum. The field work, however, will be done at different northern field stations and arboreta to be established in the future (Fig. 5). The whole system of study sites takes into consideration both the north-south latitudinal gradient as well as oceanic-continentiality differences.

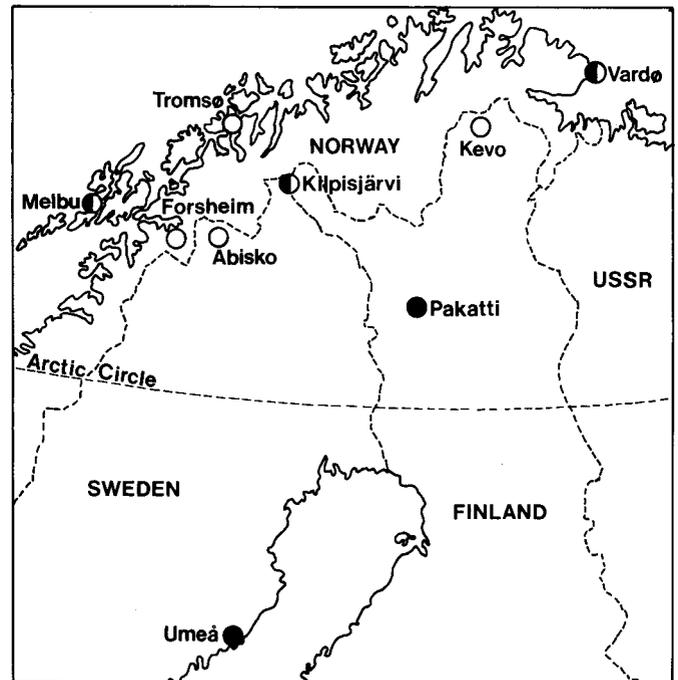


FIG. 4. Research sites (open circles), birch arboreta (solid circles) or both (circles with solid halves) in the internordic mountain birch ecosystem research program.

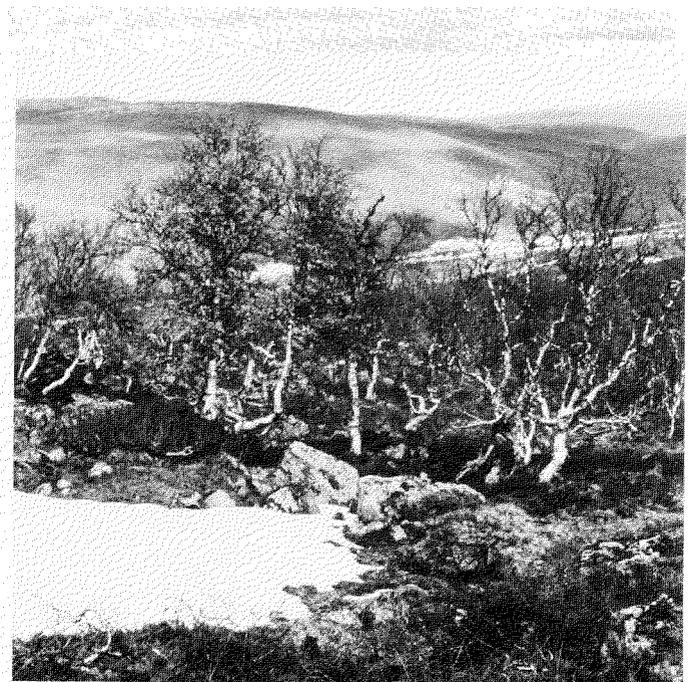


FIG. 5. Typical mountain birch forest in Finnish Lapland, Norwegian fells in the background. Photo S. Koponen, June 1983.

### Sub-projects

The study program is divided into five sub-projects: 1) variation and evolution of birch, 2) ecology of the birch, 3) ecological studies of the field layer, 4) plant-animal interaction, and 5) mapping. Some of the projects are meant to be short-term studies (2, 3, 4), whereas others require a longer period before useful results can be obtained (e.g., 1).

Studies of the variation and evolution of birch have long

traditions in both Finland and other Fennoscandian countries (Gunnarsson, 1925; Vaarama and Valanne, 1973; Sulkinoja, 1981; Kallio *et al.*, 1983), in Iceland (Elkington, 1968) and in Greenland (Böcher, 1979). Hybridization and introgression are the leading factors in the evolution of mountain birch.

A system of six arboreta provides a new possibility for variation and evolution studies in birch. The seed material is collected from 30 mother trees in each of the 25 populations representing participating countries. Some data on these populations are gathered for later use. The birches are raised in the Pakatti nursery in Finland. This provides the same population material with approximately the same variation of *ca.* 5000 trees to each arboretum. This material is also used in the Tromsø phytotrone in controlled ecophysiological studies. It will take years before the trees are old enough for reliable analyses and results from this sub-project can be obtained.

In the ecological part of the project the nutrient circulation and energy flow studies are of main interest. Analyses from different parts of birches in different seasons are made at all sites by the same laboratories. In addition to the analyses of minerals (K, Ca, Mg, Fe, P, Mn), the N-content, stored carbohydrates and lipids are also monitored. The latter is important in order to understand how the mountain birch adapts to the great climatic fluctuations in the subarctic and how this adaptation has proceeded mostly via the quantitative and qualitative storage of energy. Moreover, the birch mycorrhiza is a most important tool for nutrient uptake in the poor subarctic soil, especially of phosphorus and nitrogen. Photosynthesis studies in the birch arboreta and in the field complete this sub-project.

To study the ecology of the field layer vegetation, mineral analyses are made of the main vascular and lower plant species. The sites are the same as in sub-project 2. The idea is to follow the seasonal changes in mineral content and to make biomass measurements over three growth periods in *Vaccinium myrtillus*, *Empetrum hermaphroditum*, *Deschampsia flexuosa* and some lichens and moss species. Depending on the species, the material is divided into current-year shoots, older green shoots, brown above-ground parts, standing-dead and below-ground parts, or simply into green, non-green and dead parts. In late summer biomass samples are taken from an area of 0.25 m<sup>2</sup>. Soil conditions are also analyzed.

The study of fluctuations in population density both in invertebrates and vertebrates is the main task in the animal-plant interaction sub-project. Herbivory fluctuation is affected by climatic cycles and nutrient levels. The variation in the defence capacity of birch (and also other species) plays a certain role. To understand defence mechanisms in plants it is necessary to study the relationship between nutrients as well — e.g., polyphenols and the usability of the plant for its herbivore (Haukioja *et al.*, 1983). In these problems the treeline arboreta at Kevo (described earlier in this article) and the new arboreta are important for studies of variation in the herbivory strategy of birch. This sub-project is specially important for land usage planning in northwestern Europe, Iceland and Greenland, where grazing by reindeer and/or sheep can drastically affect plant communities and even soil stability.

The data for vegetation maps will be gathered mainly as a by-product of the other sub-projects during the course of the field work. An ideal compact unit for mapping would be one catchment area from every unit, where the main nutrient input and output could be measured to improve understanding of the dynamics of the birch ecosystem.

The cooperation among different units does not only mean common planning but also keen constant contacts among participating scientists and field stations through regular visits and meetings, methodical supervising and, partly, common financing.

## REFERENCES

- AHTI, T., HÄMET-AHTI, L., and JALAS, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5:169-211.
- BJARNASON, H. 1968. Forestry in Iceland. *Journal of the Royal Scottish Forestry Society* 22(1):55-60.
- BÖCHER, T. 1979. Birch woodlands and tree growth in southern Greenland. *Holarctic Ecology* 2(4):218-221.
- DUNBAR, M.J. 1968. Ecological development in polar regions. A study in evolution. Englewood Cliffs, N.J.: Prentice-Hall. 119 p.
- ELKINGTON, T.T. 1968. Introgressive hybridization between *Betula nana* L. and *B. pubescens* Ehrh. in North-West Iceland. *New Phytologist* 67:109-118.
- FOGELBERG, P. 1981. The written work of Ilmari Hustich. *Fennia* 159(1): 5-13.
- GORCHAKOVSKY, P.L., and SHIYATOV, S.G. 1978. The upper forest limit in the mountains of the boreal zone of the USSR. *Arctic and Alpine Research* 10:349-363.
- GUNNARSSON, J.G. 1925. Monografi över Skandinavien Betulae. Arlöv. 136 p.
- HAGEM, O. 1917. Furuens och granens frosetning i Norge. *Medd. fra Vestlandets Forst. Forsökstat.* 2:1-188.
- HAUKIOJA, E., KAPIAINEN, K., NIEMELÄ, P., and TUOMI, J. 1983. Plant availability hypothesis and other explanations of herbivore cycles: complementary or exclusive alternatives? *Oikos* 40:419-432.
- HÄMET-AHTI, L. 1963. Zonation of the mountain birch forests in northernmost Fennoscandia. *Annales Botanici Societatis Zoologicae Botanicae 'Vanamo'* 34(4):1-127.
- HUSTICH, I. 1945. The radial growth of the pine at the forest limit and its dependence on the climate. *Societatis Scientiarum Fennica Commentationes Biologicae* 9(11):1-30.
- . 1948. The Scotch Pine in northernmost Finland its dependence on the climate in the last decades. *Acta Botanica Fennica* 42:1-75.
- . 1958. On the recent expansion of the Scotch pine in northern Europe. *Fennia* 82(3):1-25.
- . 1966. On the forest-tundra and the northern tree-lines. *Reports from the Kevo Subarctic Research Station* 3:7-47.
- . 1970. On the study of the ecology of subarctic vegetation. *Proceedings of the Helsinki symposium 1966 'Ecology of the subarctic regions.'* Paris: UNESCO. 235-240.
- . 1975. The next phase in northern ecological research. *Proceedings of the Circumpolar Conference on Northern Ecology, Ottawa 1975.* Section V:1-10.
- . 1979. Ecological concepts and biogeographical zonation in the North: the need for a generally accepted terminology. *Holarctic Ecology* 2:208-217.
- HYVÄRINEN, H. 1975. Absolute and relative pollen diagrams from northernmost Fennoscandia. *Fennia* 142:1-23.
- KALLIO, P., NIEMI, S., SULKINOJA, M., and VALANNE, T. 1983. The Fennoscandian birch and its evolution in the marginal forest zone. *Nordica* 47:101-110.
- KIHLMAN, A.O. 1884. Anteckningar om floran i Inari Lappmark. *Meddelanden pro Societatis pro Fauna et Flora Fennica* 11:45-135.
- . 1890. Pflanzenbiologische Studien aus Russisch Lappland. Ein Beitrag zur Kenntniss der regionalen Gliederung an der polaren Waldgrenze. *Acta Societatis pro fauna et flora Fennica* 6(3):1-263, 14 Tafel.
- KJELVIK, S., and KÄRENLAMPI, L. 1975. Plant biomass and primary production of Fennoscandian subarctic and subalpine forests and of alpine willow and heath ecosystems. In: Wielgolaski, F.E., ed. *Fennoscandian tundra ecosystems, Part 1.* New York: Springer-Verlag. 111-120.
- KULLMAN, L. 1981a. Some aspects of the ecology of the Scandinavian birch forest belt. *Wahlenbergia* 7:99-112.
- . 1981b. Recent tree-limit dynamics of Scots pine (*Pinus sylvestris* L.) in the southern Swedish Scandes. *Wahlenbergia* 8:1-67.
- MIKOLA, P. 1952. Havumetsien viimeaikaisesta kehityksestä metsänrajaseudulla. (English summary: On the recent development of coniferous forests in the timber-line region of northern Finland.) *Communications Instituti Forestalis Fenniae* 40(2):1-35.

- \_\_\_\_\_. 1970. Forests and forestry in subarctic regions. Proceedings of the Helsinki symposium 1966 'Ecology of the subarctic regions.' Paris: UNESCO. 295-302.
- ØDUM, S. 1979. Actual and potential tree-line in the North Atlantic region, especially in Greenland and the Faroes. *Holarctic Ecology* 2(4):222-227.
- POHTILA, E. 1980. Climatic fluctuations and forestry in Lapland. *Holarctic Ecology* 3(2):91-98.
- RENVALL, A. 1912. Die periodischen Erscheinungen der Reproduktion der Kiefer an der polaren Waldgrenze. *Acta Forestalia Fennica* 1(2):1-154.
- RUDEN, T. 1949. Trekk fra Nord-Norges skoger. *Det Norske Skogselskap* 1898-1948, II:224-243. Oslo.
- SIRÉN, G. 1961. Skogsgränställen som indikator för klimatfluktuationerna i norra Fennoskandien under historisk tid. *Communicationes Instituti Forestalis Fenniae* 54(2):1-66.
- SJÖRS, H. 1963. Amphi-atlantic zonation, Nemoral to Arctic. In: Löve, A., and Löve, D., eds. *North Atlantic Biota and their history*. New York: Pergamon Press. 109-125.
- SULKINOJA, M. 1981. Lapin koivulajien muuntelusta ja risteytymisestä. (English summary: On the variation and hybridization of *Betula* species in Lapland.) *Lapin tutkimusseura Vuosikirja XXII*:22-30.
- TIKHOMIROV, B.A. 1970. Forest limit as the most important biogeographical boundary in the North. Proceedings of the Helsinki symposium 1966 'Ecology of the subarctic regions.' Paris: UNESCO. 35-40.
- TRETER, U. 1984. *Die Baumgrenzen Skandinaviens*. Wiesbaden: Steiner. 111 p.
- VAARAMA, A., and VALANNE, T. 1973. On the taxonomy, biology and origin of *Betula tortuosa* Ledeb. Reports from the Kevo Subarctic Research Station 10:70-84.
- WAHLENBERG, G. 1812. *Flora Lapponica*. Berolini. 550 p.
- WIELGOLASKI, F.E., ed. 1975a. *Fennoscandian tundra ecosystems*. Part 1. Plants and microorganisms. *Ecological Studies* 16. New York: Springer Verlag. 366 p.
- \_\_\_\_\_, ed. 1975b. *Fennoscandian tundra ecosystems*. Part 2. Animals and systems analysis. *Ecological Studies* 17. New York: Springer Verlag. 337 p.