WORKING PAPER

SURVEY OF ECOLOGICAL CHARACTERISTICS OF BOREAL TREE SPECIES IN FENNOSCANDIA AND THE USSR

Harry Helmisaari
Nedialko Nikolov

September 1989
WP-89-65

PUBLICATION NUMBER 95 of the
Biosphere Dynamics Project

IIASA
International Institute
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ABOUT THE AUTHORS

During the summer of 1988, Harry Helmisaari and Nedialko Nikolov studied in IIASA's Young Scientist's Summer Program (YSSP) on the work described in this paper. As a result of the excellence of their work, and the close cooperation they displayed, they were subsequently awarded the Peccei Scholarship for 1988.

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FOREWORD

The circumpolar boreal forest in the northern hemisphere is the source of life and culture for several distinctive and indigenous, nomadic peoples and is home to many economically-important and rare and endangered plant and animal species. Yet, in comparison with other forested regions, it contains few species, all of which are adapted to surviving months of darkness and extremely low temperatures. These conditions may soon change. Due to increases in radiatively-active pollutants (greenhouse gases), climates that occur nowhere today in the boreal forests may soon displace the boreal temperature and precipitation regimes under which the northern ecosystems currently exist. Increased growing season length threatens to reduce snow-cover rapidly during spring and fall seasons, further increasing radiation absorption, drying the boreal deserts and providing additional stress to the permafrost-dependent biotic systems in continental boreal zones.

On the other hand, positive changes may also be occurring. Increasing warmth may eventually lead to increased productivity and species diversity. Acidic deposition may be providing a temporary supply of nutrients previously unknown in boreal regions, and enhanced atmospheric CO_2 concentrations could directly increase the growth of plants, shifting competitive relationships between and among species. Whether positive or negative, these changes represent a profound metamorphosis of northern ecosystems, generated from sources outside the systems and only indirectly reflecting the activities of man. However, the changes would transform boreal forests no less drastically than does the current destruction of tropical ecosystems by bulldozers and burning.

This issue is now under scrutiny in the project Biosphere Dynamics Project at IIASA. A study has begun to provide a data- and model-based scientific "scoping" of the problem, and to develop options for institutional response and political action, should the research results warrant. The objective is to answer questions concerning the times and regions at which the boreal forest ecosystems and species will be most vulnerable to even slight changes in environmental variables, and which species might be endangered. IIASA's unique capabilities in examining east-west problems has allowed interaction among scientific experts on boreal-forest natural history, including experts from seven of the eight nations which possess northern boreal ecosystems.

The overall hypothesis is that global environmental changes will be critical determinants of future species diversity, biotic losses, and potential survival of endangered species in the boreal forest ecosystems. A sequential, three-part approach is being followed to test the hypothesis. First, the forestry literature from several languages is being gathered to document the important relationships within the circumpolar boreal forest among dominant plant species, current endangered and threatened species, and environmental variables including climate and nutrients. This effort is represented in part by the current working paper, and by a companion working paper, " The Silvics of Some East European and Siberian Boreal Forest Tree Species," by M. Korzuchin, and others. Second, this and other documentation is being used to modify existing forest-stand simulation models. The first efforts in these modifications appear in the working paper by Gordon Bonan, as "A Simulation Model of Environmental Processes and Vegetation Patterns in Boreal Forests: Test Case Fairbanks, Alaska" (IIASA WP-88-63). Third, plausible future developmental trends will be quantified and applied to the simulation models, allowing the interrogation of the models to reveal potential environmental vulnerabilities and to identify early indicators of such changes.

The data will be used to modify the available mixed-species and mixed-age forest stand simulators (for example, JABOWA, Botkin et al. 1972; FORET, Shugart and West 1977; FORENA, Solomon 1986). These models have been developed over the past 15 years to simulate forest-stand dynamics through the effect of changing resources (e.g., light, soil moisture, nutrients) on the regeneration, growth, and death of individual trees on a small forest plot corresponding to the size of a forest gap remaining after the death of a mature tree. The models have been very well documented (Shugart 1984; Solomon et al. 1984; Pastor and Post 1985; Aber et al. 1982; Dale et al. 1986; Leemans and Prentice 1989). Their application to the entire suite of circumpolar boreal-forest conditions requires the identification and implementation of the most appropriate available routines. Also, some origination of new routines will be required. It will be particularly important to expand on the routines which handle effects of winter low temperatures, to incorporate the known direct effects of warming on tree vigor (i.e., frost damage with the disappearance of seasonal low-temperatures that control winter hardening and dehardening; excessive tree mortality on coarse soils with increased summer drought).

The data represented by the content of this paper were assembled for use in forest stand simulation models. The data document important relationships between the biotic characteristics of dominant and endangered species (present abundance and geographic location of populations; maximum age and size; physiological responses to seasonal temperature, extreme temperatures, and precipitation; response to shading, mortality characteristics, insect pests and diseases, and so on), and the current environmental constraints to their reproduction and growth in boreal regions, such as growing-season length, warmth, precipitation, soil-fertility requirements, and so on. The data are selected to reveal reactions to environmental change by the critical sensitive characteristics of individual species. These species depend upon the direct influences of environment, as well as on the presence of the ecosystems in which they germinate and grow. The book by Shugart (1984) describes the logic for the data we are collecting and its use in model development.

These data form the basis for generating or enhancing model routines which handle processes peculiar to boreal forests, such as permafrost dynamics (Bonan 1988), nutrient turnover (Pastor and Post 1985), and heat accumulation (Kauppi and Posch 1988, 1985). The critical feature of the class of models over other available model approaches is that they can translate physiological responses and limits of individual species into behavior of ecosystems, over time steps of successive seasons and years. This feature is required if we are to assess the impacts of environmental changes which could induce boreal-forest destruction, such as change in permafrost distributions (Van Cleve and Dyrness 1983), shifting nutrient dynamics (Billings et al. 1982), and expansion of heat-unit accumulation with attendant increases in growing season length, decreased snow-persistence times, and loss of winter-temperature severity (Dickinson and Cicerone 1986).

As models continue to be modified and verified on field data, needs for new processes and routines will become evident, necessitating additional kinds of data on the natural history of individual species. However, for now, the data to follow, combined with that for North American species (Harlow, Harrar, and White 1979; Fowells 1965), represent as complete a data set as possible for examining behavior of the circumpolar boreal forest via stand simulation models.

Allen Solomon, Leader
Biosphere Dynamics Project

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ABSTRACT

The paper presents results from a literature study on autecological characteristics of North European and Asian boreal and boreo-nemoral tree species. It also provides general ecological information about the main forest types in the boreal region of the USSR and Fennoscandia. The work has been mainly done during the Young Scientist's Summer Program of 1988 and is a part of the Biosphere Dynamics Project activities.

Species natural history data have been collected and assembled in such a way that they can be used in parameterization and modification of existing (or new-formulated) mixed-species forest stand simulators (e.g., gap models).

The ecological survey involves 27 tree species devided into two groups. The first one, called "dominant tree species", includes 13 major forest-forming species of the present-day boreal forests of the USSR and Fennoscandia, while the second one, "important species", contains species which either dominate forests at the boreal-border areas (i.e. boreo-nemoral forests) or have restricted distribution within the boreal zone. Each species is attempted to be characterized as completely as possible by the following categories: systematics (scientific name, author and synonymies), spatial distribution (description and maps of continuous range of natural growth), habitat requirements (climate, soil types, associated species, and forest types), life history (reproduction and growth), response to environmental factors (light, soil moisture, nutrients, frost, permafrost, fire, windstorm, flooding and poludification), races and hybrids, enemies and diseases.

The data from the autecological reviews are summarized as 24 input model parameters in the Appendix.

The paper should be considered as a first step in building a boreal tree species natural history database to be used with simulation models. It is also the first attempt to compile autecological data about North Asian tree species for modeling purposes.

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SURVEY OF ECOLOGICAL CHARACTERISTICS OF BOREAL TREE SPECIES IN FENNOSCANDIA AND THE USSR

Harry Helmisaari and Nedialko Nikolov

1. INTRODUCTION

This report is a result of studies conducted at IIASA during the Young Scientist's Summer Program (YSSP) of 1988. It is a part of the Biosphere Dynamics Project. The aim of our work was to compile data concerning autecology and life histories for major boreal and boreo-nemoral tree species (78) in Fennoscandia and in the USSR and to initiate the development of a computerized silvics data base.

This report is the first comprehensive presentation of life history data for the main tree species in the boreal zone of Fennoscandia and the USSR. It includes also data about tree species occurring at the margins or having a limited distribution within the boreal zone. The compiled data are presented as 27 autecological reviews, one for each tree species and as a summary table of the life history data in the Appendix. The summary table provides key parameters which can be used as input data for boreal forest stand simulators (74).

This study is based on the literature in the IIASA library, that which was available through interlibrary loans, and that obtained through personal contacts and searches in international databases. The two main literature sources were the Higher Institute of Forestry and Forest Technology in Sofia, which provided most of the Russian literature and the University Library of Helsinki which supplied literature for boreal forests in Fennoscandia and in the USSR. The University Library of Helsinki has a very good collection of literature about the ecological characteristics of boreal forests in Fennoscandia and in the USSR because they have a good collection of Soviet Journals and older Russian literature. Searches in international databases gave very few new references since most of the studies included were from North America and Fennoscandia.

The selection of the 27 tree species included is based on distribution maps (73, 75) and information from literature (1, 5, 17, 18). The selected species were classified as:

1. Dominant species: the major forest forming or widely distributed species in boreal forests of the USSR and Fennoscandia, species 1-12.

    1. *Abies sibirica* Ledeb.
    2. *Betula pendula* Roth.
    3. *Betula pubescens* Ehrh.
    4. *Larix gmelinii* Rupr.
    5. *Larix sibirica* Ledeb.
    6. *Larix sukaczewii* Dylis.
    7. *Picea abies* (L) Karst.
    8. *Picea obovata* Ledeb.
    9. *Pinus pumila* Reg.
    10. *Pinus sibirica* Rupr.
    11. *Pinus sylvestris* L.
    12. *Populus tremula* L.

2. Important species: species occurring at the border areas or having a restricted distribution within the boreal region, species 13-27.

    13. *Abies sachalinensis* Mast.
    14. *Alnus glutinosa* Gaertn.
    15. *Alnus incana* Willd.
    16. *Carpinus betulus* L.
    17. *Fagus sylvatica* L.
    18. *Larix decidua* Mill.
    19. *Larix kurilensis* Mayr.

20. *Picea ajanensis* Fisch.
21. *Picea koraiensis* Nakai.
22. *Picea orientalis* (L.) Link.
23. *Picea schrenkiana* Fisch et Mey
24. *Pinus koraiensis* Sieb. et Zucc.
25. *Quercus mongolica* Fisch.
26. *Quercus robur* L.
27. *Tilia cordata* Mill.

The latter group "important species" were included to encompass species which may immigrate to the boreal zone due to the potential climatic warming over the next 100 years (68). Autecological reviews for the 27 species were prepared to parallel those of Fowells (56). They are as follows:

1. Systematic classification - This category provides the genus, species and authorities for the names. The nomenclature follows mainly Czerepanov 1981 (80). Such information is critical for specifying the taxonomic entity under consideration; the characteristics we subsequently provide do not necessarily apply to other species or varieties.

2. Spatial distribution - This category describes the continuous range of natural growth of each species (planted trees and urban ornamentals are excluded).

3. Habitat requirements - The category describes the climatic conditions, soil types and soil preferences as well as the associated species and the forest types with which the species occurs.

4. Life history - This category describes the species' reproductive behavior and growth patterns.

5. Response to environmental factors - This category characterizes species responses to light, soil moisture, nutrients, frost, permafrost, fire, wind and flooding.

6. Races and hybrids give examples of closely related species, races and hybrids.

7. Enemies and diseases are included to describe potential threats to the species.

The data from the reviews were summarized in a table of 24 model parameters presented in the Appendix.

2. FUTURE NEEDS

This report is the first step in building an ecological data base for boreal and boreo-nemoral tree species in Fennoscandia and in the USSR. Certain data still missing from the ecological reviews must be collected, and more information regarding autecological responses in different areas for the broadly distributed species has to be included. It is also important to search and include so called "gray literature" found in local libraries, and research institutes in Fennoscandia and in the USSR. Collaboration with scientists working with boreal forests in Fennoscandia and in the USSR is very important for obtaining as much published and unpublished data as possible. The future data base should include the following features:

1. A hierarchical structure with several levels of resolution corresponding to different model applications.

2. Parameters within each level which are compatible with input and output needs of the model corresponding to that level.

3. Coverage by data involved for the entire boreal zone.

4. Characterization of important environmental gradients (e.g., soil moisture and nutrients) should be the object of data collected.

5. Independent data should be assembled for model testing and validation.

We expect to continue the compilation of silvics of boreal tree species and to take part in the data base development in the near future.

3. THE BOREAL FOREST ZONE, THE TAIGA: A SHORT DESCRIPTION

The boreal conifer forest zone, also called taiga in Soviet Union (70), is circumpolar in extent and covers the northern parts of North America, Fennoscandia and the Soviet Union. Geographically the northern border of the boreal forest follows the coasts of Sweden, Finland and the arctic coast in northern Soviet Union, except in Siberia where it is further inland. See map, Figure 1 (73, 78).

The northern border of the boreal forest in Canada and Eurasia approximately coincides with the 13° C (55 F) July isotherm with marked departures in regions with montane or oceanic climatic influences (23). The northern limit of the boreal forest in the Soviet Union is influenced by the proximity to the cold arctic seas, river valleys and mountains (54). The southern limit is more difficult to delimit because the biome boundary is not well defined and differs in different vegetation types. The southern border is bounded roughly by the 18° C (65 F) July isotherm. In drier areas the southern edge of the forest border is north of this isotherm (23).

The northern border of the boreal forest is more sparsely forested than more central areas, with a transition into tundra roughly north of the July 13° C isotherm (23). The southern area is densely forested with conifers and at the southern edge of the boreal forest the conifer species are intermixed with a larger proportion of broad-leaf deciduous species (23). The main forest types of North Europe and Soviet Union are presented in Figures 2 and 3 (73, 79).

The climate in the forest zone is characterized by marked seasonal contrasts with mean summer temperatures of less than +10° C. In the forest zone there are long and cold winters and summers are short and generally cool with only a few days in midsummer in which afternoon temperatures reach 25° C (80 F). Moisture from precipitation exceeds loss by evaporation. Surface waters are abundant with rivers, lakes and marshlands (23).

Soil podzolization is intense in the boreal region as a consequence of cool temperatures, low evaporation rates, and the predominance of precipitation. Litter decay and nutrient turnover are slow because of slow decomposition of organic matter. Soil is acidic and has a low content of strong bases such as calcium. There is permafrost near the surface in most of the taiga. The vegetation canopy is mostly single-layered. The tree layer is composed mainly of evergreen coniferous trees. Ground layer is dominated by low shrubs, mosses and lichens.

The main forest types occurring in the boreal zone of USSR are dominated either by *Pinus*, *Picea*, *Abies* or *Larix*, as shown in Figure 3 (73). Below follows a short presentation of the main forest types. The data are from (54).

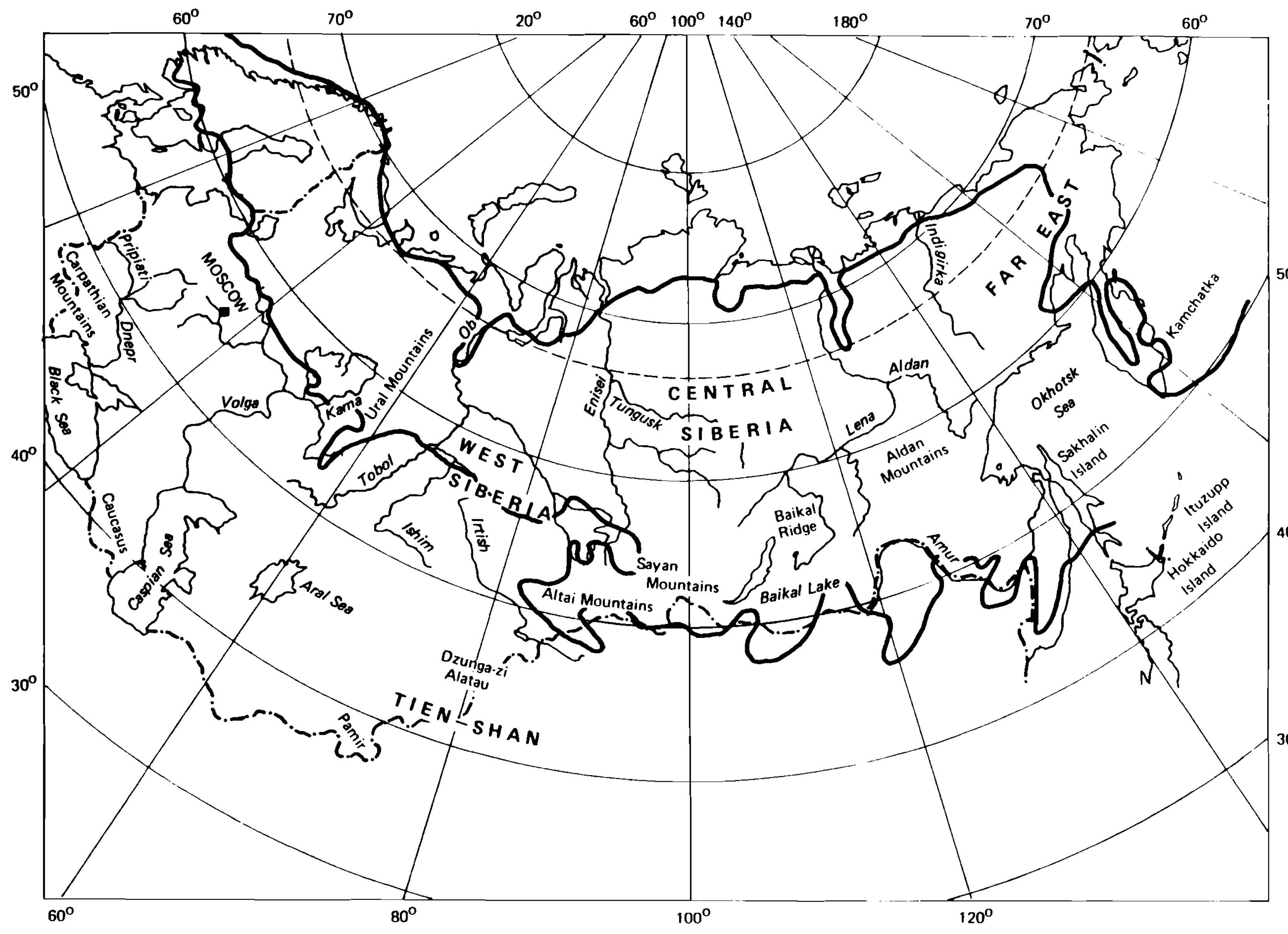

Figure 1. Boreal zone of Fennoscandia and the USSR.

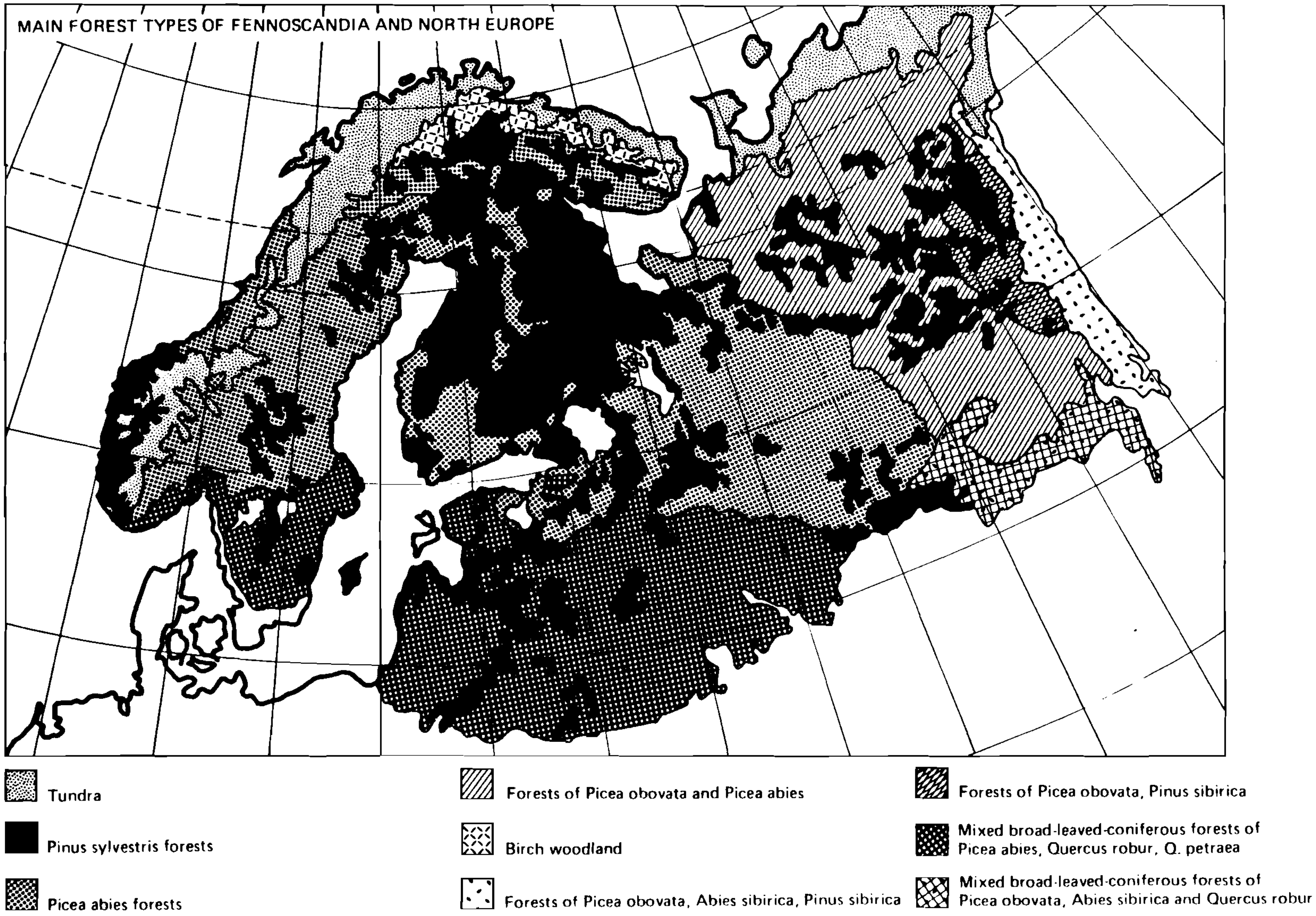

Figure 2. Main forest types of Fennoscandia and North Europe.

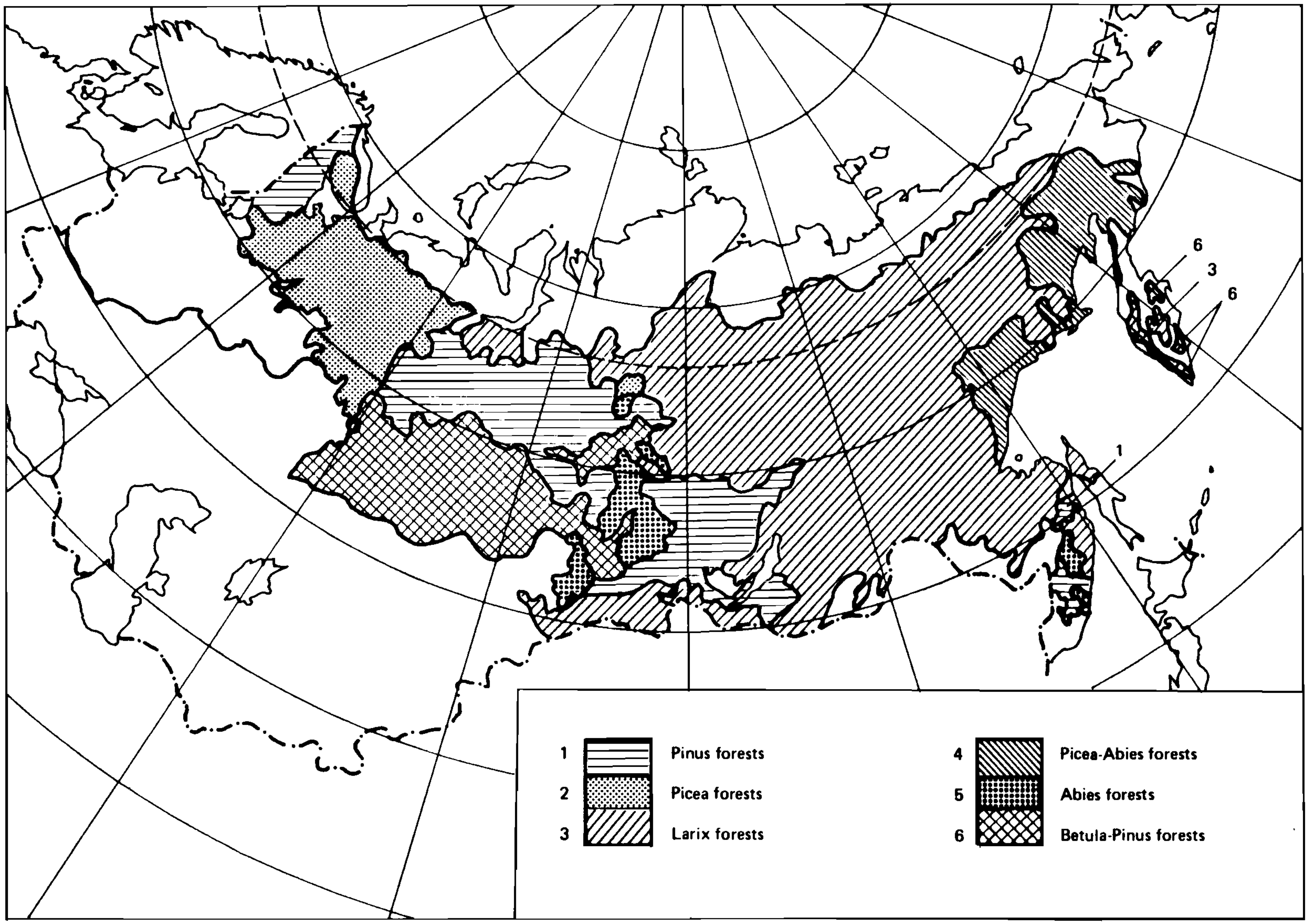

Figure 3. Main boreal forest types in the USSR.

3.1 *Pinus* Forests

Below is a short presentation of the climate in the *Pinus sylvestris* distribution area in the USSR.

Annual mean temperature	+8° - 12° C
Extreme temperature	+40° - 60° C
Precipitation per year	200 - 2000 mm

a) *Pinus-Picea* forests occur mainly in the northern Karelian, Ural and Enisei taiga.

b) *Pinus-Abies* species form mountain forests in Southern Urals, in Altai, Sayan, and in Transbaikalian mountain taiga.

c) *Pinus* forests occupy large territories of the western Siberian taiga, Angara taiga, and lower parts of Altai, Sayan, and Transbaikalian mountain taiga.

d) *Pinus-Larix* forests are found in Enisei, Angara and Yakutian taiga.

e) *Pinus-Quercus* forests form a belt at the southern edge of boreal forests as mixed and broad-leaf forests, and occur in the forest steppe zone.

f) *Pinus-Betula* and *Pinus-Populus* forests are found throughout the pine zone.

g) *Pinus sibirica*, Siberian cedar, is found in the northeast of European USSR, in western Siberia, on Altai and Sayan mountains, in Transbaikalia, the southern part of Yakutia and in the Far East.

h) *Pinus cembra* forests occur in the Carpathian mountains.

i) *Pinus koraiensis* is found in maritime areas of the Far East and in the southern part of the Khabarowsk territory. The last three pine stands mentioned are also referred to as cedar forests.

The grade, stand density, average increment, and wood reserves of pine forests improve from the north to the south and along all longitudes. The mean age of pine forests decreases gradually from north to south.

3.2 *Picea* Forests

The dominant tree species are listed below:

a) *Picea abies* (L). Karst. is a species of temperate rather than boreal climate. It is found in the Baltic region, Belorussia, Ukraine and in the Urals.

b) *Picea obovata* Ledeb. occurs mainly in western and central Siberia, as well as in the mountains of Altai and Sayan. It is better adapted to continental climate than are other species of spruce.

c) *Picea ajanensis* Fisch. is adapted to maritime climates and is found at the Far East seaboard.

d) *Picea orientalis* Link. is a species of maritime climates, which also grows in the mountain forests of Western Caucasus.

3.3 *Abies* Forests

The largest fir forests are situated in areas with precipitation of greater than 550-600 mm per year. *Abies* species occur in the eastern part of the west Siberian region and on moist slopes in the south Siberian, Uralian, Caucasus and Carpathian mountains. Distribution of fir on suitable sites is not uniform even in the humid and cool climate that fir needs (20).

The main species are:

a) *Abies sibirica* Ledeb. is found in the northeastern part of the European USSR, in the forest zone of western Siberia, on Altai, on the Sayan mountains, in the southern half of Central Siberia, in the western Tien-Shan and on the Dzungarian Alatau.

b) *Abies sachalinensis* Mast. is found on Sakhalin and Kuril islands.

3.4 *Larix* Forests

The dominant tree species are listed below:

a) *Larix sibirica* Ledeb. forests, dominated by *Larix sibirica*, are found in Western Siberia, Altai mountains, southeastern part of Eastern Siberia, northern Mongolia, and northwestern China. *Larix sukaczewii* occurs usually in stands with *Pinus sylvestris*. It also occurs in forests with *Picea obovata*, *Pinus sibirica*, and *Abies sibirica* (75).

b) *Larix sukaczewii* Dylis. forests are found in the European USSR, in the Ural mountains, and in the southwestern part of Western Siberia. *Larix sukaczewii* occurs seldom in pure stands or as a dominant species. It is usually associated with *Pinus sylvestris*, *Picea abies*, and *Picea obovata* (75).

c) *Larix gmelinii* Rupr. forests are found in Eastern Siberia, Far East, northern Mongolia, and northeastern China. Stands dominated by this species are found on many different soil types and soil textures, at different altitudes and also on permafrost. *Larix gmelinii* forms usually pure stands. *Larix gmelinii* is also found in association with *Chosenia arbutifolia*, *Populus suaveolens*, *Picea obovata*, *Picea ajanensis*, *Abies sibirica*, *Pinus sylvestris*, and *Betula pendula* (75).

4. ECOLOGICAL CHARACTERISTICS OF BOREAL TREE SPECIES

4.1 The Dominant Tree Species

1. **ABIES SIBIRICA** Ledeb. Syn. *Abies pichta* Forb., *Abies semenovii* B. Fedtsch.

<u>Distribution</u>: Its distribution is continental. *Abies sibirica* is found from the central and eastern parts of USSR to the northern tree limit, in Amur in the north and from the Urals to Turkestan and southern Mongolia to the south, and at the border to Turkestan (25). See map, Figure 4.

<u>Habitat</u>: The northern and southern limits of *A. sibirica* coincide with the 16.5° C and 20° C July isotherms respectively. Its western limit seems to be determined by increased humidity (11).

Abies sibirica requires for its optimal growth (20):
- A growing season of 120 days.
- A mean temperature for the growing season of 12° C, and for July 16° C.
- Not less than 700 mm precipitation during the growing season and not less than 900-1500 mm during the whole year.
- Maximum snow cover not exceeding 120 cm.

A. sibirica thrives on nutrient rich soil and relatively moist sand-loams and slightly podzolized soils (22). *A. sibirica* is found on river banks (19) and in mountainous areas in Siberia (1). It grows in the middle and upper elevations of mountains, but usually not as high as the timberline. It does not grow on bogs (20). After forest fire, *A. sibirica* dominates stands in the middle phases of succession, when the forest is dominated by deciduous trees

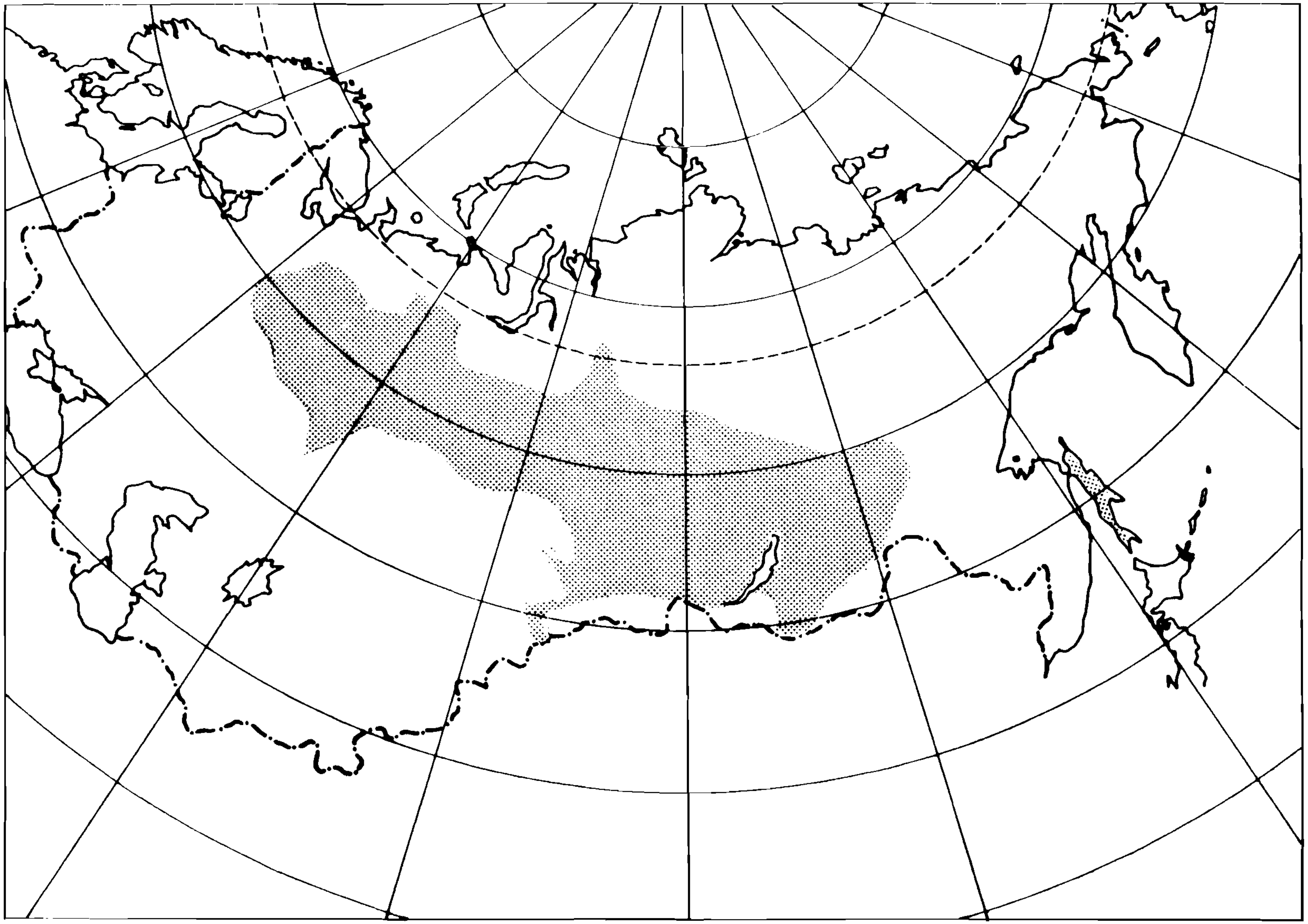

Figure 4. Distribution map of *Abies sibirica* Ledeb.

and herbs (11). At the tree line of mountains and close to the polar forest limit its growth form is shrubby (18).

Associated species: *A. sibirica* grows mainly in mixed stands with *Picea obovata*, *Pinus sibirica*, *Populus tremula* and *Betula* species (18, 75).

Life history: The seeds of *Abies sibirica* are dispersed by wind in autumn (19,20). Seed production seems to occur more often during dry and hot years (6). In closed stands, seed production begins at 40-70 years. Solitary trees produce seeds already at 20 years (18). *A. sibirica* reproduces better than *Pinus sylvestris*, *Picea abies* and *Larix* species on shady and grassy sites (11, 18). Good seed crops occur at intervals of 2-3 years in the southern USSR (18, 20) and at 4-6 year intervals in the northern parts of the country (18); on the western Siberian plains every 6-7 years, and 10 years in the region of Enisei River (20). In Kazakhstan, good seed years occur every 2-3 years and in the Urals every 3-4 years (20). *A. sibirica* is able to reproduce by layering (6). However, vegetative regeneration occurs only at the limits of its distribution and at the tree line (18, 22). Saplings of *A. sibirica* grow very slowly in the first 5-8 years (22). Young trees continue to grow slowly, reaching one meter in 15-25 years. Thereafter the growth rate increases (20).

Maximum values for height, diameter and age:

Height: 30-40 m (1, 5, 9, 15, 22), for a good site in USSR 37-38 m (2O).

D.B.H: 50 cm (22), 55 cm (15), and 30 cm at a height of 38 m (18). The largest DBH quoted is 60-80 cm (20).

Age: Range is between 150-200 years (18, 22) and 300 years (20). Maximum age is dependent on climatic conditions: in wet climates, individuals seldom reach 220-260 years because they are attacked by fungi (22). For example, in the west Siberian plains and at periodically flooded sites near rivers, maximum age is 160 years, while on drier sites in the same area it is 220-240 years (20).

Response to environmental factors

Light: *Abies sibirica* is one of the most shade-tolerant species, as it can withstand shade under canopy cover for more than 60 years (20). *A. sibirica* has similar light requirements as *Picea abies* (20, 18). Although *A. sibirica* is quite shade tolerant, it usually dies under canopies of faster growing *Pinus* and *Picea* (22).

Soil moisture: *Abies sibirica* favors moist, fertile and well-aerated soils, and weakly podzolic soils. It competes successfully with *Pinus sylvestris* on fertile soils, but the latter is a stronger competitor on poor soils and in paludified forests (11). *A. sibirica* does not grow on peat soils (18) or bogs (22). In mountainous areas, it prefers well drained and slightly elevated sites with moist soils (22).

Nutrient stress: *Abies sibirica* is less tolerant of nutrient stress than *Picea abies*, *Picea obovata*, *Pinus sibirica* (22), and *Larix* species (5).

Frost and fire: Although *Abies sibirica* can withstand temperatures as low as -50° C without damage (20), it is sensitive to late spring frosts (15, 24). Its fire tolerance is poor because it has thin bark, but fires are rare in the humid forests where it grows (20).

Flooding and wind storm: *A. sibirica* has been characterized both as tolerant of occasional flooding (19) and as having good flooding tolerance (20). It is tolerant of disturbance by wind until old age, when its tolerance has been reduced by insect damage (22).

Races and hybrids: *A. sibirica* is closely related to *Abies nephrolepis* and *Abies sachalinensis* (18).

2. **BETULA PENDULA** Roth. *Betula verrucosa* Ehrh. Syn. , *Betula alba* L., *Betula alba* v. vulgaris Rgl., *Betula alba* subsp. pendula var. vulgaris Rgl.

Distribution: *Betula pendula* is found in the European part of USSR, west Siberia, Altai, Caucasus and in Western Europe up to 2100-2500 m (22). See map, Figure 5.

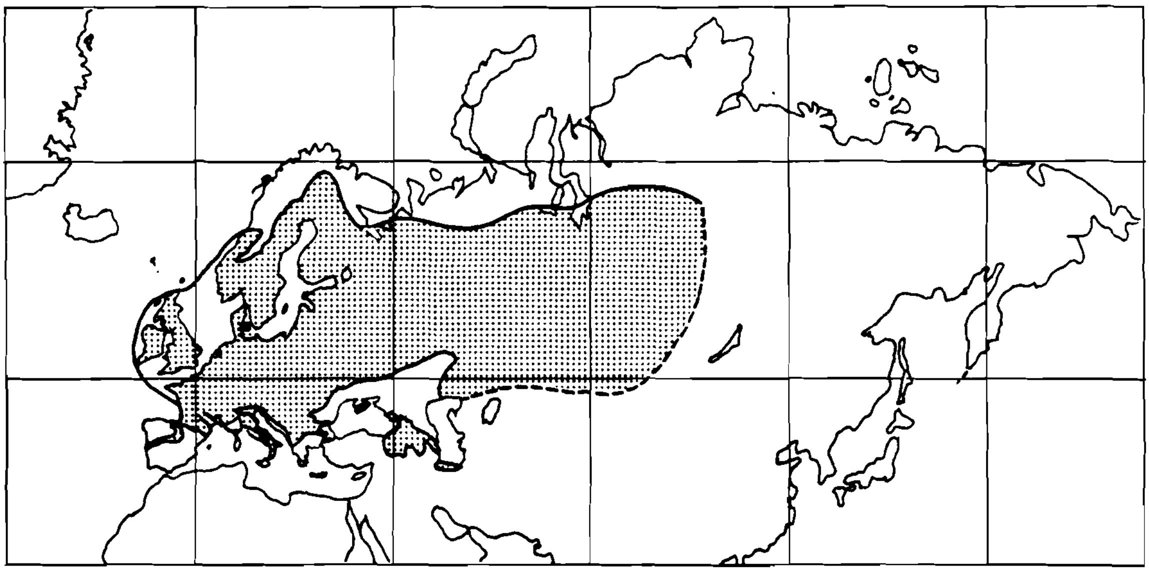

Figure 5. Distribution map of *Betula pendula* Roth.

Habitat: *B. pendula* forms both pure stands and grows in admixture with other tree species. It is a pioneer species on burned, cleared or old field sites (22). It grows best on drained loam-sand and podzol soils in the forest and in the forest-steppe zones (65). It is tolerant to acidic and saline soil but not to paludified soils (65). In the steppe region *B. pendula* becomes larger and older than in other parts of USSR (65).

Associated species: On good sites *B. pendula* is found in association with *Populus tremula*, *Picea obovata*, *Abies sibirica* and *Pinus sibirica*. On poor sites, *B. pendula* is found in association with *Betula pubescens*. *B. pendula* occurs also in association with *Picea abies*, *Quercus robur*, *Acer platanoides*, *Carpinus betulus*, *Fraxinus excelsior* and *Sorbus acuparia* (75).

Life history: The wind dispersed seeds of *B. pendula* are formed annually (8). This species regenerates both from seed and stump sprouts (8, 22). Regeneration from stump sprouts can continue until 30 years of age (65). *B. pendula* regenerates well on grassy sites (19),where it is fast growing (22). Fire is also important for its regeneration as it is unable to regenerate under a closed canopy (65). The increase in height and diameter of *B. pendula* in steppe regions is highest between the ages of 5-15 years (65). Young *B. pendula* grow faster than *Pinus sylvestris* (65).

Maximum values for height, diameter and age:

Height:	30 m in central Europe (3), 27-30 m in Finland (8) and 20 m in the USSR (22).
D.B.H:	> 60 cm in central Europe (3), 40-45 cm in Finland (8).
Age:	125-135 years in moist moss forest in southern Finland (8).

Response to environmental factors:

Light: *B. pendula* is a light-demanding species (2, 3). Only *Larix* species are more light-demanding (65). Table 1 shows the relationships between production of *Betula pendula* and illumination.

Table 1. Light level (% of full sunlight) and CO_2 uptake (mg/g dry matter) (65).

Light level	CO_2 uptake
1	0.18
30	6.0
100	9.4

Soil moisture: *B. pendula* does not grow well on wet soils (8). Nevertheless, it requires higher relative air and soil moisture than *Pinus sylvestris* (65).

Nutrient stress: *B. pendula* can grow on very poor soils (2), but it has a higher nutrient demand than *Pinus sylvestris* (65).

Fire and frost: *B. pendula* can survive forest fires (8) and is very frost tolerant (2, 65). It tolerates frosts also in late spring and in early autumn (65).

3. BETULA PUBESCENS Ehrh. Syn. *Betula alba* L. sensu Roth., *B. alba* subsp. pubescens Rgl.

Distribution: *Betula pubescens* is found in Central and Northern Europe, and in Siberia (25) throughout most of the boreal forest region. See map, Figure 6.

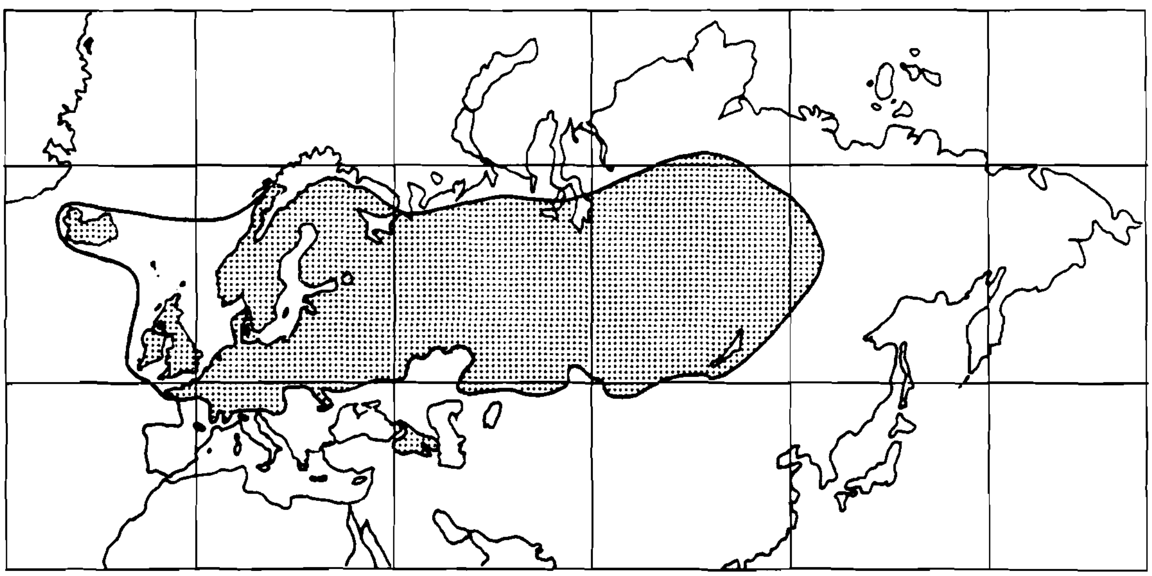

Figure 6. Distribution map of *Betula pubescens* Ehrh.

Habitat: *B. pubescens* grows on loamy sand, podzolic and marshy soils (65). It is a pioneer species in the arboreal colonization of non-forested land (54).

Associated species: It grows with most other tree species.

Life history: The seeds of *B. pubescens* are wind dispersed. The species is able to regenerate every year from seed and also from stumps. Regeneration from stumps is especially common among young individuals (8). Trees also regenerate well on grassy sites (19). Seedlings of *B. pubescens* survive better under forest canopy than seedlings of *Betula pendula* (65).

Maximum values for height, diameter and age:

Height:	ranges from 20 m (3, 22, 25, 65) to 30 m (5, 8).
D.B.H:	seldom more than 30-40 cm (3, 8). In FRG diameters of 40-60 cm have been found (12).
Age:	seldom more than 100 years (8).

Response to environmental factors

Light: *B. pubescens* is a light-demanding species (2, 54). It is more shade tolerant than *Betula pendula* (65).

Soil moisture: *B. pubescens* grows on a range of dry to wet soils (8). It tolerates wetter growing conditions and prefers moister sites than *Betula pendula* (22), and is also found on sphagnum bogs (65).

Nutrient stress: *B. pubescens* is able to grow on very poor soils (2, 54).

Fire and frost: *B. pubescens* is able to survive forest fires (8) and is very frost tolerant (2). Extreme frost tolerance allows it to reach the forest tundra zone in north, and to reach the mountain timberline (65).

4. LARIX GMELINII (Rupr.) Litv. Syn *Larix dahurica* Turcz.

Distribution: *Larix gmelinii* is broadly distributed in northeastern Asia. Its range covers wide areas in East Siberia and in the Far East (21). It forms continuous forests over nearly its whole range (21). See map, Figure 7.

Habitat: *L. gmelinii* grows under many different conditions: in mountainous areas, on plains, along river valleys, along sea-shores, in the taiga, on tundra and in forest steppe regions (21). Over most of its distribution, the climate is continental and the soil has permafrost (21). Its occurrence is characterized by areas having peat bogs and permafrost (22). *L. gmelinii* often forms a thick litter layer (21).

Associated species: North of 66° N, the tree layer is more discontinuous and is dominated by *Larix gmelinii* (4). On mountains and plains, *L. gmelinii* forms large forests both as pure stands and together with *P. sylvestris*, *Picea obovata* and other species (22). While *L. gmelinii* often forms monospecific stands with only few individuals of *Betula*, in warmer regions, in southern Yakutia and Zaibaikal, it grows with *P. sylvestris*. In mountainous areas, it grows with *Pinus sibirica* and in river valleys with *Picea obovata* (21). In the Amur area and on Sachalin Island it occurs with *Picea ajanensis* (1, 15). In the southeast, it grows with *Picea ajanensis*. *L. gmelinii* forests are usually 4-5 layered with a understory of *Betula* and other shrubs. Most stands of *L. gmelinii* are even-aged with an age difference of approximately 20-40 years. A reason for this may be the absence of competitors during colonization in severe climates (49, 50).

Life history: Seeds of *L. gmelinii* are wind dispersed. Good seed years occur at least every third year (18). Regeneration is best on bare, burned sites, but the species is also able to regenerate under closed canopies. Regeneration under its own canopy is poor because of its thick litter layer (21).

L. gmelinii grows slower than *Larix sibirica* but faster than *Pinus sylvestris* (22). Most of its height growth takes place before it is 60 years, afterwards the growth decreases to near zero by 100-120 years (21).

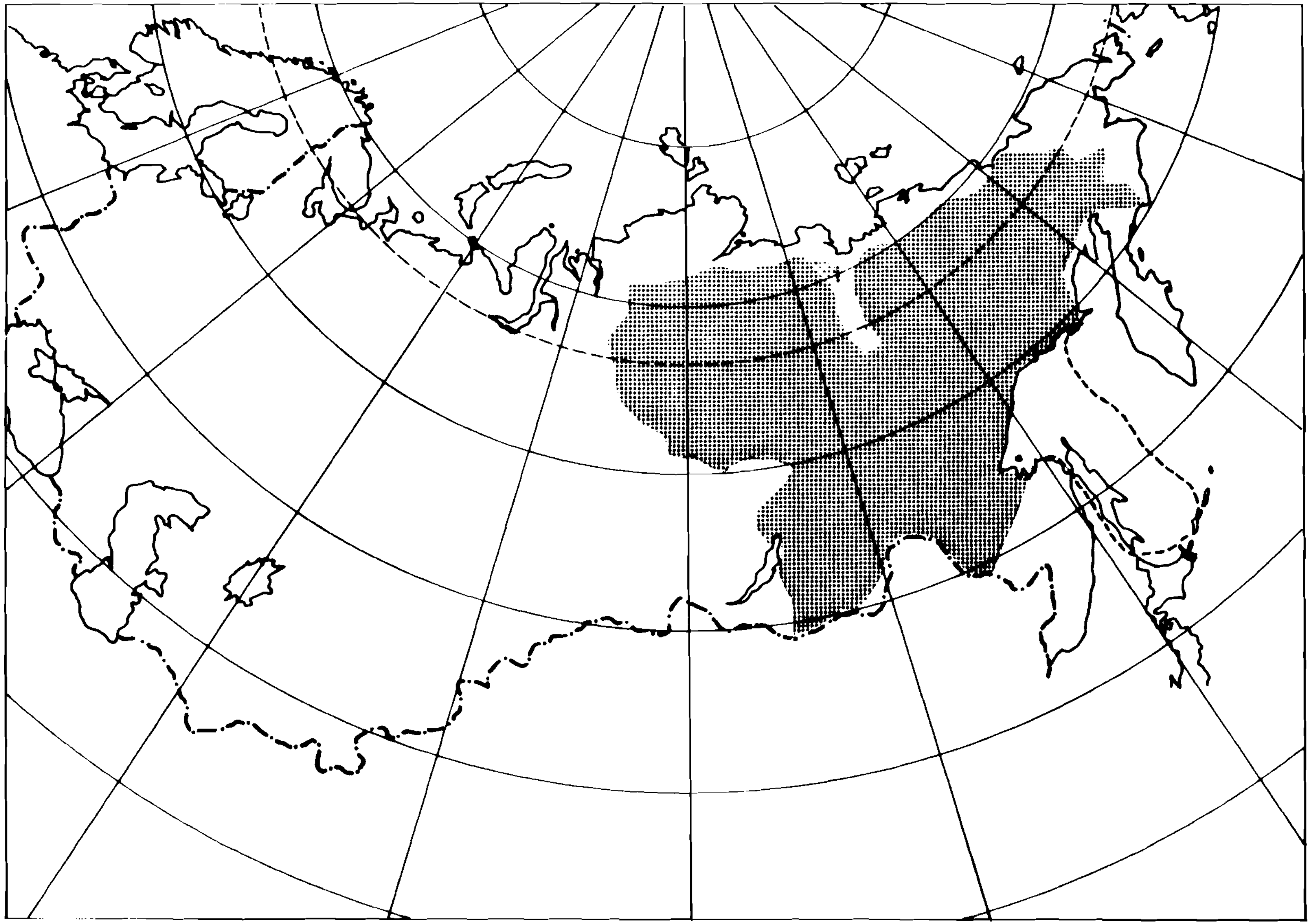

Figure 7. Distribution map of *Larix gmelinii* Rupr.

The growth pattern on best sites in Yakutia (22) is shown below:

Age (years)	Height (m)
10	1-1.5
20	2-4.0
50	6-11.0
100	15-23.0
200	20-29.0

In the north of its distribution and at tree line in mountains, *L. gmelinii* becomes shrubby, 20 cm height (18).

Maximum values for height, diameter and age:
Height: between 20 m (6, 15, 21) and 30-40 m (1, 18, 22).
D.B.H: 0.5-1 m (1, 6, 15, 21, 22). DBH of 1.40 m is rare (18).
Age: between 250-400 years in the USSR (21, 22).

Response to environmental factors

Light: *L. gmelinii* is very shade intolerant (18, 21).

Soil moisture: *L. gmelinii* grows best on moist to well drained soils (21, 22), but it also grows well on bogs (18). On swampy sites it becomes shrubby (15). *L. gmelinii* grows better on bogs than the other species of *Larix* and *Pinus sylvestris*, because it is able to produce adventitious roots (22).

Nutrient stress: *L. gmelinii* is very nutrient stress tolerant (21, 22). It grows on many different substrates (18), including saline soils (22).

Fire and frost: *L. gmelinii* is very frost tolerant (18); it can withstand extended periods of cold (21), and it also grows on permafrost (18). The temperature gradient between air and soil associated with permafrost may even be necessary for the normal growth of *L. gmelinii* (49, 50).

Flooding: *L. gmelinii* does not tolerate flooding. When it grows near rivers it always occupies elevated sites (22).

Races and hybrids: *L. gmelinii* has many local races (6). Two local races have been distinguished on the basis of climatic tolerance, one eastern and western type (21).

Enemies: The Siberian silkworm reduces both the growth in height and diameter of *L. gmelinii* (22).

5. **LARIX SIBIRICA** Ledeb. Syn. *Larix europaea* v. sibirica Lonnd, *Larix decidua* v. rossica Henk et Horst, *Larix decidua* v. sibirica Rgl. (22), L. russica Endl. (24)

Distribution: *Larix sibirica* is distributed over a range of 3000 km in direction west to east (21). In the east its range borders that of *Larix gmelinii* and in the west, that of *Larix sukaczewii* (21). It is found from 58° W longitude to 119° E (Lake Baikal), from tundra in the north (70° latitude) to mountains of Altai and Sayan in the south (46° latitude). *Larix sibirica* is the dominant species in the north, where it forms the polar forest timberline (21) in Ural Mountains and in west Siberia (north of 63° latitude) as well as in southern Siberia, Altai, Tanu-Ola, and on Baikal Ridge (21, 22). In Altai Mountains, it reaches the upper timberline at 2000-2400 m (22). In the south, it reaches the steppes and arid regions of Kazakhstan and central Asia. It is most abundant in the southern parts of its range: Altai, the Sayan mountains, the Baikal region and the central Siberian Plain. In western Siberia, the abundance of *L. sibirica* increases only in the polar zone, where it forms the forest tundra vegetation (21). See map, Figure 8.

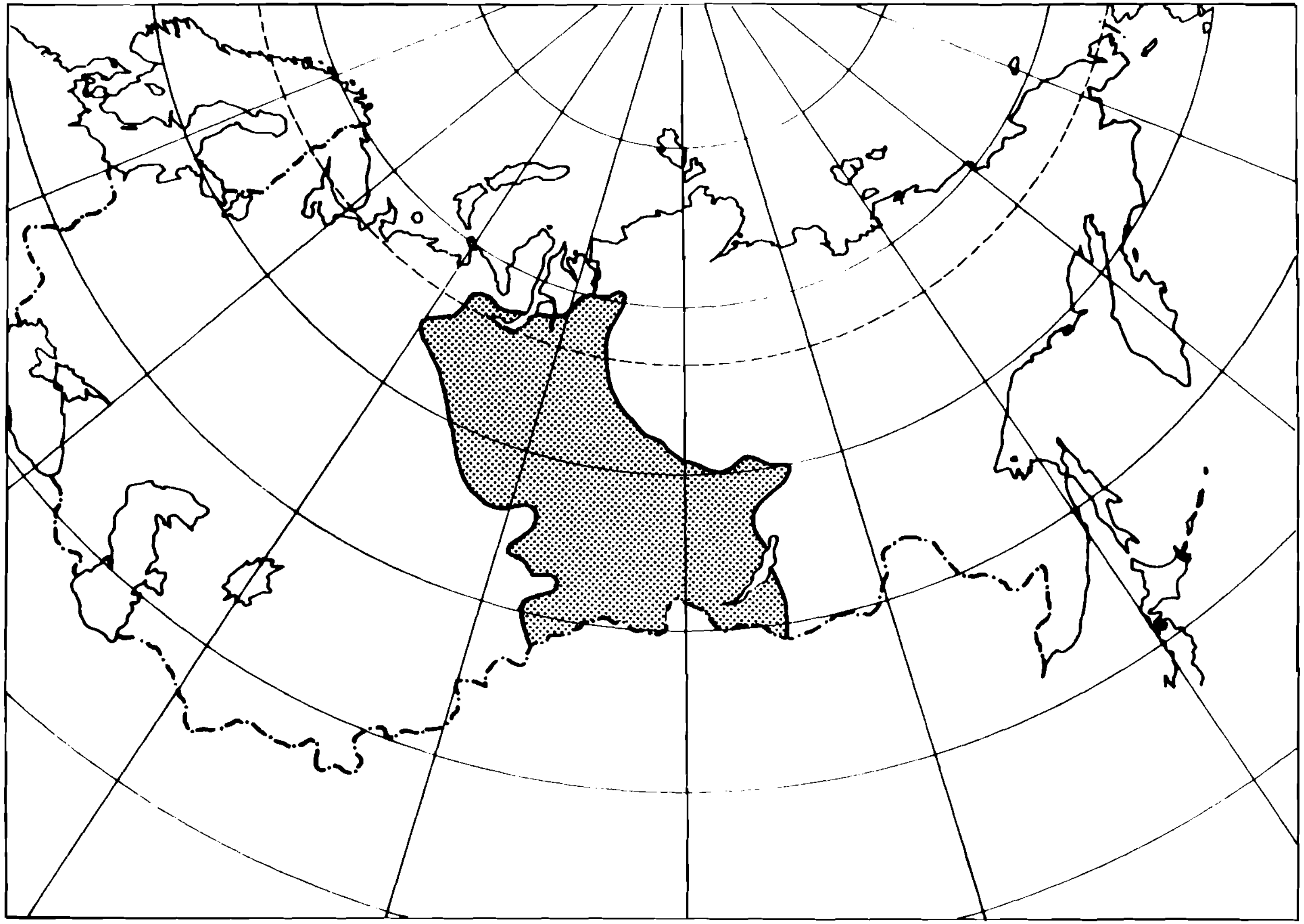

Figure 8. Distribution map of *Larix sibirica* Ledeb.

Habitat: *L. sibirica* grows on many different kinds of soils. In the upper part of Lena River valley *L. sibirica* grows on loamy soils, and near the Ob and Poluy Rivers on well-drained podzol soils. Near the polar timberline, it grows on dry sandy as well as on sand-loam soils, and in the lower parts of the Sayan mountains from the River Enisei to Lake Baikal, *L. sibirica* occurs only on nutrient rich redzina soils (21). *L. sibirica* forms moss, grass-bog and sphagnum bog forests (22). In the taiga peatlands, it grows in mixed forests with other conifer species on sandy soils, but also on marshy soils around rivers and bogs (21). In artificial plantations it grows successfully on any kind of soil (21). Continental climates, with great seasonal temperature fluctuations are most favorable for growth of *L. sibirica* (5, 22).

Associated species: *L. sibirica* often grows in pure and mixed stands with *Pinus sylvestris*, *Picea obovata*, and *Picea abies* (21), but only seldom with *Pinus sibirica* (21, 22). More often, it grows in mixed forests with *Pinus sylvestris*, preferring well drained and potassium-rich soils (21).

Life history: The seeds of *L. sibirica* are wind dispersed but they are not carried far from the mother tree (18). Good seed years occur every 6-7 years in the north and every 3-4 years in the south (19, 21). Seed production starts at the age of 12-15 years (22). The most intensive seeding occurs at 30-40 years (22) and between 70-100 years (22). Seeding continues to a very old age (22). Its growth rate is highest between 80-100 years (21), but also peak at the age of 20-40 years (22). Increase in height and diameter growth continues until 300 years (21). *L. sibirica* grows faster than the other coniferous species occurring in USSR, but slower than *Larix decidua* (21).

Table 2. Age and heights increase for individuals of *L. sibirica* growing on sites with good soils (22).

Age (years)	10	20	50	100	150
Height (m)	3.6	9.9	22.7	31.2	36.2

Larix sibirica regenerates best after forest fire (19) or on bare soils (22). It also regenerates well on moist sites with moss cover. Thick litter or grass cover prevents regeneration (21). *L. sibirica* does not regenerate at all under *Pinus sibirica* and *Pinus sylvestris* and its regeneration is weak under its own canopy (22).

The litter of *L. sibirica* decays much faster than that of other coniferous species because it contains fewer toxic substances which inhibit decay (21).

Maximum values for height, diameter and age:
Height: between 30-45 m (1, 18, 19, 21, 22).
D.B.H: 80-100 cm (18, 21), 1.8 m has been recorded as an extreme value (22).
Age: 120-150 years in natural forests (19), and 182 and 187 years in plantations (22), 400-500 (75).

Response to environmental factors

Light: The information on shade tolerance of *Larix sibirica* is contradictory. It is agreed that it is shade intolerant (18, 22) but the degree of shade tolerance is unclear. One reference (22) classifies it as very shade intolerant. Another (21) states that between 12-15 years, it can tolerate more shade and grow faster than *Picea obovata* (21). *L. sibirica* occupies sites which are not suitable for the shade tolerant Siberian species *Picea obovata*, *Pinus sibirica* and *Abies sibirica* (21).

Soil moisture: *L. sibirica* prefers moist soils. On boggy soil or soils with standing ground water, its growth is poor (18). It is very sensitive to degrees of soil aeration. For good growth it needs well-aerated soils; therefore, it does not grow well in the Siberian taiga or on peatlands around rivers (21).

L. sibirica is drought tolerant, less so than *Pinus sylvestris* and *Larix gmelinii*, and more so than *Larix decidua*, *Picea obovata* and *Pinus sibirica* (22).

Nutrient stress: The nutrient requirements of *L. sibirica* are somewhere between those of *Pinus sylvestris* and *Picea abies* (19). It can grow under poorer conditions than *Larix decidua* (21). It is able to grow on different kinds of soils, but requires good soils at the margins of its distribution (18). On podzolized soils, its growth response to fertilizer application is not as strong as for *Betula pendula* but stronger than for *Picea abies* (22).

Fire and frost: *L. sibirica* is a fire tolerant species (18) because of its thick bark (22).

Flooding and windstorm: No information was found.

Ability to grow on permafrost: This species is able to grow on permafrost (6, 18).

Palaeodata: Palaeodata show that the distribution range of *L. sibirica* was broader in the past. During the postglacial hypsithermal, it grew 2° latitude further north than today. At the end of Pliocene and during the Pleistocene, its eastern limit was several thousand kilometers further east than it is today (21).

Races and hybrids: *L. sibirica* forms hybrids with *Larix decidua* (6).

6. LARIX SUKACZEWII Dylis.

Distribution: *Larix sukaczewii* is found in the northeastern part of the European USSR, in the Urals and in Siberia. To the east it reaches Ob and Irtish valleys (21). See map, Figure 9.

Habitat: *L. sukaczewii* grows best when the soil is slightly podzolized and humus layer is thick. However, it does not grow on bogs and peatbogs (21). Optimal climatic conditions for its growth are found in the southern taiga and in the mixed forests zone (21).

Associated species: *L. sukaczewii* rarely forms pure stands (21). In Archangelsk region *L. sukaczewii* often grows on steep river slopes, where it can form up to 70% of the two-layered canopy. The upper stratum consists of *L. sukaczewii* and some *Pinus sylvestris*, and the lower stratum consists of *Betula* (21).

Life history: *L. sukaczewii* requires mineral soils without litter for natural regeneration. These conditions are found on mountain slopes, along river valleys, and only after forest fires in the plains (21). *L. sukaczewii* belongs to the faster-growing coniferous species. On good sites it grows faster than any *Picea* and *Pinus* species. Its growth is particularly fast during the first 30-40 years (21).

Maximum values for height, diameter and age:
Height: 40 m (21).
D.B.H: 100-120 cm (21).
Age: No information was found.

Response to environmental factors

Light: *L. sukaczewii* is very shade intolerant (21).

Soil moisture: *L. sukaczewii* grows best on well drained, aerated soils. It tolerates drought (21).

Nutrient stress: No information was found.

Fire and frost: *L. sukaczewii* is fire tolerant because old trees have thick bark (21). Its occurrence at the northern forest limit is a sign of its ability to tolerate frost (21).

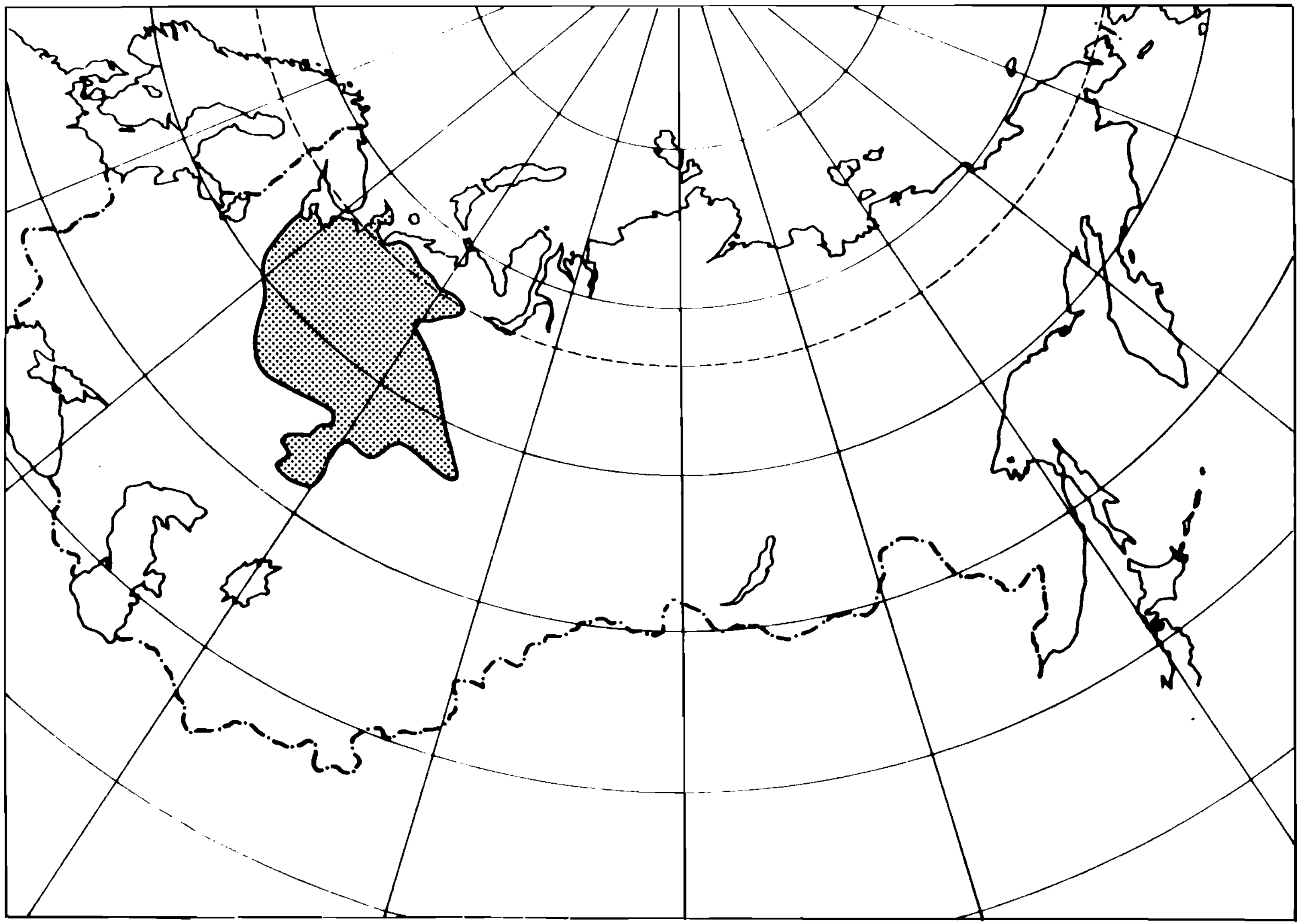

Figure 9. Distribution map of *Larix sukaczewii* Dylis.

Flooding and windstorm: No information has been found.

Races and hybrids: *Larix sukaczewii* is a subspecies of *Larix sibirica* (6).

7. PICEA ABIES (L.) Karst. Syn. *Picea excelsa* Link

Distribution: *Picea abies* is found in northeastern and central parts of the USSR. In the east, it reaches the Kama River, in south the Pripiati River and Ukrainian Carpathians (27). It is also found in mountainous areas of central Europe (18). Its northern limit is determined by the duration of the growing season: it needs at least 2-2.5 months with a temperature above +10° C. The southern limit is determined by drought, the western by oceanic climate and eastern limit by drought and competition from other trees and grasses (17). See map, Figure 10.

Habitat: *P. abies* grows naturally in areas with continental climate and high amounts of precipitation, but grows outside its 'natural' range in plantations. *P. abies* is a very flexible species (2) because it grows in many different climatic conditions (17).

It is found where:
- the minimum heat sum is 1450° C during the growing season.
- the length of the frost period is at least 3 months.
- optimal rainfall in the alps is 600-800 mm during May to August (66). Another author sets the lower limit to 230 mm (17); the difference is, of course, dependent on the temperature conditions at the site.

The soil moisture availability determines the temperature requirements of *P. abies* (17).

Associated species: *P. abies* forms mixed stands mainly with *Pinus sylvestris*, *Larix sukaczewii*, *Pinus sibirica*, *Betula pendula*, *Betula pubescens*, *Populus tremula* (17, 18), *Picea obovata*, and *Abies sibirica* (75).

Life history: The seeds of *P. abies* are light; 4.8 g/1000 seeds in northern Europe and 8.0 g/1000 seeds in central Europe (18). The wind dispersed seeds are spread between March and April in the year following flowering (17). Seed production starts at an age of 40-60 years in closed canopy, and earlier in open conditions (6). Seeding occurs every 4-8 years in USSR (27) and 12-13 years in Finland (18). This species regenerates also by layering (27). The increase in height of *P. abies* is intensive until the age of 150-170 years (27). Seedlings are very shade tolerant; they can survive under closed canopy for a long period (71).

Maximum values for height, diameter and age:

Height: from 30-60 m (12, 15, 17). In the Russian plains it is 35-40 m while it reaches 50 m in the Carpathian mountains (27); in Sweden it is 45 m (6).

D.B.H: in Sweden 1.7 m (6) and in FRG 2 m (1, 5).

Age: seldom up to 400-500 years in the USSR (27). However, 1000 year-old trees have been found in primeval forests in the alps (1). In managed forests the oldest trees are 150 years (1). The oldest trees found in Sweden are seldom more than 400 years (6).

Response to environmental factors

Light: *P. abies* belong to the group intermediate between light demanding and shade tolerant species (2). The ability to tolerate shading depends both on its age and site conditions: young individuals are more shade tolerant than older trees (67, 68).

Soil moisture: *P. abies* grows preferably on moist or wet soils (2). However, it does not thrive on wet anaerobic soils (71).

Nutrient stress: *P. abies* is a tolerant species (2). *P. abies* prefers acidic soil pH 4-5 (17) but it needs good nutrition to grow well (18).

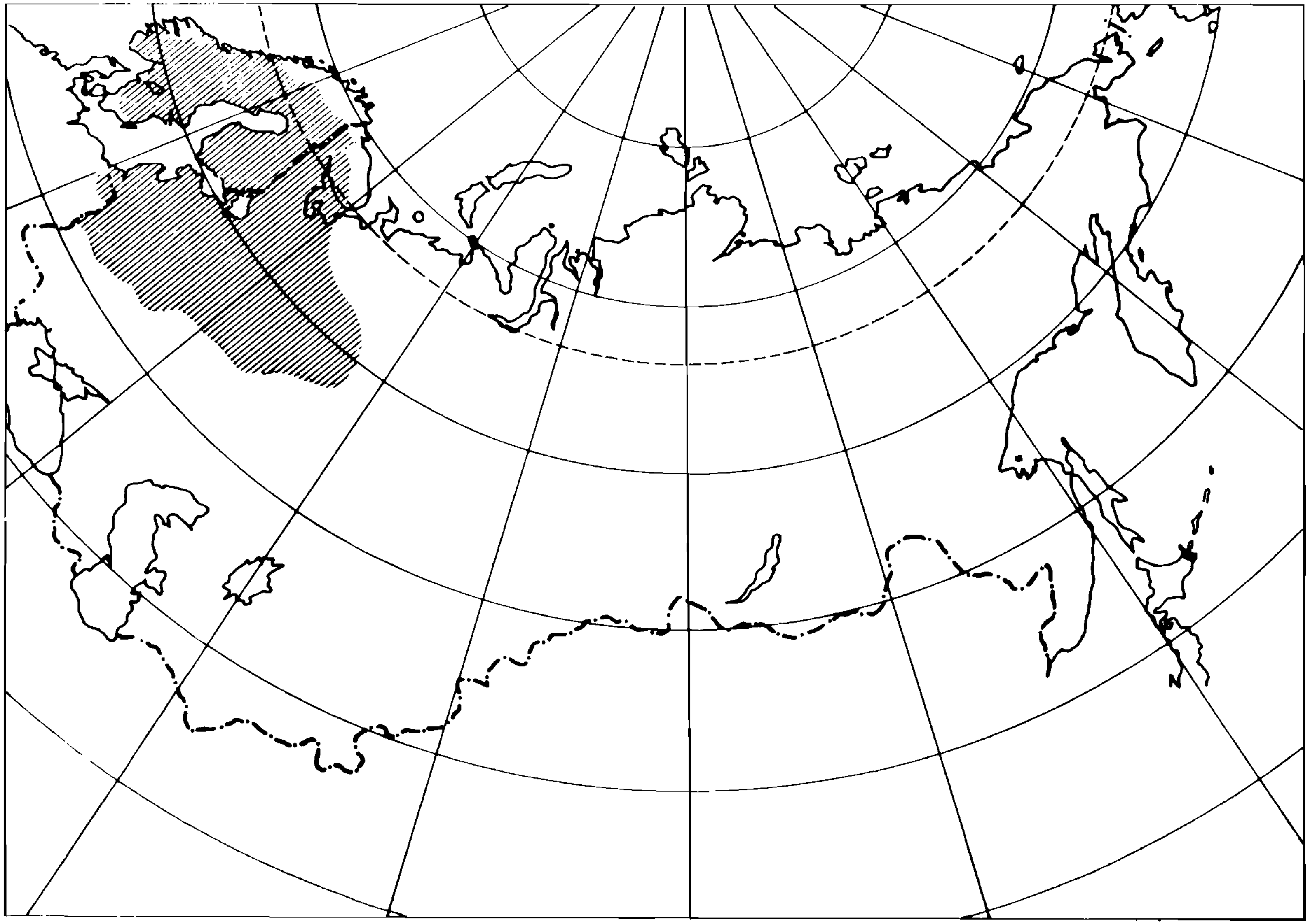

Figure 10. Distribution map of *Picea abies* (L) Karst.

Fire and frost: Fire tolerance of *P. abies* is very poor (5), but it is quite frost tolerant (2). Ability to survive late frosts depends on the place of origin. Siberian subspecies are very resistant to spring frosts (17). At early ages, however, damage can occur from spring frosts (27, 71). The species tolerates winter frosts well (71).

Flooding and windstorm: No information was found.

Races and hybrids: *P. abies* has formed many races with different ecological requirements (17, 1). Based on differences in cone scales the following tree varieties are recognized (17):

1. *Picea abies* var. acuminata, found in the Alps.
2. *Picea abies* var. europaea, found in Northern Europe as far east as Ural Mountains.
3. *Picea abies* var. obovata, found east of Ural Mountains.

8. PICEA OBOVATA Ledeb. Syn. *Picea abies* var. obovata

Distribution: *P. obovata* usually grows in continental areas (17). It occurs from 70-71° N to 54-56° N latitude (27), from north eastern parts of European USSR to Okhotsk Sea in the east (65). To the north, it reaches the tundra forest region, and to the south, the taiga zone (65). It grows on Siberian plains and in the upper Ural, Altai, and Sayan Mountains (64). See map, Figure 11.

Habitat: *P. obovata* grows on well-drained to moist, sandy-loam soils but has a poor growth on marshy soils in central and south taiga regions (65).

Associated species: *P. obovata* forms pure and mixed stands (27). It grows with *Pinus sylvestris*, *Larix sukaczewii*, *Betula pendula*, *Betula pubescens* and *Populus tremula* (18, 27) and with *Abies sibirica*, *Larix sibirica* and *Pinus sibirica* (24, 27). It forms large forests in western and eastern Siberia, in the Urals, and in the mountains of the Far East mountains (65). Higher in the mountainous regions of Far East taiga, it forms forests with *Abies sibirica*, *Larix* species, *Pinus koraiensis* and *Betula* species. At lower elevations in this region, it forms forests with *Fraxinus*, *Tilia*, *Acer*, and *Populus tremula* (64).

Life history: *P. obovata* has good seed years once every 12-13 years (8). The seeds are dispersed in September of the year of flowering (17). It regenerates on bare, burned soil and under canopies of all forest types. However, its regeneration is poor on sphagnum bogs (64).

Maximum values for height, diameter and age:

Height:	30 m (15, 27, 65), 40 m (8, 1).
D.B.H:	40-50 cm (8).
Age:	in southern Finland maximum age is 250-350 years, while in northern Finland it is 400-500 years (8).

Response to environmental factors

Light: *P. obovata* is able to withstand even strong shading (8). However, it tolerates less shading than *Abies sibirica* (65).

Soil moisture: *P. obovata* grows on humid and swampy areas (4), but not on soils with standing water (8).

Nutrient stress: *P. obovata* has higher nutrient and moisture demands than *Pinus sylvestris* (8).

Fire and frost: *P. obovata* tolerates winter frosts but is sensitive to spring frosts (64). Its seedlings are very sensitive to fire (65).

Flooding and windstorm: No information was found.

Races and hybrids: *P. obovata* has many different varieties (1). *Picea obovata* itself is a "cold climate variety" of *Picea abies* (69).

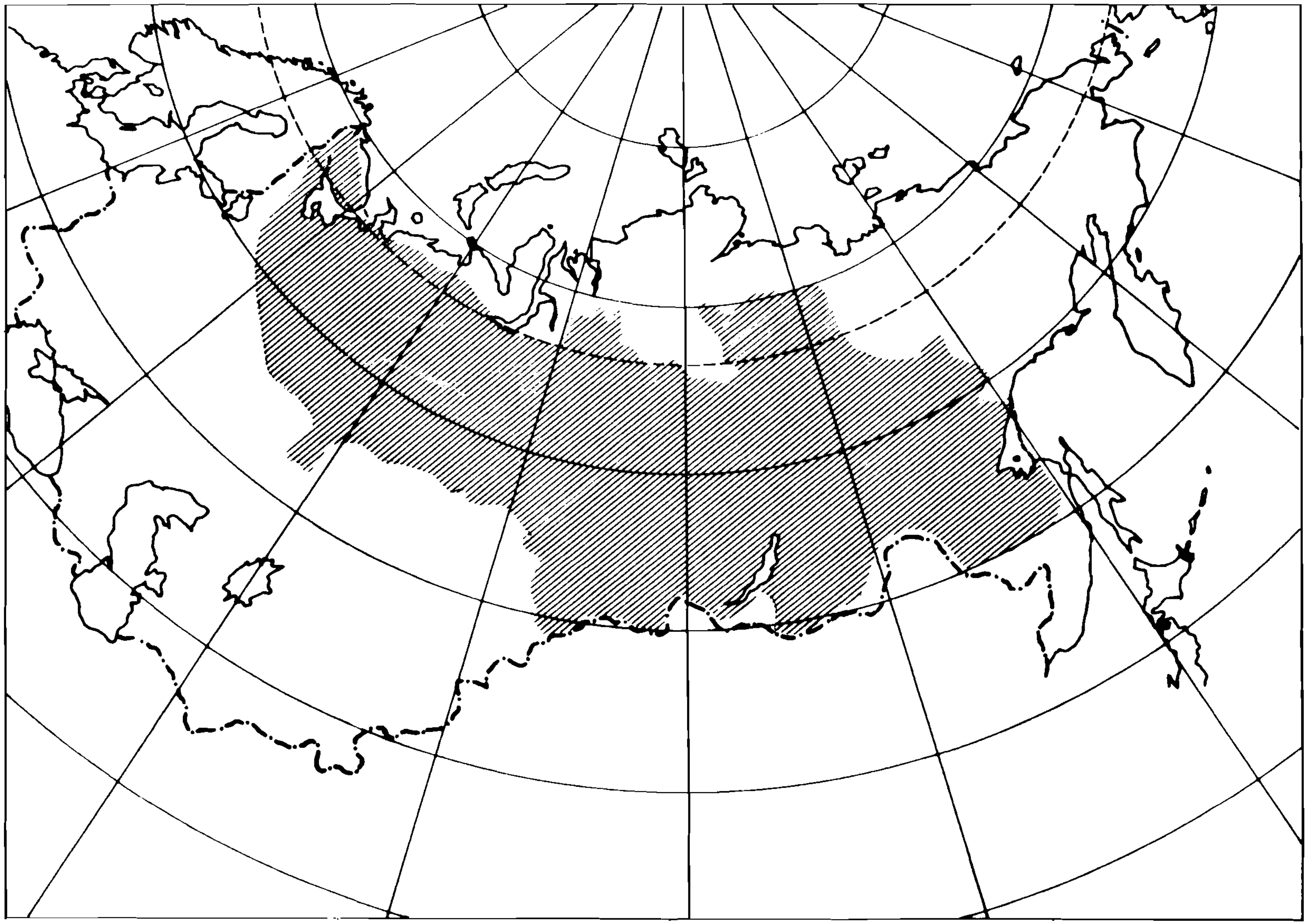

Figure 11. Distribution map of *Picea obovata* Ledeb.

9. PINUS PUMILA Regel (Pall.) Syn. *Pinus cembra* var. pumila Pall. Fl. Ross.

Distribution: *Pinus pumila* is found in northeastern Siberia, Kamchatka, Sakhalin and on Kuril Islands in northern Japan (1). See map, Figure 12.

Habitat: *P. pumila* forms the alpine treeline together with *Larix* species (5).

Associated species: *P. pumila* grows often in the shrub layer in forest with *Picea ajanensis*, *Larix gmelinii* forests (18) and in association with *Picea obovata*, *Pinus sibirica* and *Pinus sylvestris* (75).

Life history: *P. pumila* has good seed years nearly every year. One thousand seeds weigh 97 g. Seeds are dispersed by animals, and especially birds. Close to the tree limit it also regenerates by layering (18). Its growthform is shrubby (18).

Maximum values for height, diameter and age:

Height:	7 m (1), usually not more than 3 m (18), 4-5 m (22).
Dbh:	unknown.
Age:	unknown.

Response to environmental factors

Light: No information was found.

Soil moisture: No information was found.

Nutrient stress: It is nutrient stress tolerant (22).

Fire and frost: *P. pumila* is fire intolerant (18), but it is a frost tolerant species (22).

Flooding and windstorm: No information was found.

Races and hybrids: *P. pumila* is closely related to *Pinus cembra* var. sibirica (5).

10. PINUS SIBIRICA Loud. (Rupr.) Mayr. Syn. *Pinus cembra* subsp. sibirica (Rupr.)

Distribution: *Pinus sibirica* is found in the European Alps (18). In the USSR, its northern border goes between 66° N 30' and 57° north latitude, crossing the Ural Mountains. The southern border passes through northern Mongolia, the county of Tobolsk and the Altai mountains, and its western limit is the river Vitschegda (22). Its distribution range has become broader in the last 80-100 years (41, 42). See map, Figure 13.

Habitat: *P. sibirica* has different soil requirements at its northern and southern limits. In the north it grows in river valleys (18), but prefers drier, drained slopes with sandy-loam to sandy soils and seldom grows on bogs (31, 59, 57, 44), while in the south it prefers drained moist soils and grows on sphagnum bogs (31, 59, 57). Its ability to tolerate a variety of soil conditions is also noted: parent material, soil structure and soil fertility have only minor influence on the distribution and it is able to grow on sites with thin soil layer as well as on sphagnum bogs (22, 28). *P. sibirica* and *Picea obovata* tolerate swamp soils only if they are aptotroph or mesotroph bogs. On oligotroph bogs, *P. sibirica* is replaced by *Pinus sylvestris* (61).

The climatic requirements of *P. sibirica* have been described as:

- A mean annual relative humidity of 62% seems to be optimal for *P. sibirica* (46). Humidity above 70% during the growing season limits the normal growth of *P. sibirica* (47), but other references (30, 44) state that it prefers sites with higher humidity. The lowest relative humidity tolerated by *Pinus sibirica* without affecting its growth is 45% (48).

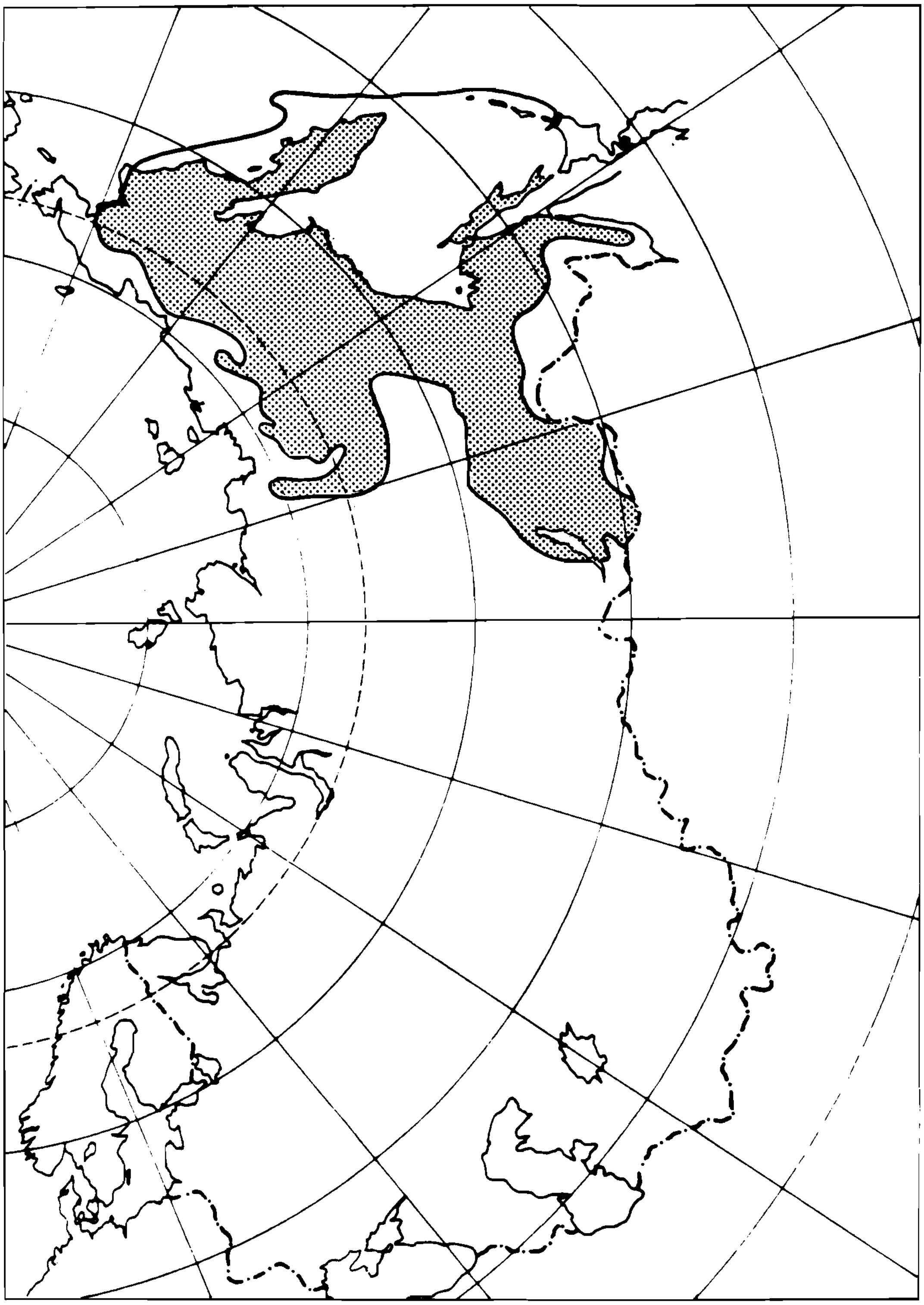

Figure 12. Distribution map of *Pinus pumila* Reg.

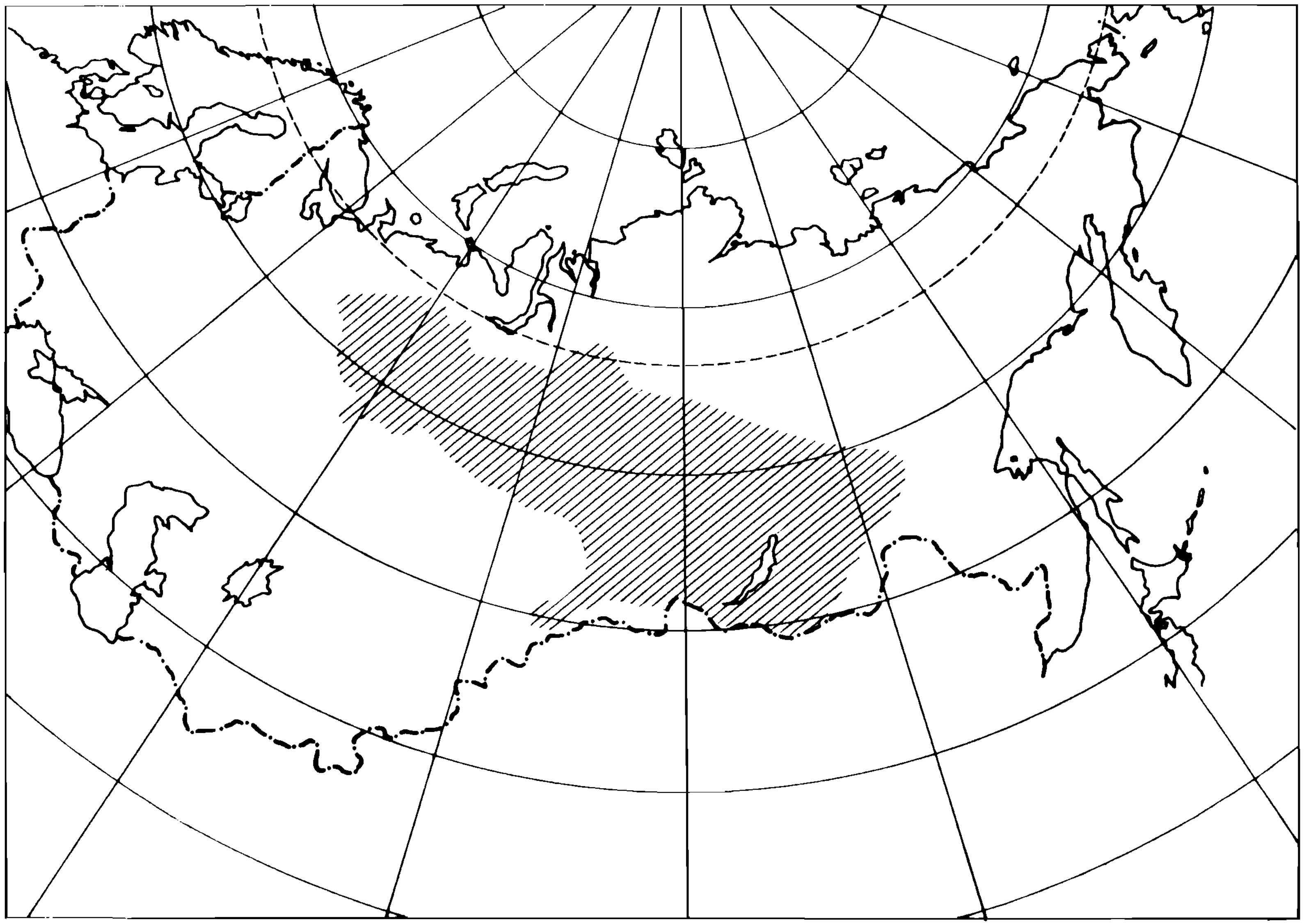

Figure 13. Distribution map of *Pinus sibirica* Loud.

- The optimal amount of annual precipitation for *P. sibirica* is 500-600 mm (48, 57) and 800-1400 mm per year in the mountains of south Siberia (47).

Associated species: *P. sibirica* is associated with *Picea obovata* , *Abies sibirica*, *Larix sibirica*, *Larix gmelinii*, *Larix sukaczewii*, *Pinus sylvestris*, *Populus tremula*, *Betula pendula* and *Betula pubescens* (75).

Life history: *P. sibirica* has good seed crops in the European part of USSR every 8-9 years, every 4-6 years in west Siberia (37) and every 3-4 years in Baikal area (22). The annual frequencies of seed production are

- in the southern regions of central Siberia 81%.
- in the north Taiga 68%.
- in the south Taiga 64%.

Seed-producing trees are found in stands every year but in some years the percentage of seeding trees is 80-90% instead of 50% in non-seeding years (40). On bogs the seeding frequency is reduced (62).

In the European part of USSR solitary trees form seed crops when they are 25-30 years old (18, 22). In closed forests seed crops are formed at 60-80 years (22). Seed production reaches its peek at the age of 80-160 years (18) and 170-240 (300) years (31). Seeding continues until 400-450 years (34). The seed-bearing cones fall to the soil and the seeds are released when the cone decays (18). *P. sibirica* seeds are eaten and dispersed by animals (22) and humans (18). The number of cones per tree ranges from 71 to 120 (35). Mean number of seeds per cone is 80 (36). The seeds may be dispersed 5-7 km per year (38). *P. sibirica* seeds germinate at a soil temperature of 5° C (31). Light requirements of *P. sibirica* increase with age (28). The relationship between seedling age and minimum light requirements for growth (52) are shown below:

Age	Light level of full sunlight (%)
1-2	1-3
3-5	3-6
6-10	6-9
11-15	9-13

Under dense canopies of *P. sibirica* seedlings can survive 10-15 years, some individuals up to 30-35 years (28). The roots of *P. sibirica* are shallow (33). *P. sibirica* is able to produce adventitious roots, enabling growth on wet sites (33).

Maximum values for height, diameter and age:
Height: between 30-40 m (1, 9, 14, 18, 19, 22, 31).
D.B.H: 1.80-1.90 m (18, 31).
Age: usually 400-600 years (12, 22, 30, 31, 32), but 800 year-old trees have been found (30, 31, 32).

Response to environmental factors

Light: *P. sibirica* is classified as a shade tolerant species (22, 28). It is less shade tolerant than *Abies* but more shade tolerant than *Picea* (51, 53).

Soil moisture: *P. sibirica* grows on different soil conditions from dry (4) to humid and wet (14, 22) and on bogs (61). *P. sibirica* and *Picea obovata* tolerate swamp soils well only if they are nutrient rich or intermediately nutrient rich bogs. On nutrient poor bogs *P. sibirica* is replaced by *Pinus sylvestris* (61). The former is able to grow under similar moisture conditions to *Picea abies* (19), and is able to grow better on bogs than *Pinus sylvestris* (18).

Nutrient stress: *P. sibirica* is nutrient stress tolerant (55, 56, 57), but on marshy sites its growth is poor (22).

Fire tolerance: *P. sibirica* is more fire tolerant than *Picea abies* and *Betula* (19).

Frost tolerance: *P. sibirica* is a frost tolerant species (19, 22, 30, 31, 43). It tolerates low soil temperatures and grows well on permafrost (47). *P. sibirica* tolerates -60° C in winter; -50° C in the spring can be tolerated (31).

Flooding and windstorm: *P. sibirica* grows poorly on undrained soil, but it tolerates periodic flooding. This feature, along with its high tolerance of low temperatures, permits growth in river valleys (18, 31).

Races and hybrids: *P. sibirica* has formed several varieties within its range (28). *Pinus cembra* L. is usually divided into two geographically separated races: *Pinus cembra* L. var. typica in the European Alps, and *Pinus cembra* L. var. sibirica Loud. in the USSR (18). *Pinus sibirica* f. furfosa. (H. max 6-7 m) is found on bogs (22). In Altai, Sayan and Transbaikal mountains a shorter variety *Pinus cembra* var. coronans is found (18).

11. PINUS SYLVESTRIS L.

Distribution: *Pinus sylvestris* is the most widely distributed pine tree in the world (5). It is found in central Europe, and in the western, central and eastern parts of the USSR (18). See map, Figure 14.

Habitat: *P. sylvestris* occurs in areas with continental or submaritime climate (18). It thrives best in lowland areas; on mountains it is found mainly on warm eastern and western slopes (18). It grows well on peat, sand and rocky soils (70).

Associated species: *Pinus sylvestris* is found together with most species in the boreal zone.

Life history: *P. sylvestris* regenerates only from seed (8). It has good seed production once every 6-7 years (8, 18). Solitary trees start seeding at 8-20 years (18). In closed stands, seeding starts at 30-40 years (6). Seeding occurs more seldom in northern parts of the country (6). For a successful regeneration on pine heaths a good seed year has to be followed by one or two wet summers (18). Fire is also required for successful regeneration (5), since seedlings of *Pinus sylvestris* are light demanding (6). In southern Sweden, growth in height is most rapid from 5-30 years while in northern Sweden it is fastest from 15-30 years (6).

Maximum values for height, diameter and age:

Height:	maximum is 40-48 m under most optimal growth conditions in the FRG (1), in Sweden 37 m (5) and 35.5 m in Finland (18).
D.B.H:	in Sweden 1.9 m (6), 5.9 m is the maximum measured, but trees 2.5 m in diameter are already uncommon (5).
Age:	in southern Finland, 250-300 years on dry morainic soils; on fresh soils it can be 600 years, in northern Finland 700-800 years (8).

Response to environmental factors

Light: *P. sylvestris* belongs to the group of light demanding species, but it is also able to grow in shady habitats when the soil is humid (2, 18). On fertile soils, it is more shade tolerant (71).

Soil moisture: *P. sylvestris* grows both on wet and dry soils (2), but on wet soils it is outcompeted by *Picea abies* (8).

Nutrient stress: *Pinus sylvestris* is a very tolerant species (2). It grows under many different conditions from very dry, nutrient-poor to wet, nutrient rich conditions (8, 71). It thrives on humid sand-loam soils (71).

Fire and frost: *P. sylvestris* survives forest fires and regenerates on burned areas (8). *P. sylvestris* is also very frost tolerant (2).

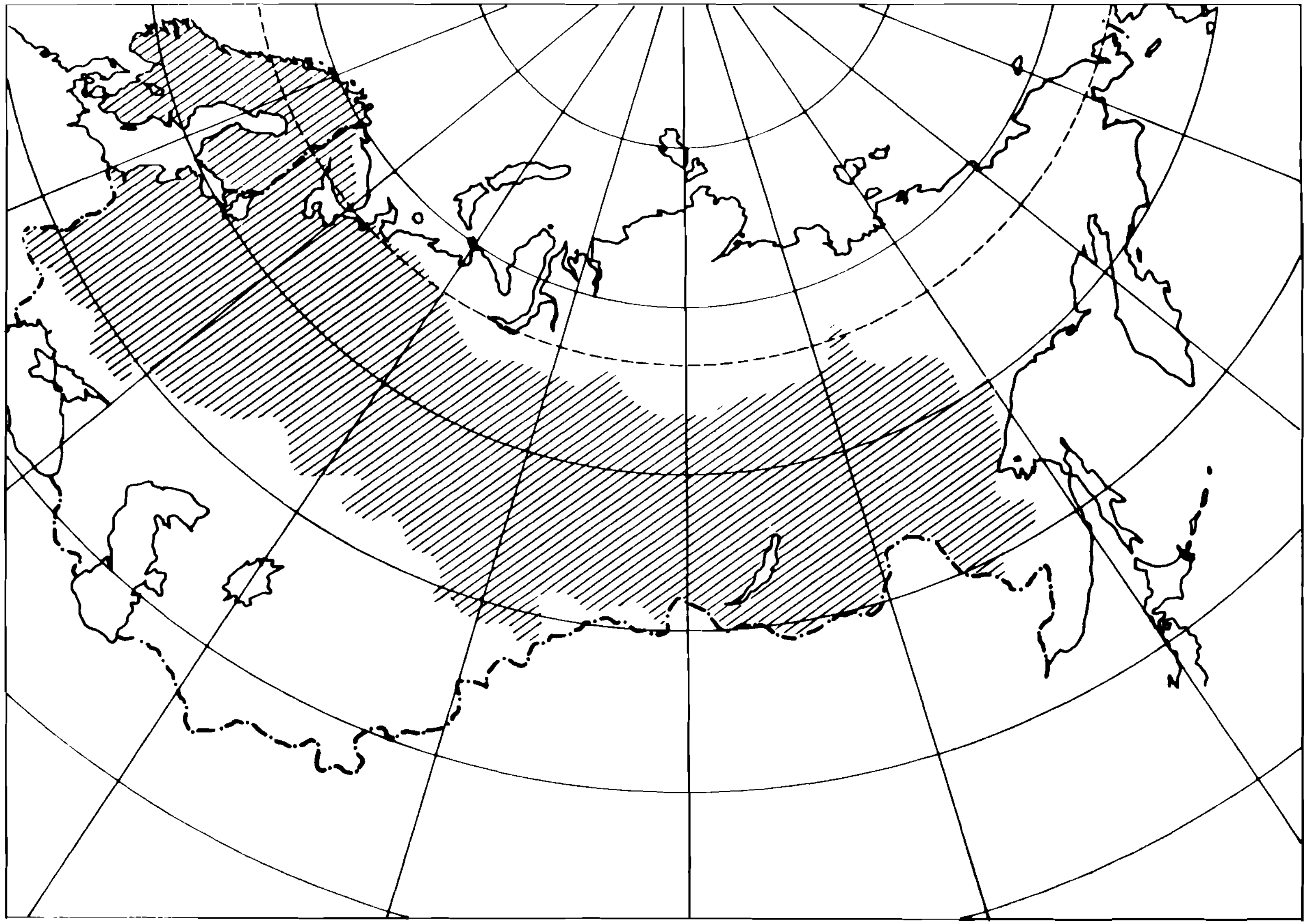

Figure 14. Distribution map of *Pinus sylvestris* L.

Flooding and windstorm: No information was found.

Races and hybrids: *P. sylvestris* has many different subspecies (1). Two clines of *Pinus sylvestris* are recognized (18):

1. *Pinus sylvestris* var. lapponica Hartm., found on northern Fennoscandia, north of 66°.
2. *Pinus sylvestris* var. septentrionalis Schott., in central and southern Fennoscandia, reaching to southern parts of Sweden.

12. POPULUS TREMULA L.

Distribution: *P. tremula* occurs as a tree until 70° N (3), from the western borders of USSR to Kamchatka (54). See map, Figure 15.

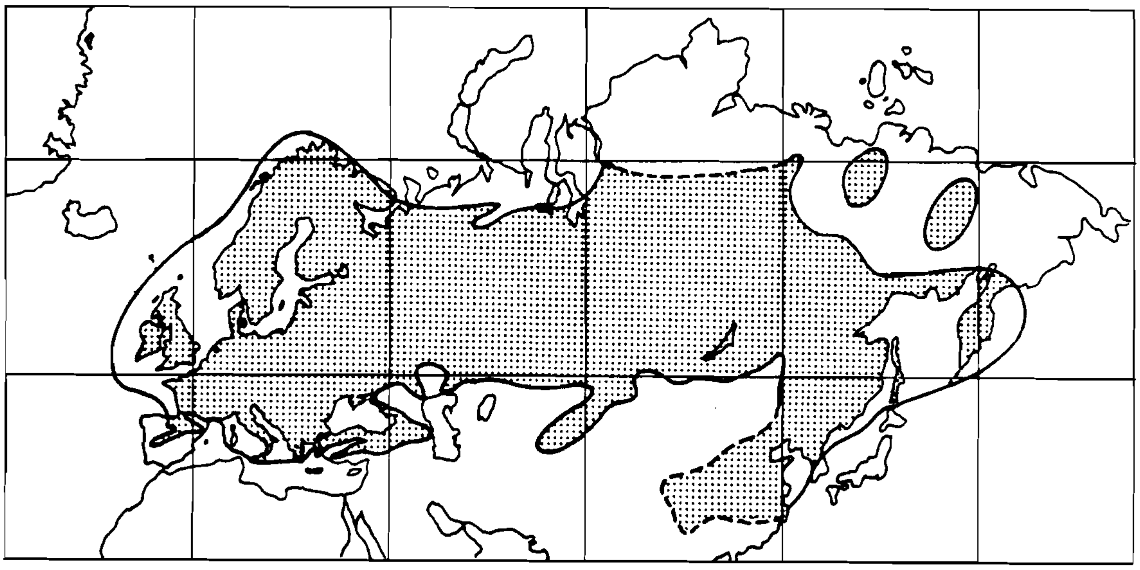

Figure 15. Distribution map of *Populus tremula* L.

Habitat: *P. tremula* has few habitat preferences and can essentially grow everywhere. In harsh environments in eastern Siberia, it grows only in river valleys and on lower parts of mountain slopes (54).

Associated species: *P. tremula* is a constant associate of *Betula* (54).

Life history: *P. tremula* regenerates from seed and from stump and root suckers. Stump suckers do not form trees (8).

Maximum values for height, diameter and age:

Height: 10-35 m in Central Europe (1); in Finland and around the Balticum 30 m (8, 3).

D.B.H: from 35 cm to 1 m in Europe and in the USSR (1); and 35-40 cm in Finland (8).

Age: 100 years (1); *P. tremula* rarely grows more than 150 years of age (8).

Response to environmental factors

Light: *P. tremula* is light demanding (3, 54).

Soil moisture: *P. tremula* grows best on soils with good water supply and aeration (3). On soils with a high water table its growth form becomes shrublike.

Nutrient stress: *P. tremula* grows on all soil types (3) except stony and marshy soils, and loose sands (54).

Fire and frost: *P. tremula* tolerates summer frosts and cold winters (3). *P. tremula* tolerates freezing as well as heat (54).

Flooding and windstorm: No information was found.

Races and hybrids: No information was found.

4.2. The Important Tree Species

13. ABIES SACHALINENSIS Mast.

Distribution: *Abies sachalinensis* is found in northern Japan (5), in the western and southern parts of Sakhalin Island and in the Hokkaido district (1, 18).

Habitat: *Abies sachalinensis* grows on thick fertile soils (13).

Associated species: Near Hokkaido it grows together with *Picea ajanensis* (18). In the central parts of Sakhalin Island it forms the lower stratum in *Picea ajanensis* forests (20). In the southern part of its distribution area, *A. sachalinensis* forms the upper stratum in the forest (20).

Life history: Seeds of *A. sachalinensis* weigh 11-13 g/1000 seeds and they are wind dispersed (18).

Maximum values for height, diameter and age
Height: 40 m (1, 9, 18) and 25 m in the USSR (20).
D.B.H: from 50 cm (20) to 1 m (18).
Age: 240-280 years (20).

Response to environmental factors

Light: *A. sachalinensis* is either intermediately or very tolerant, as are all *Abies* species (18).

Soil moisture: *A. sachalinensis* prefers humid climates (9). This is characteristic of *Abies* species (18).

Nutrient stress: *A. sachalinensis* is less tolerant of nutrient stress than *Abies sibirica* (20). *Abies* species generally require nutrient rich soils (18).

Fire and frost: *Abies* species are classified as fire intolerant, but they are less sensitive to fire than *Picea* species (18). *A. sachalinensis* has been classified as frost intolerant (18), and is less frost tolerant than *Abies sibirica* (20).

Races and hybrids: *Abies sachalinensis* var. Mayriana Maybe et Kudo. is found in northern Japan (18).

14. ALNUS GLUTINOSA Gaertn. Syn. *Alnus rotundifolia* Mill. and *Alnus vulgaris* Hill.

Distribution: Its main distribution area is central Europe (65).

Habitat: *A. glutinosa* requires high summer temperatures (3). In cold climates it becomes contorted (7). It thrives on wet or inundated sites, such as shores and river banks where it occurs as a tree, while on swamps it grows poorly, and becomes contorted (8, 54, 64).

Associated species: *A. glutinosa* is found together with *Salix* species, *Betula* species and *Picea abies* (64).

Life history: *A. glutinosa* regenerates from seeds and stump suckers, but does not form root suckers (8, 64). The formation of trees from stump suckers can continue for many generations but their growth is poorer than the older and higher-originating rootstock (64). Seeds are dispersed within 6-8 m from the parent tree except near lakes, where they are dispersed by water (64). On shorelines seeds are formed nearly every year. Seeds mature in October and are dispersed between February and April (64). Seeds are formed at the age of 12-20 years in open stands, while in closed stands or on sites with poor soils or harsh climatic conditions, seed formation occurs later (64). Because seedlings of *A. glutinosa* do not tolerate competition and need a continuous water supply, they are found only on newly exposed land, such as shorelines undergoing isostatic rebound, on river-banks and on bogs (64). The form and extension of the root system is dependent on the site conditions (64). *A. glutinosa* grows best on well aerated and moist soils (64).

Maximum values for height, diameter and age :

Height:	30-35 m in FRG (1, 3, 12) and 20-25 m in Finland (8, 64). At the northernmost site in Finland, the height is 12 m and DBH 25 cm (65).
D.B.H:	50-60 cm in FRG (1, 3), 25-30 cm (8), 30-40 cm and 75 cm in Finland (64).
Age:	100-120 years (1, 8, 12, 64) on soils with good nutrient, water and light availability, and high relative humidity (12, 8).

Response to environmental factors

Light: *A. glutinosa* is shade intolerant (3, 8). It seems to have light requirements similar to (8) or somewhat less than *Betula* (2).

Soil moisture: *A. glutinosa* requires wet soils and high relative humidity. It is able to survive inundations (3). *A. glutinosa* requires moist soil and prefers wetting by flowing water (54, 64).

Nutrient stress: *A. glutinosa* needs more fertile soils than *Alnus incana* (54).

Fire and frost: Fires do not occur where *A. glutinosa* grows (64).

Flooding and windstorm: *A. glutinosa* tolerates inundations better than *Alnus incana* and any other tree species in Finland (64).

15. ALNUS INCANA Willd.

Distribution: *Alnus incana* is found in all of Eurasia except in southern parts of Europe. It also occurs in northern-most parts of Asia. It grows up to 1700 m in the Alps and 2000 m in Caucasus (65).

Habitat: *A. incana* prefers cold humid climates (63). It grows on river banks and shorelines (63). Best growth occurs on wet sites with flowing water (63). Stature is shrubby on poor sites, while on good sites it is a tree (8).

Associated species: No information was found.

Life history: *A. incana* starts seeding at 8-10 years (63). Seeds are produced annually (63). Regeneration occurs from stump and root suckers as well as from seeds (8, 65).

Maximum values for height, diameter and age:
Height: 15 m (8), 20 m (63).
D.B.H: 20-25 cm (8), 50 cm (63).
Age: 60 years (8).

Response to environmental factors

Light: *A. incana* is shade intolerant but tolerates more shade than *Betula* (8) and *Alnus glutinosa* (65).

Soil moisture: *A. incana* can grow on drier localities than *Alnus glutinosa* (8, 54).

Nutrient stress tolerance: *A. incana* requires less fertile soils than *Alnus glutinosa* (54, 65).

Fire and frost tolerance: Fires are unusual at localities where *A. incana* occurs. It is a very frost tolerant species, found in polar regions where the growing season is only 6 weeks long (63).

Flooding and windstorm tolerance: *A. incana* is more flood tolerant than *Alnus glutinosa* (63).

16. CARPINUS BETULUS L.

Distribution: *Carpinus betulus* is found in the southwestern parts of USSR (1), occasionally in the Ukraine; it occurs in Moldavia, Belorussia and Lithuania (54). In Caucasus, it grows on dry southern slopes up to 1800 m elevations (65). See map, Figure 16.

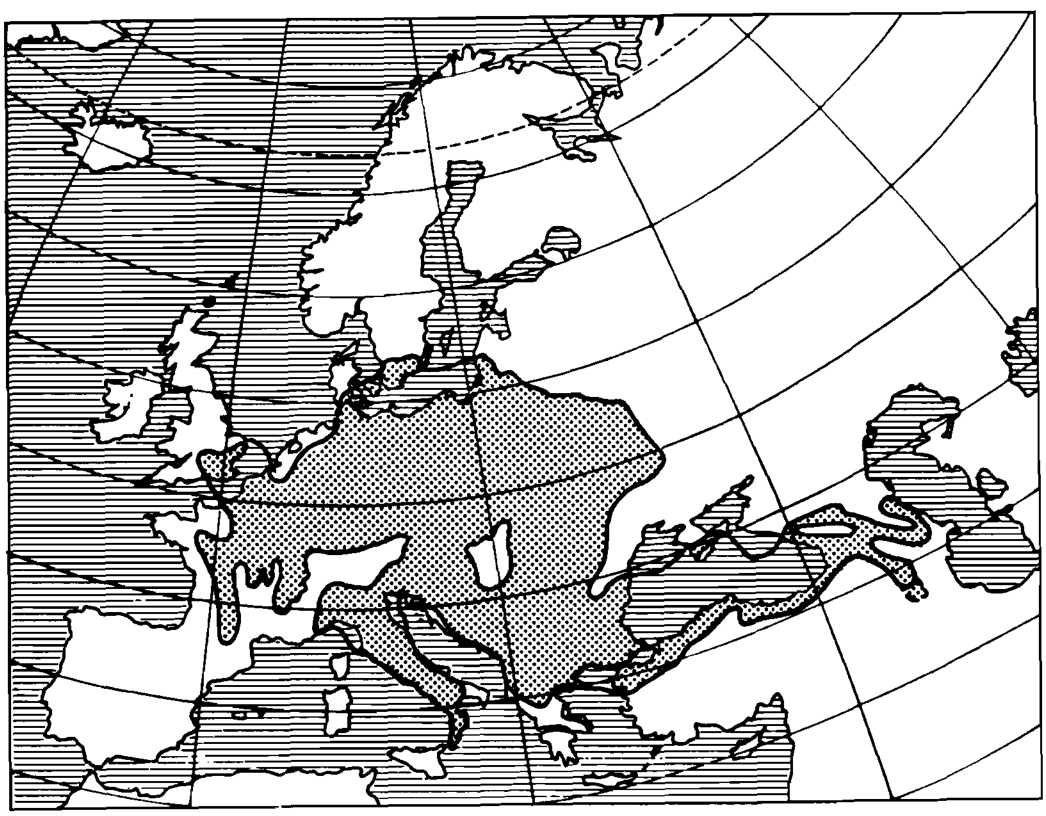

Figure 16. Distribution map of *Carpinus betulus* L.

Habitat: *C. betulus* grows best on loamy mineral-rich soils (3). It demands good soil conditions (54). It grows well on dark grey, grey, sandy-loam and on rocky soils in the mountainous regions (65). The species can tolerate drier soils than *Fagus sylvatica* (65). It does not grow on marshy or acidic soils (63). However, it develops freely under the canopy of other trees and has a high regenerative ability (54).

Associated species: It always occurs with *Fagus* and often grows in association with other broad leaved species (54) such as *Quercus*, *Tilia*, and *Acer* (65).

Life history: *Carpinus betulus* regenerates from seed both under forest canopies and on bare soil. It also reproduces from stump sprouts and by layering (65). It has good seed years once every 2-3 years and it is able to form stump sprouts until the age of 80-100 years (65). Saplings of *C. betulus* grow faster than saplings of *Quercus* (65). On optimal sites it grows 6-7 m in the first 15 years (63). At the age of 80-100 years on a good site, it can become 25 m tall and have a diameter from 30 cm to 50 cm (63).

Maximum values for height, diameter and age:

Height:	30 m (1, 2, 3, 25), 25-30 m (63).
D.B.H:	50 cm (1, 2), and to more than 80 cm in the east (3); 60 cm (63).
Age:	seldom more than 150 years (6). On good sites 300-400 years (65).

Response to environmental factors

Light: *C. betulus* is shade tolerant (54), but less so than *Fagus sylvatica*, *Tilia cordata* (2), and *Abies sibirica* (65). It is classified as intermediately shade tolerant (2, 3).

Soil moisture: *C. betulus* survives on dry soil but grows best on wet soils (2). It is more sensitive to drought than *Fagus sylvatica* (3). Nevertheless, it tolerates drought well because it has a well-developed root system (65).

Nutrient stress: *C. betulus* is classified as either intolerant of nutrient stress or intermediately intolerant (63).

Frost: *C. betulus* is frost intolerant. However, it can withstand temperatures down to -35° C (65). It tolerates late spring frosts (2), although Delkov (63) states the opposite.

Flooding and windstorm: No information was found.

17. FAGUS SYLVATICA L.

Distribution: *Fagus sylvatica* is found in western Europe, in western parts of USSR and on lowland areas of southwestern parts of the Ukraine and Moldavia (65). It occurs also in the Carpathian mountains (54). Its northern limit is 58° N (63).

Habitat: *Fagus* species are mesic to thermophilic trees (54). They do not occur in oceanic or dry continental climates (65). In the east *F. sylvatica* grows mainly in mountainous areas (3). It needs at least 600-700 mm rain annually (3). *F. sylvatica* does not occur on sandy, strongly podzolized soils (65), or on marshy or heavy loam soils (63). It grows best on nutrient rich, humid and well aerated soils (63).

The growth pattern of *F. sylvatica* on an optimal site (63) is shown below:

Age (years)	Height (m)
10	0.8
20	3.0
30	6.0
50	14.0
120	30.0

Associated species: *Acer*, *Quercus*, *Fraxinus*, *Picea*, *Pinus* and *Abies* species (63).

Life history: Seeds of *F. sylvatica* are dispersed by animals. Seed production begins at 40-50 years in a closed stand (65). Good seed years occur every 3-4 year (65). Seeding years are more frequent under better growing conditions (65). *F. sylvatica* produces stump sprouts only after cutting, and if 30-60 years old (63, 65).

Maximum values for height, diameter and age:
Height: 25-30 m in Sweden (6) and 40-45 m in FRG (1, 12), 30 m (65), 40 m (63).
D.B.H: 1.4-1.5 m in FRG (1, 12) and 6.5 m in Sweden (6), 100-150 cm (65), 120-200 cm elsewhere (63).
Age: 300 years in FRG and USSR (12, 63).

Response to environmental factors

Light: *F. sylvatica* is shade tolerant (3). It can grow well when the incoming light is 20% of full sunlight (2).

Soil moisture: *F. sylvatica* prefers moist thick soils (1). However, soils should be neither too moist or nor too dry (65).

Fire and frost: No information was found.

Flooding and wind: *F. sylvatica* is unable to survive on inundated soils (3).

18. LARIX DECIDUA Mill. Syn. *Larix europaea* DC.

Distribution: *Larix decidua* is found in northern Europe and in the Alps between 1000-1800 m elevation.

Habitat: *L. decidua* is a mountain tree (18) requiring warm summers and dry, cold winters (12).

Associated species: *L. decidua* grows with *Abies alba*, *Picea abies* and *Pinus cembra* (15).

Life history: *L. decidua* requires loamy, chalky, thick, well-aerated soils (15). It grows best on drained, moist, sand-loam soils as well as on alluvial lime soils (22). It is fast growing (15) (see also the description of *Larix sibirica*).

Maximum values for height, diameter and age:
Height: 20-30 m at an age of 60-150 years (1), 30 m (5), and more than 50 m (5, 6, 12, 24). All values are for European trees.
D.B.H: ranges from 90 cm at an age of 60-150 years (1), to about 1.6 m (6, 15).
Age: is from 600-800 years (1, 12, 24) and up to 1000 years in the mountains (18).

Response to environmental factors

Light: *Larix decidua* is a shade intolerant species (15). *Larix* species have been reported as the most light demanding species of the coniferous tree species (5).

Nutrient stress: *L. decidua* has similar nutrient requirements to *Pinus sylvestris* and *Picea abies* (2).

Soil moisture: *L. decidua* is less moisture demanding than *Picea abies* (6).

Fire and frost: No information was found.

Flooding and windstorm: No information was found.

Races and hybrids: No information was found.

19. LARIX KURILENSIS Mayr. Syn. *Larix gmelini* var. Japonica and *Larix gmelinii* var. japonica and *Larix kamtschatica* Rupr.

Distribution: *Larix kurilensis* grows in eastern Siberia (18). It is also found on the Island Iturupp (1). In the far north and close to the tree limit, it has prostrate growth form (18).

Habitat: *L. kurilensis* is able to grow on a range of dry to boggy areas (18). It tolerates nutrient stress (18).

Associated species: No information was found.

Life history: *L. kurilensis* has good seed production once every third year. It regenerates well even at the far north of its distribution. It also regenerates by layering (18).

Maximum values for height, diameter and age:

Height:	22 m (1), on good sites 30-33 m (18).
D.B.H:	70 cm (1), 1.40 m (18).
Age:	300-400 years on bogs (18).

Response to environmental factors

Light: *L. kurilensis* is more shade intolerant than *Larix sibirica* (18).

Nutrient stress: *L. kurilensis* tolerates nutrient stress (18).

Soil moisture: *L. kurilensis* is able to grow on dry to boggy areas (18).

Fire and frost tolerance: No information was found.

Flooding and windstorm: No information was found.

Races and hybrids: *L. kurilensis* has many subspecies and its growth form is variable (18).

20. PICEA AJANENSIS Lindl. et Gord., Fisch. Syn. *Picea jezoensis* (Sieb. et Zucc.) Carr.

Distribution: *Picea ajanensis* is found in Japan and on coastal areas in the southeastern USSR (5), and from Ajan along the east coast until the Amur area and on Sakhalin Island (1). In the Far East, it is found also on Kamchatka Peninsula, and on the mountains of north Korea and Japan (27). In Far East *P. ajanensis* is one of the most important species (64). On Hokkaido, where it forms pure stands, it is the most important *Picea* species (18).

Habitat: *P. ajanensis* grows on thin soils, 10-15 cm, and on rocky outcrops (27). It is found in similar habitats as *Picea abies* (9). Its occurrence is mainly in mountains (65), but it needs more humid, maritime climates than *Picea abies* (17). It grows best on moist, sand-loam soils and in moist climate near the sea (65). Its growth is poor on sandy or marshy soils (65).

Associated species: *P. ajanensis* grows both in pure and mixed stands. In mixed stands, it grows with *Abies* species, *Betula* species, *Populus tremula* and *Larix* species. On Kamchatka it grows with *Larix gmelinii* (65).

Life history: *P. ajanensis* seeds weigh 2-2.9 g/1000 seeds and are wind dispersed (18). Seedlings of *P. ajanensis* are found under different canopy densities including under open canopy (65). The growth pattern of *P. ajanensis* on a good site (65) is shown below.

Age (years)	Height (m)
10	2
50	12
100	25

Maximum values for height, diameter and age:
Height: from 30 m (1) to 50-60 m (8, 9, 17), some varieties 50 m (5), 40-45 m in USSR (27).
D.B.H: unknown.
Age: 300 years (27).

Response to environmental factors

Light: *P. ajanensis* is more shade tolerant than *Picea obovata* (17).

Soil moisture: *P. ajanensis* grows under more humid conditions than *Picea obovata* (17).

Nutrient stress: *P. ajanensis* tolerates nutrient stress (27).

Fire and frost: *P. ajanensis* is frost tolerant but it is sensitive to late spring frosts (65).

Flooding and windstorm: *P. ajanensis* has a shallow root system, and therefore it is susceptible to windthrow (27, 65).

Races and hybrids: *Picea ajanensis* var. hondoensis Rehn. is found on the Island Honshu (18).

21. PICEA KORAIENSIS Nakai

Distribution: *Picea koraiensis* is found in river valleys in the southern part of the Far East, in North Korea and in adjacent areas in Siberia and Manchuria (5, 65).

Habitat: *P. koraiensis* is dominant only in river valleys (27, 17). It has similar requirements as *Picea obovata* in the Far East (17).

Associated species: In lower elevations of mountains, *P. koraiensis* is found with *Fraxinus*, *Acer* and *Tilia* and in the upper parts with *Abies*, *Picea* and *Betula* (65).

Life history: *P. koraiensis* regenerates well under canopy cover and better on a litter layer than on bare soil (65). It grows on loamy-sandy, to sandy, alluvial, marshy and on stony soils. On stony and marshy soils its growth is poor (65).

Maximum values for height, diameter and age:
Height: is from 30-35 m (5, 17, 27).
D.B.H: unknown.
Age: unknown.

Response to environmental factors

Light: *P. koraiensis* is shade intolerant (65).

Soil moisture: *P. koraiensis* does not tolerate drought (27).

Nutrient stress: No information was found.

Fire and frost: *P. koraiensis* is less frost tolerant than *Pinus sibirica* (65).

Flooding and windstorm: No information was found.

Races and hybrids: No information was found.

22. PICEA ORIENTALIS (L.) Link.

Distribution: *Picea orientalis* forms forests on Taurus and Caucasus in USSR (1) and in northern parts of Turkey (17).

Habitat: *P. orientalis* is found mainly in mountain areas (1). It often grows at 1000-2400 m where it forms the tree limit (18).

Associated species: *P. orientalis* often forms forests with *Fagus sylvatica*, *Carpinus orientalis*, *Abies nordmanniana* and *Pinus sylvestris* (18).

Life history: No information was found.

Maximum values for height, diameter and age:
Height: 50-60 m, usually 30 m (1), 50 m (5, 9, 17, 24), 60 m (14).
D.B.H: 1.50-2.30 m (1), 1.20 m (9, 24).
Age: unknown.

Response to environmental factors

Light: No information was found.

Soil moisture: *Picea orientalis* is sensitive to drought. It grows where humid, rainy conditions prevail throughout the growing season (18).

Nutrient stress: No information was found.

Fire and frost: No information was found.

Flooding and windstorm: No information was found.

Races and hybrids: No information was found.

23. PICEA SCHRENKIANA (Fisch et Mey) Syn. *Pinus schrenkiana*

Distribution: *Picea schrenkiana* is found on 1400-3000 m on northern slopes in mountainous areas in Tien-Shan (17,65), and in Dzungari-Alatau and Pamir (18, 65) between China and Siberia (5). Its western limit is at the northern slopes of Kirgizian mountains (17). The largest forests with *P. schrenkiana* is found in Kazakhstan and in Kirgizia (65).

Habitat: *P. schrenkiana* is found in mountainous areas at elevations of 1400-3000, maximum 3500 m (17). It grows best when the annual precipitation is 700-800 mm and mean annual temperature is 3-4° C, on nutrient rich, sand-loam or slightly podzolic soils (65).

Associated species: *P. schrenkiana* forms mainly pure stands but it is sometimes found with *Abies sibirica* (18).

Life history: *P. schrenkiana* start seed production at 25-30 years. It regenerates well under canopy cover, but does not regenerate in the open and in a grass layer (65).

One growth pattern of *P. schrenkiana* is shown below (65):

Age (years)	Height (m)
10	2
50	17
100	25

Maximum values for height, diameter and age:
Height: is from 30-40 m (18), 40-45 m (65), up to 50-60 m (5, 17).
D.B.H: 200 cm (65).
Age: 400 years (18, 65).

Response to environmental factors

Light: *P. schrenkiana* is shade tolerant (65).

Soil moisture: *P. schrenkiana* is found on northern slopes because it thrives on soils with good water availability (5, 65).

Nutrient stress: *P. schrenkiana* does not tolerate nutrient stress (65).

Fire and frost: *P. schrenkiana* is less frost tolerant than *Picea abies* and is sensitive to late spring frost (65).

Flooding and windstorm: No information was found.

Races and hybrids: No information was found.

24. **PINUS KORAIENSIS** Sieb. et Zucc. Syn. *Pinus strobus* Thunb.

Distribution: *Pinus koraiensis* is found in Korea, in the central parts of Japan (Honshu), and in Manchuria at Ussur (1). In Manchuria, it is one of the most important tree species (18). In Manchuria it occurs at 300-1000 m and in Honshu at 1300-1500 m (18).

Habitat: *P. koraiensis* is found in cold deciduous forests (1).

Associated species: *P. koraiensis* forms mixed forests with *Abies holophylla* (5).

Life history: *P. koraiensis* produce seeds every second year (18). They are heavy; 1000 seeds weigh 500 g. Seeds are eaten and dispersed by animals and humans (18). *P. koraiensis* often forms multistemmed individuals (18).

Maximum values for height, diameter and age:
Height: 32 m in Manchuria and central Japan (1, 18).
D.B.H: 0.80-1.0 m (18).
Age: more than 400 years (18).

Response to environmental factors

Light: *P. koraiensis* is intermediately shade tolerant (18).

Soil moisture: No information was found.

Nutrient stress: *P. koraiensis* thrives on more fertile soils (5, 18).

Fire and frost: *P. koraiensis* is intolerant of fire and is sensitive to frosts (18).

Flooding and windstorm: *P. koraiensis* is sensitive to windthrow (18).

Races and hybrids: No information was found.

25. **QUERCUS MONGOLICA** Fisch. ex Ledeb.

Distribution: *Quercus mongolica* occurs in Korea, Manchuria, eastern Mongolia (1), East Siberia, north China and northern Japan (10).

Habitat: *Q. mongolica* grows on rocky outcrops (1).

Associated species: No information was found.

Life history: No information was found.

Maximum values for height, diameter and age:
Height: is 25-30 m (1, 10).
D.B.H: unknown.
Age: unknown.

Response to environmental factors

Light: No information was found.

Soil moisture: *Q. mongolica* prefers moist soils (54).

Nutrient stress: No information was found.

Fire and frost: *Q. mongolica* has low frost tolerance (54).

Races and hybrids: No information was found.

26. QUERCUS ROBUR L. Syn. *Quercus pedunculata* Ehrh.

Distribution: *Quercus robur* occurs over nearly all lowland Europe, the western coast of France and Britain to the Urals (26). Its northern limit is in Scotland and eastern Norway, along 'limes norrlandicus' along the Dalecarlia river in central Sweden and at the southern edge of Finland 58° N (26). The eastern limit is in Livonia and Ortsk in the Urals (26). See map, Figure 17.

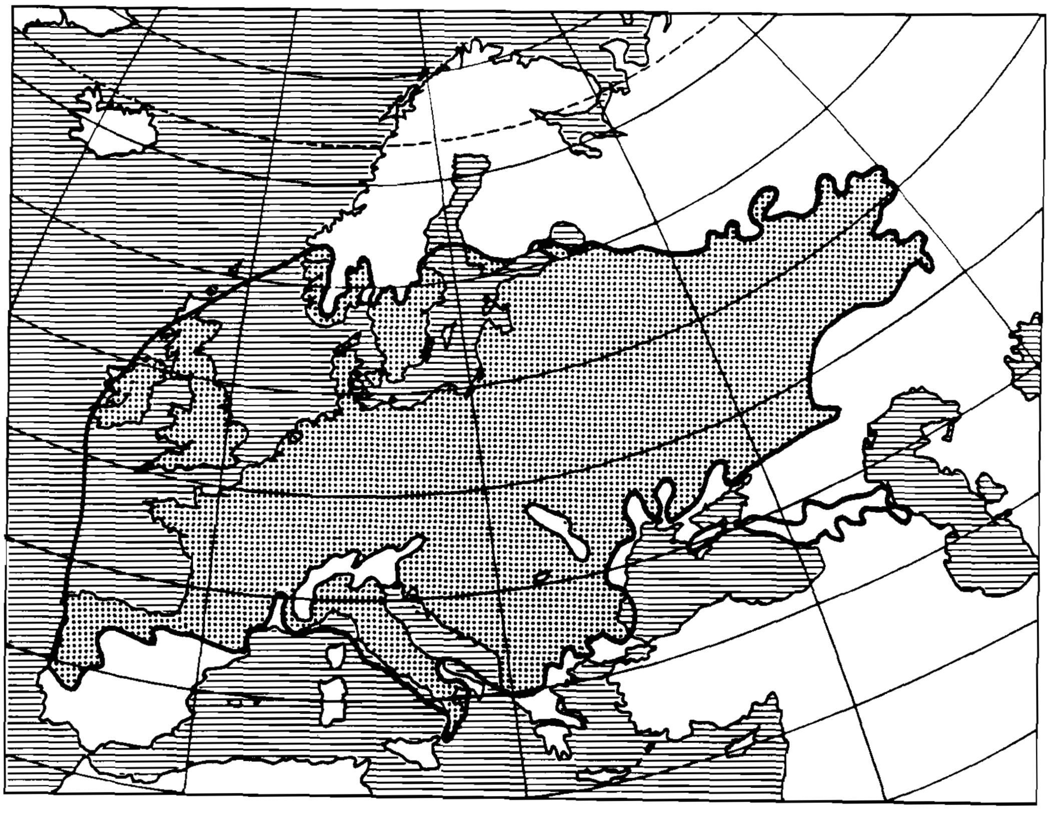

Figure 17. Distribution map of *Quercus robur* L.

Habitat: *Q. robur* has a tendency to grow in wet depressions, at rivers and streams and on lower valley slopes (26). It needs a warm, 4-5 month-long growing season (3). Climatic requirements as per data from sites in the USSR (26):

	Mean temperature ° C		Mean precipitation (mm)
	January	July	
Northern boundary:			
Leningrad	-9.3	17.7	480
Wjatka	-14.9	18.6	390
Eastern boundary:			
Orenburg	-15.9	21.6	390
Saratow	-10.8	22.0	374
Jelisatwetpol	-0.2	24.8	260

Q. robur prefers mature brown soils (26).

Associated species: In the north of its distribution *Q. robur* grows with *Pinus sylvestris*, *Picea abies* and *Populus tremula* (54). At lower altitudes, *Fagus sylvatica* is a serious competitor with *Quercus* but it is much more responsive to the concentrations of nutrients in the soil than *Q. robur* (26).

Life history: The age at which first fruiting occurs depends on climatic conditions and whether the stand is open or closed. In the south and in open stands fruiting occurs earlier, at 15-40 years. The seed set is irregular, in southern England every 6-7 years, with moderate crops at intervals of 3-4 years. *Q. robur* seeds are dispersed by mammals and birds. Burial in the ground or covering by a blanket of dead leaves is important for keeping acorns moist and protecting them from frost and predation by animals (26). *Q. robur* seedlings have a greater power to establish in closed vegetation and in grass swards than *Fagus*, *Fraxinus* and *Betula* (26). *Q. robur* seedlings cannot survive in shade for many years (2). The height growth ends at an age of 120-200 years in FRG (1).

Maximum values for height, diameter and age:
Height: normally on good soils 30-45 m (1, 3) to 50-60 m (1, 12, 26).
D.B.H: 2 m in FRG (1, 3), in GB 132 cm (26).
Age: 2000 years (1), 1200 (12) in FRG.

Quercus litter decays slowly, only *Fagus* litter decays more slowly (26).

Response to environmental factors

Light: *Quercus robur* is shade intolerant (2, 3).

Soil moisture: *Q. robur* tolerates a wide range of soils (26), from very wet to dry soils (2), but it prefers moist heavy soils (26).

Nutrient stress: *Q. robur* tolerates many different kinds of soil (2), but prefers an alkaline soil rich in mineral nutrients (26).

Flooding and windstorm: *Q. robur* tolerates prolonged flooding and waterlogging better than *Fraxinus excelsior* (26).

Frost and fire: Old *Q. robur* are quite fire tolerant because of thick bark. Seedlings and saplings whose tops have been killed by fire will often produce new vigorous shoots from the base (26).

Races and hybrids: Many different ecotypes of *Q. robur* have been found (1). *Q. robur* has a very variable growth and leaf form (26).

27. **TILIA CORDATA** L., Mill. Syn. *Tilia parvifolia* Ehrh.

Distribution: *T. cordata* is found as far as 63° N (1). See map, Figure 18.

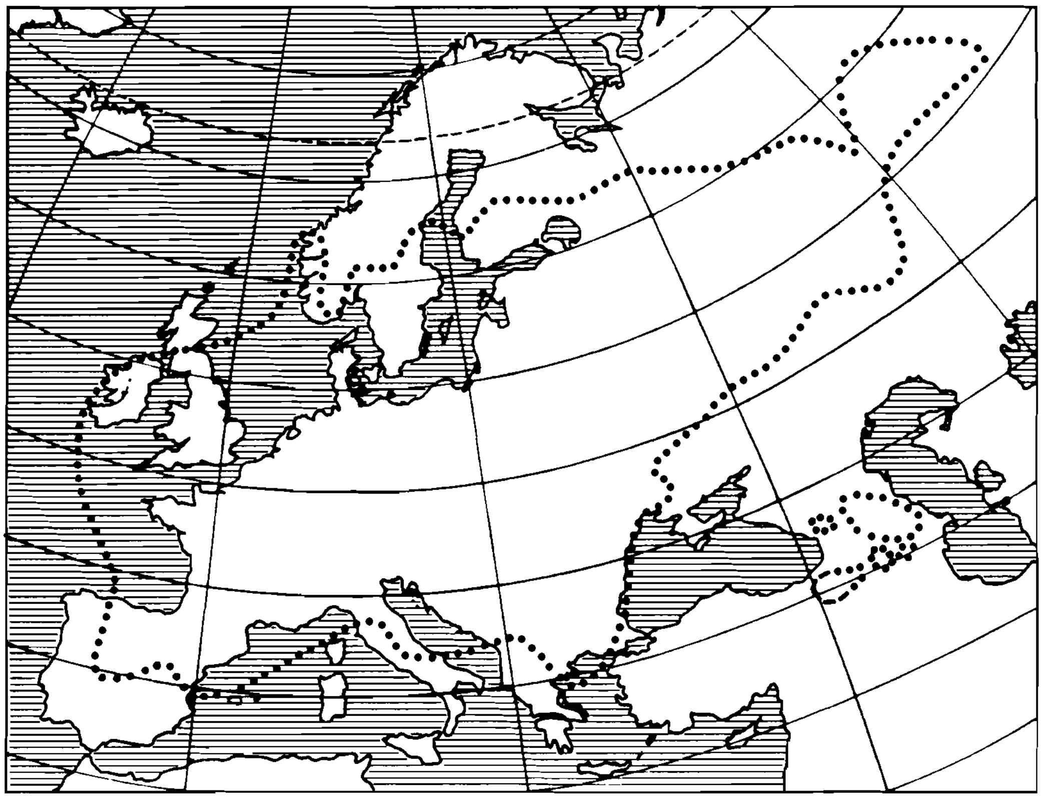

Figure 18. Distribution map of *Tilia cordata* L.

Habitat: *T. cordata* is found at lake shores and along rivers and brooks. *T. cordata* occurs mostly on rocky soils in Finland (77).

Associated species: *T. cordata* occurs together with *Quercus robur* in the USSR. In Germany it is found in combination with deciduous trees. Other associated genera are *Alnus*, *Fraxinus*, *Acer* and *Betula* (77).

Life history: *T. cordata* has a considerable shooting ability from the base (54).

Maximum values for height, diameter and age:
Height: 25-30 m (3), until 30 m (10, 25, 77).
D.B.H: more than 1 m (3).
Age: hundreds of years (25), 600 (63).

Response to environmental factors

Light: *Tilia cordata* is shade tolerant (54, 1).

Soil moisture: *T. cordata* grows mainly in wet places (1).

Nutrient stress: The information about nutrient requirements of *T. cordata* are contradictory; references state both that it is nutrient stress tolerant (1), and also that it is very demanding in regard to soil fertility (54).

Frost: *T. cordata* tolerates frost in winter and survives late spring frosts (3).

Flooding and windstorm: According to (77), *T. cordata* occurs along rivers and streams, and is found on islands and on lake shores. Therefore, it can be assumed that *T. cordata* tolerates flooding.

Races and hybrids: A related species in the USSR is *Tilia sibirica* Bayer (77).

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APPENDIX

Species life history parameters.

Parameter	Description	Unit
ETSmax	Maximum annual Effective Temperature Sum (5° C base)	° C
ETSmin	Minimum annual Effective Temperature Sum (5° C base)	° C
AGEmax	Maximum age recorded	Years
Hmax	Maximum height recorded	m
Dmax	Maximum breast height diameter recorded	cm
Tl	Shade tolerance class	1-tolerant 2,3,4, 5-intolerant
Tdr	Drought tolerance class	1-tolerant, 2,3,4, 5-intolerant
Tn	Nutrient stress tolerance class	1-tolerant, 2,3,4, 5-intolerant
Tfr	Fire tolerance class	1-tolerant 0.5-intermediate 0-intolerant
Tfl	Flooding tolerance class	0-intolerant 1-tolerates occasional flooding 2-tolerates seasonal flooding 3-tolerates year-round flooding
Bog	Growth on bogs	0-no growth 1-bad growth
Ptol	Growth on permafrost	0-bad 1-good 2-good growth
Tcold	Mean temperature of the coldest month at continental boundary of geographical range of the species	° C

Species life history parameters (continuation).

Parameter	Description	Unit
Rsl	Requirement for mineral soil for successful reproduction	T-yes F-no
Rm	Requirement for moss or litter layer for successful reproduction	T-yes F-no
Sfrq	Seed crop year frequency	%
Disp	Seed dispersal pattern	T- wind-dispersed F- not wind-dispersed
Fire	Seedling germination with respect to fire	T- requires fire F- does not require fire
Stol	Seedling germination tolerance class with respect to drought.	T- tolerant F- intolerant
Lmin	Minimum light level required for seedling growth	% of full sun light
Rlr	Ability of vegetative reproduction by layering	T- able F- unable
SprTnd	Tendency for stump or root sprouting	Mean number of sprouts per tree
SprMin	Minimum breast height diameter for sprouting	cm
SprMax	Maximum breast height diameter for sprouting	cm

Summary table of species life history data presented in the autecological reviews. Values for *ETSmax*, *ETSmin* and *Tcold* are specified on the basis of species distribution maps (73) and climatic maps prepared by W. Cramer (72). Values for *Tl*, *Tdr*, and *Tn* are derived from unpublished data by Polikarpov (personal communication). Unknown values are indicated by hyphen (-).

Species	ETSmax	ETSmin	AGEmax	Hmax	Dmax
Dominant boreal tree species					
Abies sibirica	1450	300	300	38	80
Betula pendula	2300	470	135	30	60
Betula pubescens	2050	400	100	30	60
Larix gmelinii	1500	300	400	40	140
Larix sibirica	1500	400	450	45	180
Larix sukaczewii	1750	450	-	40	120
Picea abies	2250	480	500	60	170
Picea obovata	1500	400	500	40	50
Pinus pumila	1600	270	-	7	-
Pinus sibirica	1450	520	800	40	190
Pinus sylvestris	2350	470	600	48	190
Populus tremula	3000	480	150	35	100
Important tree species					
Abies sahalinensis	1500	800	280	40	100
Alnus glutinosa	-	-	120	35	60
Alnus incana	-	-	60	20	50
Carpinus betulus	3500	1400	300	30	80
Fagus sylvatica	3700	980	300	45	150
Larix decidua	-	-	800	50	160
Larix kurilensis	1500	500	400	33	140
Picea ajanensis	1800	800	300	60	-
Picea koraiensis	2800	1200	-	35	-
Picea schrenkiana	-	-	400	45	200
Pinus koraiensis	2000	1100	600	40	100
Quercus mongolica	-	1000	-	30	-
Quercus robur	3500	1100	1200	50	200
Tilia cordata	2900	900	600	30	100

Summary table (continuation).

Species	Tl	Tdr	Tn	Tfr	Tfl	Bog	Ptol	Tcold
Dominant boreal tree species								
Abies sibirica	1	4	5	0	1	0	0	-35
Betula pendula	4	1	1	1	-	0	1	-40
Betula pubescens	4	5	1	0.5	1	1	1	-40
Larix gmelinii	5	2	2	-	2	1	2	-45
Larix sibirica	5	1	2	1	2	1	1	-33
Larix sukaczewii	5	3	2	1	-	1	1	-22
Picea abies	2	5	3	0	-	1	-	-17
Picea obovata	2	5	3	0	-	1	1	-40
Pinus pumila	3	4	1	0	-	-	2	-45
Pinus sibirica	2	4	3	0.5	2	1	1	-35
Pinus sylvestris	4	1	1	1	-	1	-	-40
Populus tremula	4	2	3	0	-	0	-	-40
Important tree species								
Abies sahalinensis	1	4	5	0	-	-	0	-21
Alnus glutinosa	3	5	5	1	3	1	0	-
Alnus incana	3	4	4	1	3	1	-	-
Carpinus betulus	2	2	4	0	-	0	0	-7
Fagus sylvatica	1	3	5	-	0	0	0	-
Larix decidua	5	3	2	-	-	0	0	-
Larix kurilensis	5	3	2	-	-	1	-	-
Picea ajanensis	2	4	3	-	-	1	-	-38
Picea koraiensis	3	4	-	-	-	1	-	-
Picea schrenkiana	2	5	5	-	-	-	-	-
Pinus koraiensis	2	3	3	0	-	-	-	-
Quercus mongolica	-	-	-	-	-	-	-	-
Quercus robur	3	1	4	1	2	0	0	-17
Tilia cordata	2	2	5	-	1	0	0	-19

Summary table (continuation).

Species	Rsl	Rm	Sfrq	Disp	Fire	Stol	Lmin	Rlr
Dominant boreal tree species								
Abies sibirica	F	T	30	T	F	F	4	T
Betula pendula	-	-	90	T	T	T	-	F
Betula pubescens	-	-	90	T	T	F	-	F
Larix gmelinii	T	F	33	T	T	T	-	F
Larix sibirica	T	F	20	T	T	T	-	F
Larix sukaczewii	T	F	-	T	T	T	-	F
Picea abies	-	-	24	T	F	F	-	T
Picea obovata	T	T	8	T	F	F	-	-
Pinus pumila	-	-	90	F	-	-	-	T
Pinus sibirica	-	-	65	F	-	F	6	F
Pinus sylvestris	T	F	24	T	T	T	-	F
Populus tremula	T	F	-	T	T	-	-	-
Important tree species								
Abies sahalinensis	-	-	30	T	F	F	-	-
Alnus glutinosa	-	-	-	T	F	F	-	F
Alnus incana	-	-	90	T	F	F	-	-
Carpinus betulus	T	F	40	T	F	T	-	T
Fagus sylvatica	F	T	23	F	F	F	-	F
Larix decidua	T	F	-	T	T	T	-	F
Larix kurilensis	-	-	33	T	T	T	-	T
Picea ajanensis	F	T	-	T	F	T	-	-
Picea koraiensis	F	T	-	T	F	T	-	-
Picea schrenkiana	F	T	-	-	F	T	-	-
Pinus koraiensis	-	-	50	F	F	-	-	-
Quercus mongolica	-	-	-	-	-	-	-	-
Quercus robur	F	T	17	F	F	F	-	F
Tilia cordata	-	-	-	-	-	-	-	-

Summary table (continuation).

Species	SprtTnd	SprtMax	SprtMin
Dominant boreal tree species			
Abies sibirica	0	0.0	0.0
Betula pendula	-	-	-
Betula pubescens	-	-	-
Larix gmelinii	0	0.0	0.0
Larix sibirica	0	0.0	0.0
Larix sukaczewii	0	0.0	0.0
Picea abies	0	0.0	0.0
Picea obovata	0	0.0	0.0
Pinus pumila	0	0.0	0.0
Pinus sibirica	0	0.0	0.0
Pinus sylvestris	0	0.0	0.0
Populus tremula	-	-	-
Important tree species			
Abies sahalinensis	0	0.0	0.0
Alnus glutinosa	-	-	-
Alnus incana	-	-	-
Carpinus betulus	-	-	-
Fagus sylvatica	-	-	-
Larix decidua	0	0.0	0.0
Larix kurilensis	0	0.0	0.0
Picea ajanensis	0	0.0	0.0
Picea koraiensis	0	0.0	0.0
Picea schrenkiana	0	0.0	0.0
Pinus koraiensis	0	0.0	0.0
Quercus mongolica	-	-	-
Quercus robur	-	-	-
Tilia cordata	-	-	-

For estimation of Effective Temperature Sums (*ETS*) the following approach is used:

$$ETS = SUM(D_i),$$

where $SUM(D_i)$ is the annual total of daily departures (D_i) of temperatures above 5°C, so that

$$D_i = \begin{cases} (T_i - 5), & \text{if } T_i > 5; \\ 0, & \text{otherwise.} \end{cases}$$

In the equation above T_i are mean daily temperatures. Values for T_i are estimated from mean monthly temperature data by assuming that the reported monthly values (MT_j) refer to the middle day of each month, and applying a linear interpolation:

$$T_i = MT_j + i(MT_j - MT_{j+1})/Days,$$

where *Days* is the number of days between two-month middles (i.e., 30 or 31).