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The Silvics of Some East European and Siberian Boreal Forest Tree Species

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PREFACE

IIASA's Biosphere Dynamics Project focuses on biotic (ecological) systems, particularly those long term (sustainable) behaviors which are produced in response to human activities, and are detected at global (biospheric) spatial scales. An important approach of the "Biosphere" project to these goals uses mathematical and gaming simulations to explore the complex natural and sociological ramifications of ecosystem responses. The central Biosphere Project study on global vegetation change is being supported by an emerging study aimed at examining the potential future responses of the world's boreal forests to changes in global climate and atmospheric chemistry. Our three-part approach includes production of boreal forest data sets, modification of forest-stand simulation models for application to the circumpolar boreal forest, and then, application of models to examine implications of climate change scenarios. One of the first steps is to document known ecological characteristics of species for incorporation into specific mathematical models, as exemplified by the content of this working paper.

The documentation of species' attributes requires careful analysis by trained forest biologists who can understand the ecological context of the mass of information presented, and can select only the relevant and most correct data. The examination requires searching out the information scattered in many sources, including books, scientific journals, and the "grey literature" of forestry project accounts, field data files, and forest experiment station records. Much of this work has been done in North America, summarized particularly in works by Harlow, Harrar and White (1979) and by Fowells (1965). In the case of boreal forests of Fennoscandia and the Soviet Union, the literature is much more difficult to summarize, being found in several languages (Norwegian, Swedish, Finnish, Russian, German, English) as well as in many widely separated locations and many poorly known report series. The difficulties of completing the literature review have been admirably accomplished by Korzukhin and others who generated this report. Their work will be immediately applicable to parameterizing individual tree species in boreal forest stand simulation models for which the data were collected. In addition, this report provides the basis of ongoing data collections, and will stand as a model of its kind, for some time.

Bo R. Döös, Leader
Environment Program

ABSTRACT

In recent years, the boreal forest has received increased scientific attention in light of projected climatic warming to boreal regions from increased concentrations of atmospheric carbon dioxide. The ecological consequences of such a warming could be significant. However, before the consequences of climatic change can be properly investigated, the ecology of boreal forest tree species must be adequately understood. Though the life-histories of many North American boreal forest tree species are well known, little comparable information has been compiled in English for the major boreal forest tree species of the Soviet Union. In this paper, we present a preliminary description of the silvics of seven of these species – their ranges, optimum climatic and soil conditions, regeneration characteristics, tree growth features, responses to sub-optimal site conditions, and reaction to fire. We hope that this information will provide a useful data base for use in modeling the ecology of these species.

CONTENTS

THE SILVICS OF SOME EAST EUROPEAN AND SIBERIAN BOREAL FOREST TREE SPECIES

M.D. Korzukhin, A.E. Rubinina, G.B. Bonan, A.M.Solomon and M.Ya. Antonovsky

INTRODUCTION

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 snowcover 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 Biosphere Dynamics Project within the Environment Program 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 problem 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 examine the problem. First, the forestry literature is being gathered from five languages 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, "Survey of Ecological Characteristics of Boreal Tree Species in Fennoscandia and the USSR," by Harry Helmisaari and Nedialko Nikolov. Second, this and other documentation is being used to modify existing and tested forest-stand simulation models. The first efforts in these modifications appear in Bonan (1988a), Antonovsky et al. (1989), and Leemans and Prentice (1989). Third, plausible future developmental trends will be quantified and applied to the simulation models, allowing the interrogation of the models to reveal the potential ecological vulnerabilities and to identify early indicators of such changes.

Data about individual tree growth which are contained in the following life histories can be used in standard gap models for the calculation of needed parameters, such as G, D_{max}, b_2, b_3 in the commonly-used tree volume growth equation (Botkin et al. 1972; Shugart 1984):

$$\frac{d(D^2H)}{dt} = GD^2\left[1 - \frac{D \cdot H(D)}{D_{max}H_{max}}\right],$$

where

$$H(D) = 137 + b_2D - b_3D^2 \; [cm] \, .$$

The data will also 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 20 years to simulate forest-stand dynamics through the effect of changing resources (e.g., light, soil moisture, nutrients) on the regeneration, growth, and mortality 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 varied, although all have shared the same basic structure and growth equations (Shugart 1984; Solomon et al. 1984; Pastor and Post 1986; Aber et al. 1982; Dale et al. 1986).

The application of available models to the entire suite of circumpolar boreal-forest conditions requires the identification and implementation of the most relevant data on species natural history attributes. Also, a few new routines will be required. Particularly, the routines which simulate effects of winter low temperatures must be enhanced if the models are to incorporate the known direct effects of warming on tree vigor (i.e., frost damage increases with increases of the seasonal low-temperatures that control winter hardening and dehardening; tree mortality increases on coarse soils with increased summer drought frequencies).

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 species (i.e., present abundance and geographic location of populations; maximum age and size; physiological responses to seasonal temperature, extreme temperatures, and precipitation; growth 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, (i.e., growing-season length, warmth, precipitation, soil-fertility requirements, etc.). The data were selected to mimic reactions to environmental change by critically-sensitive characteristics of individual species. These data form the basis for generating or enhancing model routines which handle processes peculiar to boreal forests, such as permafrost dynamics (Bonan 1988b), nutrient turnover (Pastor and Post 1986), low sun-analyses (Bonan 1988b), and 24-hour heat accumulation in summer (Kauppi and Posch 1987, 1985). The book by Shugart (1984) describes the logic for the data we are collecting and its use in model development.

The critical feature of the stand-simulation 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 future 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 snowpersistence 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 by Helmisaari and Nikolov and that for North American species (Harlow et al. 1979; Fowells 1965), represent as complete a data set as possible for examining behavior of the circumpolar boreal forest via stand simulation models.

I. Pinus silvestris

(1) *Range.* See Figure A.1. Optimum climatic conditions occur near the south-west edge of the range - (see point 7, Figure A.1). Here the general rule that the optimum conditions are found in the middle of the geographic range is inoperative. For *P. silvestris,* these conditions include both moist soils, such as in river valleys, and sufficient warmth. To the north, the warmth diminishes and to the south, the soil becomes too dry for *P. silvestris* to reproduce by seed (see Figure 1.1) and to grow successfully (Morozov 1930).

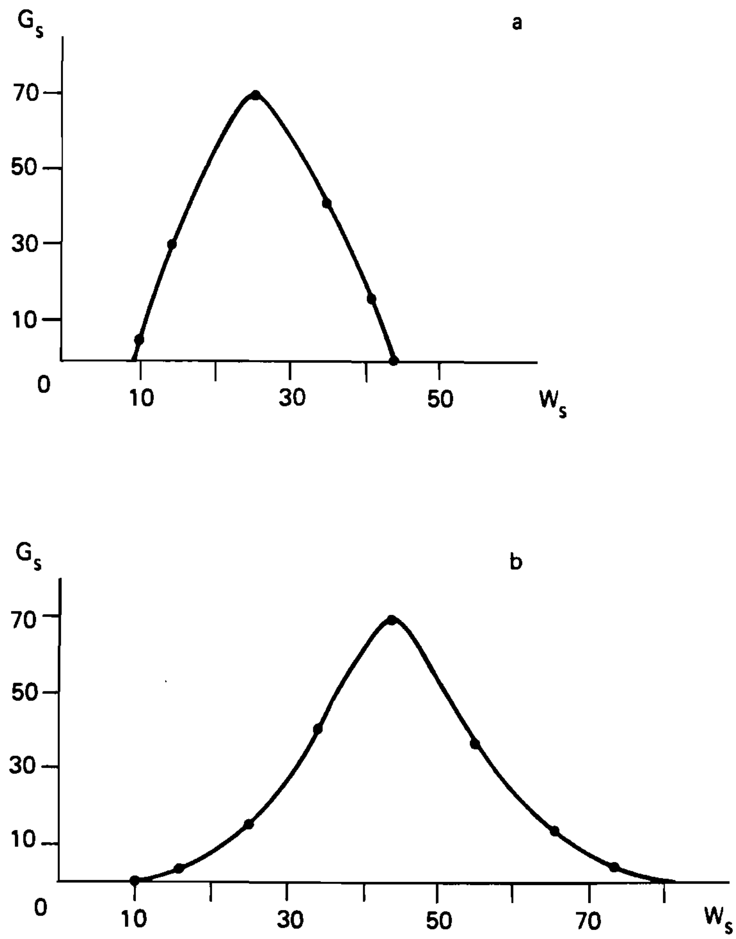


Figure 1.1. Success of seed germination G_s (%) for *P. silvestris* as a function of soil moisture W_s (% of soil volume at 16–20°C) (Popov 1957).

a – for sand and sandy loam
b – for litter

(2) *Optimum soil conditions. P. silvestris* can tolerate relatively nutrient-poor soils, although in USSR it grows on neither droughty nor flooded soils (Sannikov 1976). (See relative scales 1–3 in Section XI). Elsewhere in Scandinavia it can be found on both droughty and flooded soils.

(3) *Reproduction.* Cone production begins at 20 years for open-growth trees and at 35–40 years for trees growing inside a closed canopy forest (Sannikov 1976). Most seeds fall within 50–70 m of tree; maximum reported distance is up to 8–10 km (Shimanyuk 1964). Cone production is a function of tree age (Figure 1.2, Table 1.1c). Optimal pH for seed germination is 5.7–7.2; optimal pH for seedling growth is 5.0–6.3 (Popov 1957). Soil moisture (Figures 1.1 and 1.3) produces a definite optimum of germination when soil moisture w is near 30–40%; germination ceases when w is out of range

$$10 \leq w \leq 50-70 .$$

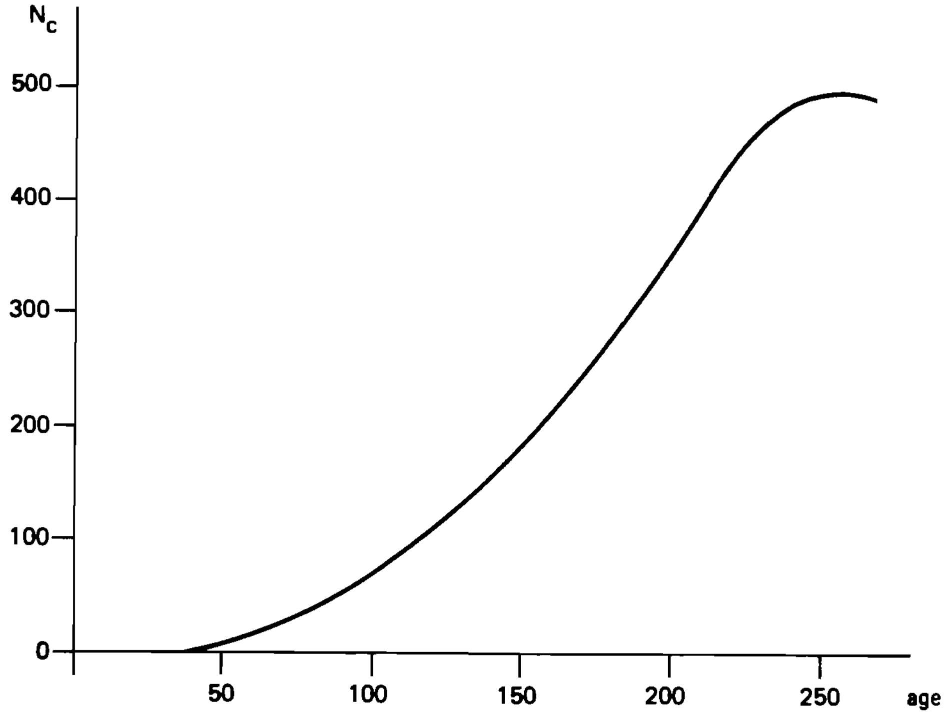


Figure 1.2. Cone productivity N_c (cones/tree · year) as a function of age for *P. silvestris*. Located at Point 3 in Figure A.1. (Sannikov 1976).

The temperature range for seed germination produces an optimum at 20–25°C, a minimum at 6–8°C and a maximum at 3–7°C. The forest floor organic layer strongly affects at the germination probability (Figure 1.4). The best germination is on open mineral soil; diminishing when the organic layer thickness increases because of difficulties for seed roots in reaching of mineral soil. When height of the litter layer is greater than 3–5 cm, or height of moss layer is greater than 6–8 cm, the probability of establishment is near zero (Sannikov 1976). The ability to reproduce vegetatively by layering is absent.

(4) *Growth.* Seedlings optimum light levels are 30–50% of full sunlight (Kravtchenko 1972). Mature trees are quite shade tolerant among boreal trees as shown in relative scale 4 (Morozov 1930). Maximum dimensions are achieved in the regions of forest islands located in the southern European portion of range: maximum height is 48 m; maximum diameter in forest stands is 1 m (Kapper 1954). Maximum age in the

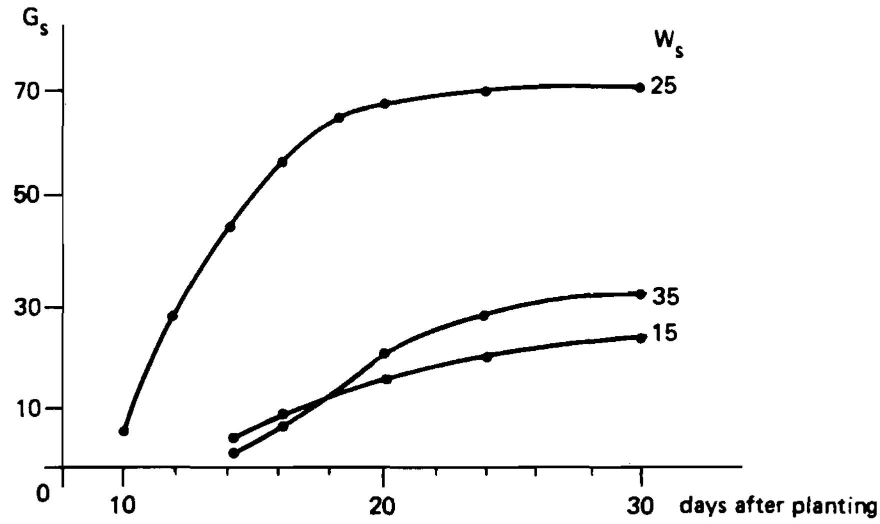


Figure 1.3. Dynamics of seed germination G_s (%) for *P. silvestris* in sand soil under various soil moisture conditions W_s (% of soil volume) (Popov 1957).

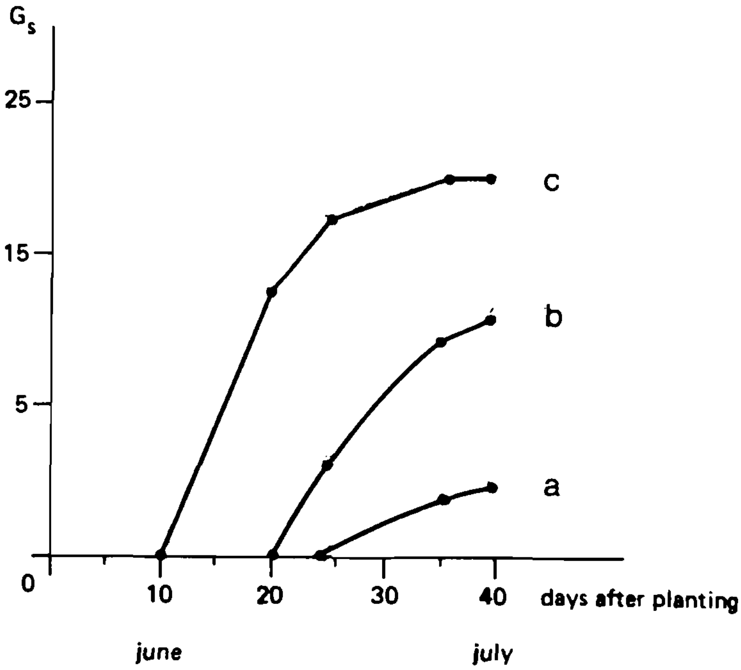


Figure 1.4. Dynamics of seed germination G_s (accumulated %) for *P. silvestris* at various types of ground surfaces (Popov 1957).

a – litter consists of weakly decomposed moss and needles, $H_{litter} \sim 3.5$ cm
b – partially burned litter, $H_{litter} \sim 0.5–0.7$ cm
c – mineralized sandy surface.

southern portion of European range is 350 years; in the northern portion of West Siberian sector, 200 years; in the southern portion of this section, 500 years (Krylov 1961).

Individual tree characteristics are shown in Tables 1.1 and 1.2.

(5) *Fire*. *P. silvestris* can tolerate fire because of its thick bark (Kolesnikov 1956).

Table 1.1. *Pinus silvestris* tree growth.

A: South Karelia (point 1, Figure A.1) (Zyabchenko 1984)

			Dry Biomass		
Age (yrs)	DBH (cm)	Height (m)	Tree (kg)	Needles (kg)	Root (kg)
5		1.4			
10	2.7	2.6			
20	8.6	7.2	4.0	0.5	0.7
40	18.0	17.0	32.0	1.7	5.4
60	25.0	23.0	120.0	4.0	16.0
80			270.0	6.3	38.0
100			430.0	8.2	56.0
120			560.0	9.4	65.0
160			630.0	9.5	74.0
200			750.0	9.8	78.0

B: Point 2, Figure A.1 (Kravtchenko 1972)

Age (yrs)	DBH (cm)	Height (m)	Volume (dm^3)	Needles (wet kg)
20	14.0	11.0	190.0	12.0
40	25.0	20.0	490.0	30.0
60	35.0	27.0	1200.0	49.0
80	43.0	31.0	2100.0	60.0
100	50.0	34.0	3000.0	63.0
110	53.0	35.0	3500.0	63.0

C: Middle Ural region (point 3, Figure A.1) (Sannikov 1976)

			Wet Biomass		
Age (yrs)	DBH (cm)	Height (m)	Tree (kg)	Cones (kg)	Number of Seeds
50	18.0	18.0	125.0	0.2	500
100	30.0	30.0	625.0	0.4	1250
150	32.0	32.0	1380.0	1.2	3400
200	34.0	34.0	1630	2.2	6400
250	35.0	35.0	–	2.7	7700

Table 1.2. *Pinus silvestris* tree growth.

East Siberia (point 4, Figure A.1) (Utkin 1965)			Far East (point 5, Figure A.1) (Kolesnikov 1956)			East Siberia (point 6, Figure A.1) (Utkin 1965)		
Age (yrs)	DBH (cm)	Height (m)	Age (yrs)	DBH (cm)	Height (m)	Age (yrs)	DBH (cm)	Height (m)
20	–	1.3	10	7.8	3.3	20	2.8	2.4
40	6.7	6.7	20	16.0	6.4	40	7.5	6.2
60	12.0	10.3	30	19.0	7.9	60	9.5	9.7
80	13.3	11.5	40	22.0	8.7	80	10.0	11.0
100	14.4	12.0	50	25.0	10.0	100	11.0	12.0
120	15.0	12.6	60	29.0	11.0	120	12.0	13.0
			70	33.0	12.0	140	13.0	14.0
			80	36.0	13.0	160	15.0	16.0

II. Picea abies

(1) *Range*. See Figure A.2. Optimum climatic conditions consist of 1000–1400 mm annual precipitation and 2800 growing degree-days (5°C base). For territory in the USSR, these conditions occur in the Karpate Mountains. The northern range limit coincides with the isoline of 375 mm annual precipitation. The southern range limit coincides with the isoline of 625 mm annual precipitation (Urkevitch et al. 1971); growing degree-days (5°C base): maximum – 2800, minimum – 800.

(2) *Optimum soil conditions*. *Picea abies* prefers podzol soils of clay to sandy loam texture. Range of pH tolerance is 3.5–7.0, optimum pH is 5.0–6.5. (See relative scales 1–3, Kiseliova 1976).

(3) *Reproduction*. Cone production begins at 20–30 years for a tree growing in the open and at 40–60 years for a tree inside a closed forest canopy (Kiseliova 1976). The usual cone yield of a mature tree is approximately 100–150 cones per year (Anonymous 1962). The number of seeds per cone varies geographically: north taiga – 230, middle taiga – 260, south taiga – 300 (Kazimirov 1983). The weight of one cone is approximately 48 g; one tree produces about one million seeds during its lifetime (Molchanov 1967). Dynamics of seed and cone production are shown in Figure 2.1. Most seeds fall within 50–70 m of the parent tree (Sannikov 1976). The maximum reported distance is 8–10 km (Sukatchov 1938). The minimum temperature for seed germination is 10–11°C and the optimal temperature is 19–22°C (Gortinsky 1964). Soil temperature effects are illustrated in Figure 2.2. Soil moisture effects are shown in Figures 2.3 and 2.4. Regeneration is hampered by dense maple and hazel leaf litter. *P. abies* regenerates well under aspen and birch canopies (Gortinsky 1964). Vegetative reproduction does not occur.

(4) *Growth*. Seedlings can develop under 5% of full sunlight (Kiseliova 1976). Light requirements increase with age (see relative scale 4). For the European part of range, maximum height reaches 35–40 m and maximum age is 250–300 years (Kiseliova 1976; Kazimirov 1983). Growth of seedlings is rather slow; height is no more than 1–2 m at 10–15 years, then growth increases and can be as high as 70–100 cm per year; fastest growth occurs between 35–65 years; see also Table 2.1 and Figure 2.5.

(5) *Fire*. This species is intolerant of fire and is strongly damaged by low intensity surface fires because of its thin bark and shallow root system (Kazimirov 1983).

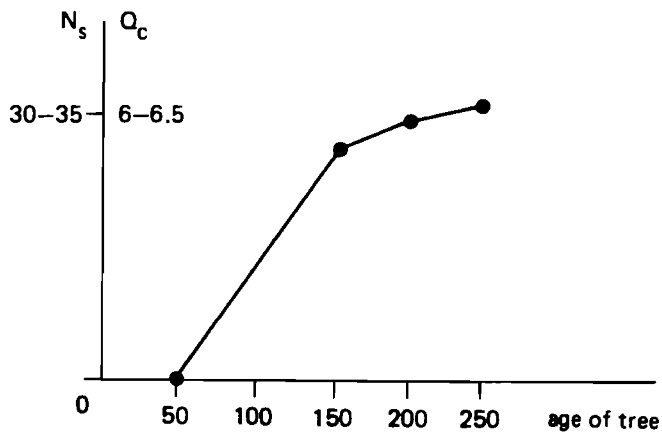


Figure 2.1. Dynamics of seed and cone production for *P. abies* (Molchanov 1967).
N_s – thousands of seeds (tree/year)
Q_c – weight of cones (kg/tree-year)

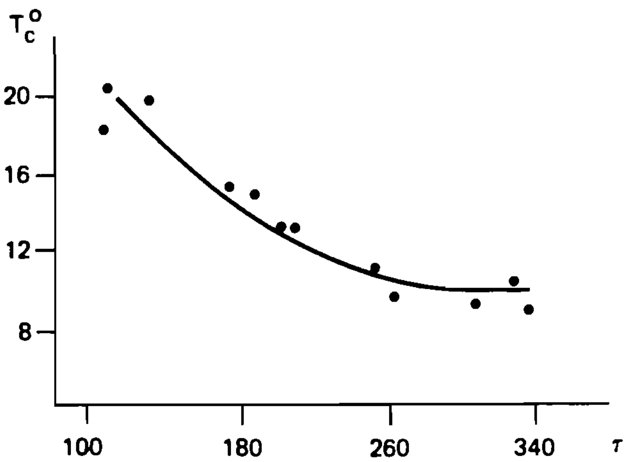
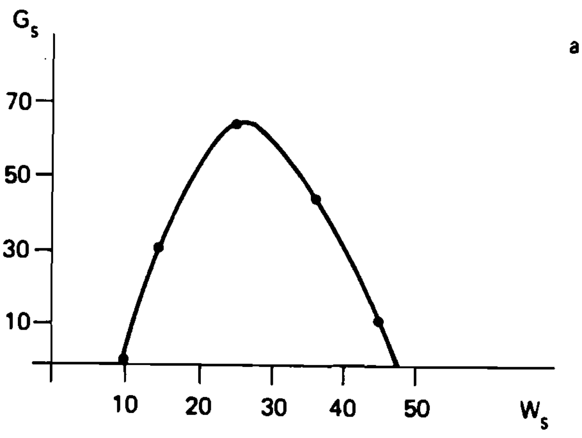


Figure 2.2. Time of germination of 50% seeds τ for various soil temperatures T_c° (Gortinsky 1964).



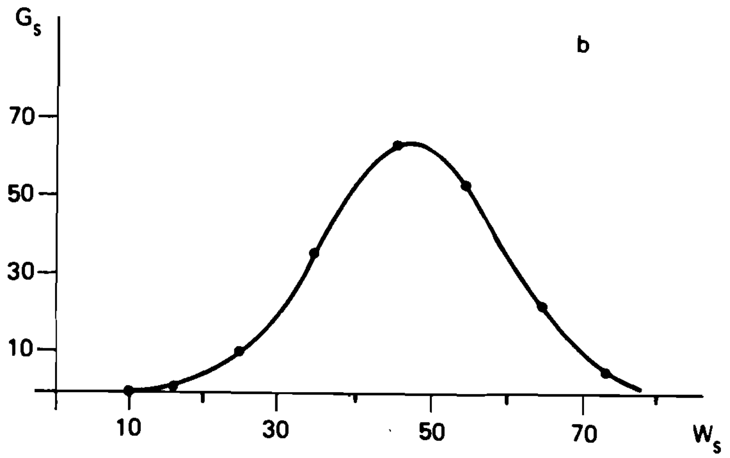


Figure 2.3. Success of seed germination G_s (%) for *P. abies* in various soil moisture conditions. W_s (% of soil volume) at 16–20°C (Popov 1957).

a – for sand and sandy loam
b – for litter

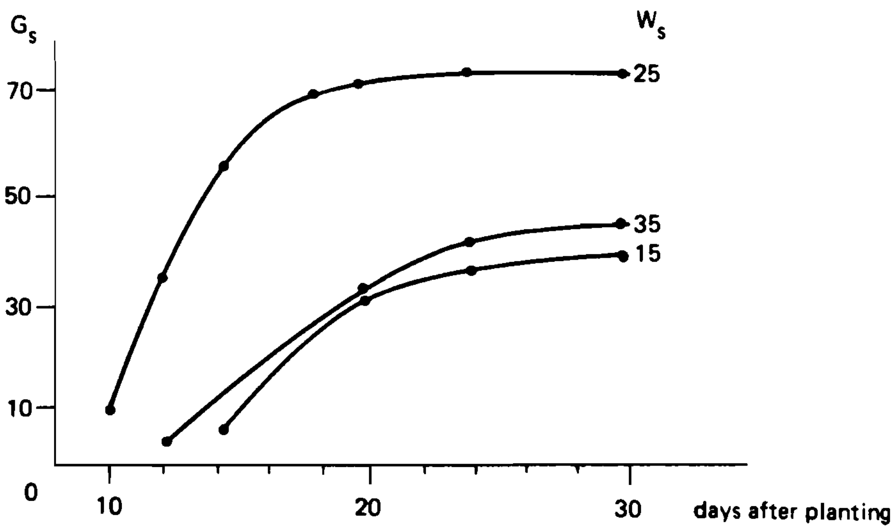


Figure 2.4. Dynamics of seed germination G_m (accumulated %) for *P. abies* in sand soil under various soil moisture levels W_m (% of soil volume) (Gortinsky 1964).

Table 2.1. *Picea abies* tree growth.

Moscow region (point 1, Figure A.2) (Anonymous 1964)				West slope Ural Mountains (point 2, Figure A.2) (Kazimirov 1983)		
Age (yrs)	DBH (cm)	Height (m)	Volume (dm^3)	Age (yrs)	DBH (cm)	Biomass (kg)
26	10.0	14.0	57.0	20	1.5	1.0
32	11.6	15.5	72.0	30	7.6	16.0
37	12.6	16.5	86.0	40	12.0	67.0
47	15.8	18.0	107.0	50	17.1	188.0
50	16.7	19.5	170.0	60	20.9	334.0
54	18.3	20.5	211.0	70	24.1	507.0
61	20.6	21.5	311.0	80	26.3	649.0
62	21.0	22.5	394.0	90	27.7	755.0
				100	28.9	844.0

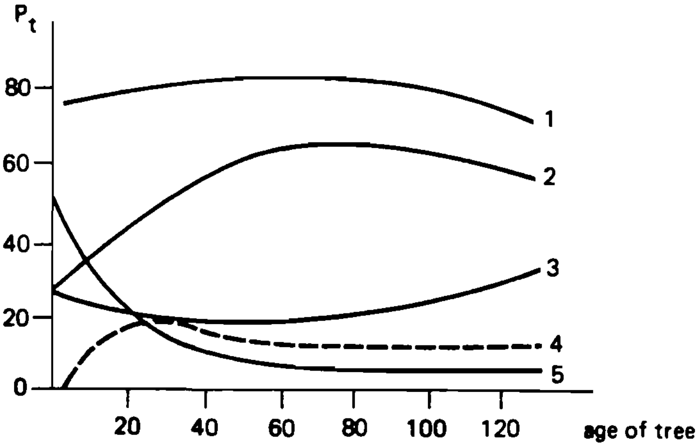


Figure 2.5. Parts of tree biomass (P_t, %) during lifetime of *P. abies* for point 3 of Figure A.2 (Palumets 1985).

1 – above ground part
2 – stem
3 – roots
4 – branches
5 – leaves

III. Picea sibirica

(1) *Range*. See Figure A.3. Growing degree-days (5°C base), maximum is approximately 2000, minimum is approximately 630.

(2) *Optimum soil conditions*. Similar to those of *Picea abies*, but concrete data are incomplete; see relative scales 1–3. *P. sibirica* has little tolerance either to flooding or to drought and requires relatively rich soil fertility.

(3) *Reproduction*. Cone production is approximately half as much as for *P. abies*. The ability to layer is absent.

(4) *Growth*. It is very shade tolerant (see relative scale 4). Its height is 30 m; maximum age varies, being 200 years in the north taiga zone, 300 years in the south taiga zone, and 500 years in the mountains of south Siberia (Krylov 1961). Individual tree growth is poorly documented, suggesting very slow growth rates. Table 3.1 provides values for young trees.

(5) *Fire*. *Picea sibirica* is intolerant of fire because of thin bark.

Table 3.1. *Picea sibirica* tree growth (Utkin 1965).

Central Yakutia (point 1, Figure A.3)			South Yakutia (point 2, Figure A.3)		
Age (yrs)	DBH (cm)	Height (m)	Age (yrs)	DBH (cm)	Height (m)
10	2.0	5.0	20	1.0	1.0
20	8.0	10.0	40	2.0	2.0
40	12.0	13.0	80	4.0	3.0
			120	7.0	5.0
			160	11.0	7.0

IV. Abies sibirica

(1) *Range*. See Figure A.4. Optimum climatic conditions occur in SE West Siberia and include an annual precipitation of 900–1500 mm, growing season of 120 days, no less than 700 mm precipitation during the growing season, maximum growing degree-days of 2000, and minimum growing degree-days of 630 (Kapper 1954; Protopopov 1975).

(2) *Optimum soil conditions*. *Abies sibirica* prefers the most productive taiga soils (loams, podzols); see relative scales 1–3 (Falaleev 1964; Nuhimovskaya 1971b; Krylov et al. 1986).

(3) *Reproduction* (Nuhimovskaya 1971b; Danilov 1951). Cone production begins at 25–30 years for a tree growing in the open, and at 40–60 years for a tree growing inside a closed forest canopy. Mean cone weight is approximately 9 g, and mean number of seeds in one cone is approximately 230. The dynamics of cone production is illustrated in Figure 4.1. The maximum reported distance for seed dispersal is 10 km. (Falaleev 1964).

Abies sibirica may produce vegetatively by laying from roots but these trees are more sensitive to rot than are trees that originate from seeds (Falaleev 1964).

(4) *Growth*. Like other *Abies* species, *Abies sibirica* is very shade tolerant (see relative scale 4). Young trees can survive under low light for up to 60 years age with almost no growth. Light demands increase with age (Table 4.1). Maximum height is 38 m, maximum dbh, 80 cm, and maximum age is approximately 300 years (north taiga zone – 200 yrs, south taiga zone – 300 yrs, mountains of south Siberia – 500 yrs). Normally, observed age is 150–180 years (Krylov 1961). Individual tree growth is

described in the data of Table 4.2. Trees are strongly subjected to rot, so that healthy trees greater than 140 years old are rare. Trees that grow fast are more susceptible to rot than are slow growing trees.

(5) *Fire*. Intolerant of fire because of thin bark.

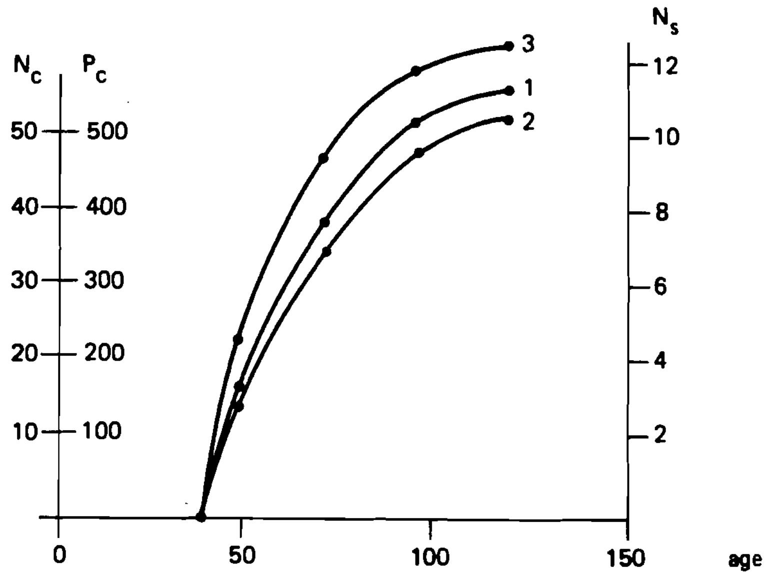


Figure 4.1. Dynamics of reproduction for *Abies sibirica* (point 1, Figure A.4).
1 – N_c – number of cones (1/tree/year)
2 – P_c – weight of cones (g/tree/year)
3 – N_s – number of seeds (thousands/tree/year) (Danilov 1951).

Table 4.1. Minimum light intensity necessary for survival of *Abies sibirica* (Savchenko 1970).

Height of Tree (m)	Age (yrs)	Percent Full Sunlight
< 0.05	5	1.0
0.05 – 0.25	10	1.4
0.25 – 0.50	21	5.0
0.50 – 1.0	27	4.9
1.0 – 1.5	39	5.2
> 1.5	64	6.8

Table 4.2. *Abies sibirica* tree growth.

Point 2, Figure A.4 (Nuhimovskaya 1971a)		Point 3, Figure A.4 (Pozdniakov 1961)			Point 4, Figure A.4 (Nuhimovskaya 1971b)	
Age (yrs)	Height (cm)	Age (yrs)	DBH (cm)	Height (m)	Age (yrs)	Height (m)
10	15	20	0.5	0.5	20	5.0
20	40	40	1.0	1.0	40	11.0
30	100	80	2.0	2.5	60	17.0
		120	4.0	4.0	80	22.0
		160	7.0	6.0	100	25.0
					120	27.0

V. Larix sibirica

(1) *Range.* See Figure A.5. Growing degree-day (5°C base) maximum is 2300, and minimum is 700.

(2) *Optimum soil conditions. Larix sibirica* is intermediate in tolerance to drought, flooding and soil nutrient stresses (relative scales 1–3). It prefers neutral or slightly acidic podzols without permafrost (Dilis 1961).

(3) *Reproduction.* Cone production begins at 12–15 years (Dilis 1961). Seed production is a function of age (Figure 5.1). Most seeds fall within 50 m of tree (Anonymous 1962). Optimum soil moisture for seed germination is 20–45% (by volume) (Safonova 1949). Probability of seed germination is usually (60–70%); regeneration is good following fire. Regeneration is suppressed by dry soil conditions and by thick litter and grass cover (Dilis 1981). The ability to layer is absent.

(4) *Growth. Larix sibirica* is a shade intolerant species (relative scale 4). Its light demands are relatively low for the first 12–15 years, but then increase (Dilis 1981). *Larix sibirica* is a long-lived species. Stands 200–300 years old are common. Maximum height is 45 m, maximum diameter 1 m, and maximum age is 500–600 years (Dilis 1981; Pozdniakov 1983). The most vigorous growth occurs before 80–100 years of age (Figure 5.2, see also Table 5.1).

(5) *Fire. Larix sibirica* is moderately tolerant of fire. All mesic soils in Siberia are mainly occupied by dark conifers and *Larix sibirica* can only persist due to recurring fires.

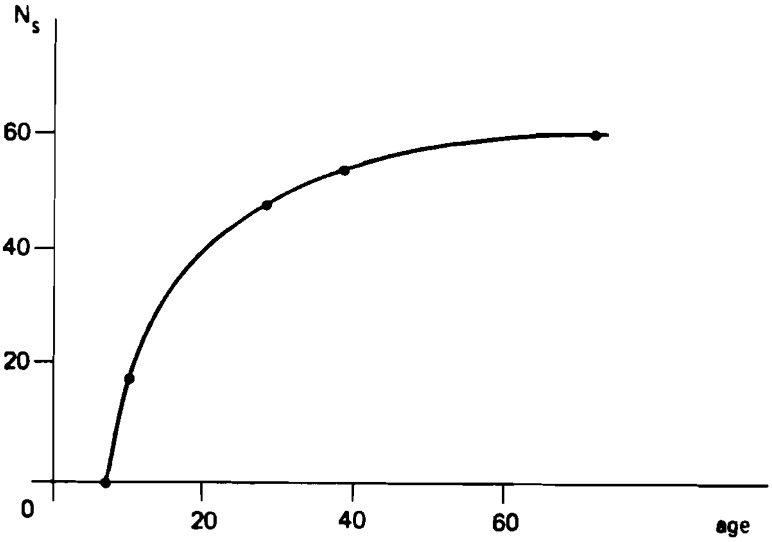


Figure 5.1. Dependence of seed productivity N_s (thou/year/tree) upon age for *L. sibirica* (Dilis 1961).

Table 5.1. Biomass distribution for individual *Larix sibirica* trees. (Safronova and Nypa 1979).

Above-ground Biomass					Below-ground
Age (yrs)	Total	Stem	Branches	Needles	
10	80%	38%	25%	17%	20%
16	74	39	27	8	26

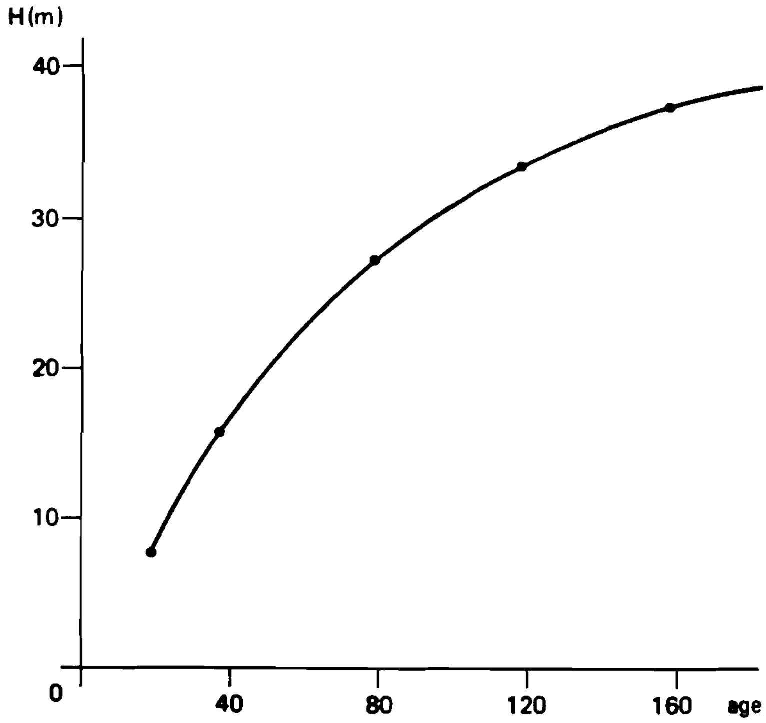


Figure 5.2. Height growth of *L. sibirica* (for point 3 on Figure A.5) (Safronova and Nypa 1979).

VI. Larix sukachewii

(1) *Range.* See Figure A.6. Growing degree-day (5°C base) maximum is 1700, and minimum is 800.

(2) *Optimum soil conditions* are moderate with respect to nutrient demand and soil moisture (relative scales 1–3, Dilis 1981; Pozdniakov 1983).

(3) *Reproduction.* Cone production is similar to that of *Larix sibirica.* Probability of seed germination is usually no greater than 20% (Tymofeev 1961). The ability to layer is absent.

(4) *Growth.* Reaction to light is similar to that of *Larix sibirica.* Its maximum dimensions are also similar to those of *Larix sibirica.* Maximum height is 45 m, maximum diameter is 1 m, and maximum age is 500–600 years (Dilis 1981). Individual tree growth is illustrated in Table 6.1.

(5) *Fire. Larix sukachewii* is moderately tolerant of fire.

Table 6.1. *Larix sukachewii* tree growth.

Point 1, Figure A.5 (Kalinin 1965)				Point 2, Figure A.6 (Konovalov and Surin 1979)		
Age (yrs)	DBH (cm)	Height (m)	Volume (m3)	Age (yrs)	DBH (cm)	Height (m)
10	3.4	4.0	0.01	20	7.0	8.0
20	9.2	12.0	0.04	40	16.0	17.0
30	14.0	18.0	0.14	60	23.0	22.0
40	17.0	23.0	0.30	80	30.0	27.0
50	22.0	26.0	0.48	100	34.0	32.0
60	28.0	29.0	0.88			

VII. Larix dahurica

(1) *Range.* See Figure A.5. Western and eastern range borders coincide with –30 °C mean January temperature isotherm and to isoline of 200–300 mm annual precipitation; northern border is result of short growing season and heat deficiency.

(2) *Optimum soil conditions. Larix dahurica* can grow on a wide range of soil types: poor sands, thin stony soils, wet peaty soils, and black earthy soils. Optimum soil conditions (see relative scale 1–3) are well-drained, mesic sites with a thick soil active layer (Dilis 1981).

(3) *Reproduction.* Cone production begins at approximately 15 years age. The maximum number of cones per tree per year is 1800. The maximum number of seeds per tree per year is 700,000 (Milutin 1984). The ability to layer is absent. Seed germination depends on soil moisture (Table 7.1).

(4) *Growth. L. dahurica* is slightly less tolerant of shade than *Larix sibirica* and *L. sukachewii* (see relative scale 4). Its maximum height is about 30 m, and maximum age is approximately 250 years (Dilis 1981). Individual tree growth is illustrated in Table 7.2.

(5) *Fire. L. dahurica* is moderately tolerant of fire.

Table 7.1. Seed germination: probability of seed germination as a function of soil moisture (Utkin 1965).

water content (% volume)	12	12-22
germination (%)	0	4

Table 7.2. Growth of *Larix dahurica.*

Central East Siberia Point 4, Figure A.5 (Utkin 1965)		
Age (yrs)	DBH (cm)	Height (m)
20	1.5	4.0
40	4.5	6.0
60	9.0	11.0
80	11.0	14.0
100	14.0	17.0

VIII. Pinus sibirica

(1) *Range.* See Figure A.6. Optimum climatic conditions occur in the mountains of SW Siberia (point 2, Figure A.6). Optimum growing degree-days (5°C base) are 1700 and annual precipitation is 800–1400 mm. Minimum growing degree-days are 650, and minimum annual precipitation is 450 mm. Maximum growing degree-days are 2100, and maximum annual precipitation is 2000 mm. The western range border is of anthropogenic origin. The other borders represent climatic effects. The eastern limit is explained by the presence of permafrost and the dry continental climate. The southern limit reflects low moisture conditions. The northern limit reflects low

temperature limitations (summarized in Katayeva and Korzukhin 1987).

(2) *Optimum soil conditions. P. Sibirica* can grow on a wide range of soil types (stony soils, sphagnum bogs, dry sands, and permafrost soils with shallow soil active layers). Optimum soil conditions (see relative scale 1–3) are moist humid soils (summarized in Katayeva and Korzukhin 1987).

(3) *Reproduction.* Cone production variables are described in Table 8.1. Seeds are dispersed mainly by birds *(Nucifraga caryocatactes macrorhynchos* Brehm) up to 5–7 km distant (Vorobiev 1982; Bech 1974). Approximately 2% of seeds in the soil germinate. The most suitable substrate is green moss with a thickness of 5–20 cm (Bech 1974). There is a qualitative difference in the dependence of germination on thickness of moss layer for *Pinus sibirica* and species with small seeds (e.g., *Pinus, Betula)* as shown in Figure 8.1 (Sedych 1979; Katayeva and Korzukhin 1987). The ability to layer is absent.

(4) *Growth. P. sibirica* is relatively tolerant of shade (relative scale 4) as shown in Table 8.2. (Krylov et al. 1983; Zubov 1971; Rhysin 1970). Maximum dimensions occur in the southern mountains of West Siberia (point 2, Figure A.8). The maximum height is 40 m and maximum diameter, 1.8 m. Maximum age in the northern taiga is 300 years, and in the southern taiga, 500 years. However, in the mountains of south Siberia, *P. sibirica* reaches 850 years (Bech 1974; Sukatchov 1938; Krylov 1961). Individual tree growth is described in Table 8.3.

(5) *Fire. P. sibirica* is moderately tolerant of fire.

Table 8.1. Cone and seed production parameters for *Pinus sibirica* (Sergyevskaya 1971; Nekrasova 1960; Kirsanov 1981).

Beginning of cone production	
tree in the open	15–20
tree in closed canopy	60–70
Age of maximum seed production	
Number of cones per tree	
alone	180–300
tree in closed canopy	120–140
Number of seeds per cone	80
Average number of seeds per tree per year	
alone	3000–7000
tree in closed canopy	2000–3000
Frequency of seed production (per ten years)	2–3

Table 8.2. Minimum light demands for survival (Polykarpov and Babintceva 1963).

Age (yrs)	1–2	3–5	6–10	11–15	>15
Percent Full Sunlight	1–3	3–6	6–9	9–13	13

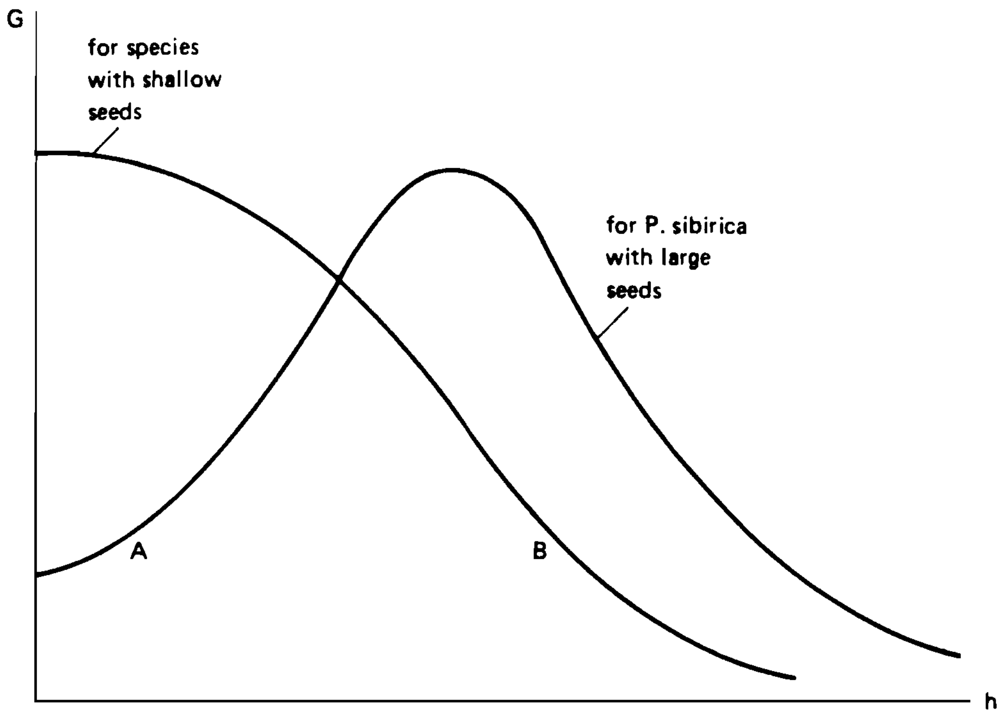


Figure 8.1. Qualitative dependence of G – combined probability of seed destruction and germination of undestroyed seeds – upon thickness of moss h for two types of tree seeds (summarized in Katayeva and Korzukhin 1987). Curve A is peculiar to *P. sibirica*. It has a low probability of avoiding destruction at low moss-layer thickness because of enhanced probability of being eaten by mice, drying on droughty soils, being buried by birds, etc. Decrease of probability of germination at large moss thicknesses arises because of inability of *P. sibirica* seed root to reach mineral soil.

Table 8.3. *Pinus sibirica* tree growth.

West Siberia (point 1, Figure A.8) (Sedych 1979)			
Age (yrs)	DBH (cm)	HT (m)	Volume (m3)
40	3.0	3.0	–
80	8.0	6.0	0.02
120	23.0	17.0	0.32
160	36.0	25.0	1.20

Point 2, Figure A.8 (Semetchkin 1970)		Point 3, Figure A.8 (Pozdniakov 1961)		
Age (yrs)	Height (m)	Age (yrs)	DBH (cm)	Height (m)
25	3.0	20	4.0	2.0
50	9.0	40	7.0	7.0
100	21.0	60	12.0	9.0
150	25.0	80	16.0	10.0
200	26.0	120	18.0	11.0
		160	22.0	12.0

IX. Betula pubescens and B. pendula

(1) *Range*. See Figure A.7. The maximum growing degree-days (5°C base) are 2800 and minimum growing degree-days are 600.

(2) *Optimum soil conditions*. The birches require fewer nutrients than any other species described here. They are also very tolerant of droughty and flooded (boggy) soils. (See relative scales 1–3, Grozdova 1979).

(3) *Reproduction*. Seed production begins at approximately 10–15 years age for an open stand, 20–30 years for a closed stand. Probability of seed germination is generally less than 60%. Successful germination requires high light levels and wet mineral soil. Root sprouts can occur, but they have less vitality than trees that have originated from seeds (Ivanov et al. 1975).

(4) *Growth*. The birches are shade intolerant (see relative scale 4, Grozdova 1979). Maximum height is about 30 m. Maximum diameter is 60–80 cm. Maximum age is approximately 150 years.

Individual tree growth is illustrated in Table 9.1.

(5) *Fire*. Thin bark makes these species intolerant of fire.

Table 9.1. Growth of *Betula* species.

South Karelia Point 1, Figure A.9 (Zyabchenko 1984)			Central Yakutia Point 2, Figure A.9 (Utkin 1965)		
Age (yrs)	DBH (cm)	Height (m)	Age (yrs)	DBH (cm)	Height (m)
10	2.2	3.0	10	1.0	4.0
20	7.7	8.0	20	3.0	6.0
30	13.0	12.0	40	10.0	13.0
40	17.0	14.0	60	13.0	15.0
50	20.0	16.0	80	16.0	17.0

X. Populus tremula

(1) *Range*. See Figure A.8. Maximum growing degree-days (5°C base) is 3300. Minimum growing degree-day is 600.

(2) *Optimum soil conditions*. *P. tremula* grows on wide range of soil types (podzols, grey forest soils, alluvial soils), but avoids extremely dry and wet soils. pH range is 4.3–5.8 (see relative scales 1–3). *P. tremula* is resistant to flooding (Demidenko 1978).

(3) *Reproduction*. Seed production begins at approximately 10–15 years, but regeneration by seed is rare (Demidenko 1978). Vegetative reproduction is much more common. Prolific root sprouts occur beginning at an age of 7–9 years. One tree can produce up to 500 sprouts per year. Successful sprouting requires high levels of soil moisture and aeration (Demidenko 1978).

(4) *Growth*. *P. tremula* is shade intolerant (Demidenko 1978, see relative scale 4). Maximum height is about 35 m, maximum diameter is 100 cm, maximum age is approximately 80–90 years (Shimanyuk 1964). Individual tree growth is illustrated in Table 10.1. *P. tremula* has low resistance to rot.

(5) *Fire*. Thin bark makes this and other *Populus* species intolerant of fire, although vegetative reproduction by root sprouts allow *P. tremula* to dominate early post-fire successions.

Table 10.1. Growth of *Populus tremula*.

A: Middle Taiga, Central West Siberia
(point 1, Figure A.10)
(Demidenko 1978)

Age (yrs)	DBH (cm)	Height (m)	Volume (m3)
10	2.0	5.0	-
20	5.0	9.0	0.02
40	13.0	18.0	0.12
60	22.0	22.0	0.40

B: south taiga, central West Siberia
(point 2, Figure A.10)
(Demidenko 1978)

Age (yrs)	DBH (cm)	Height (m)	Volume (m3)
10	3.0	4.0	-
20	7.0	8.0	0.03
40	17.0	18.0	0.16
60	23.0	24.0	0.43

XI. Relative Ecological Scales

The relative sensitivity of tree species to environmental factors, illustrated in Figure 11.1, are constructed from numerous qualitative field observations made by Russian forest ecologists. Some of them (Morozov 1930; Sukatchov 1938; Polykarpov et al. 1986) illustrate relative ecological properties for most of the tree species mentioned in our paper, and the others (Demidenko 1978; Dilis 1981; Bech 1974; Krylov 1961; etc.) tell about the properties of one species in relation to another one or two species. Not all these observations are comparable, and some of them contradict one another (e.g., at shade tolerance scale, *Pinus sibirica* is sometimes placed between *Abies sibirica* and *Picea abies*). These contradictions cannot be resolved on the basis of qualitative "naturalistic" field observations and need assessment of ecophysiological data. Moreover, the position of tree species on the scales must depend on the species locations inside their geographic ranges, so the "fixed" scales are only rough approximations which are probably correct for centers of the ranges.

```
(1)  Nutrient-stress tolerance

    poor soil                                       rich soil
(high stress tolerance)                                 (low stress tolerance)

      |------|------|------|------|------|------|------|
      9     10      1      7      5      8      2      4
                                  6             3


(2)  Soil moisture drought tolerance

    dry soils                                       wet soils
(high drought tolerance)                                 (low drought tolerance)
      |--|---|------|------|------|------|------|------|
      9  9  10      1      5      7      8      4      2
                           6                           3


(3)  Soil oxygen demands:  tolerance to flood-induced oxygen shortage

   low oxygen                                      high oxygen
(high flood tolerance)                                 (low flood tolerance)
      |--|---|------|------|------|------|------|------|------|-----|
      9  9  10      7      5      1      8      2      4     6
                                                3


(4)  Shade tolerance

   shade tolerant                                       shade intolerant
      |------|------|------|------|------|------|------|
      4      2      8      1      5      7      9      10
             3                    6


(5)  Growing season temperature demands

    cold                                             warm
      |---------|---------|---------|---------|---------|
      7         8         2         4         9         1
      5                   3
      6
```

Species:

1. *Pinus silvestris*
2. *Picea abies*
3. *Picea sibirica*
4. *Abies sibirica*
5. *Larix sibirica*
6. *Larix sukachewii*
7. *Larix dahurica*
8. *Pinus sibirica*
9. *Betula pubescens and B. pendula*
10. *Populus tremula*

Figure 11.1. Relative ecological tolerances of ten tree species.

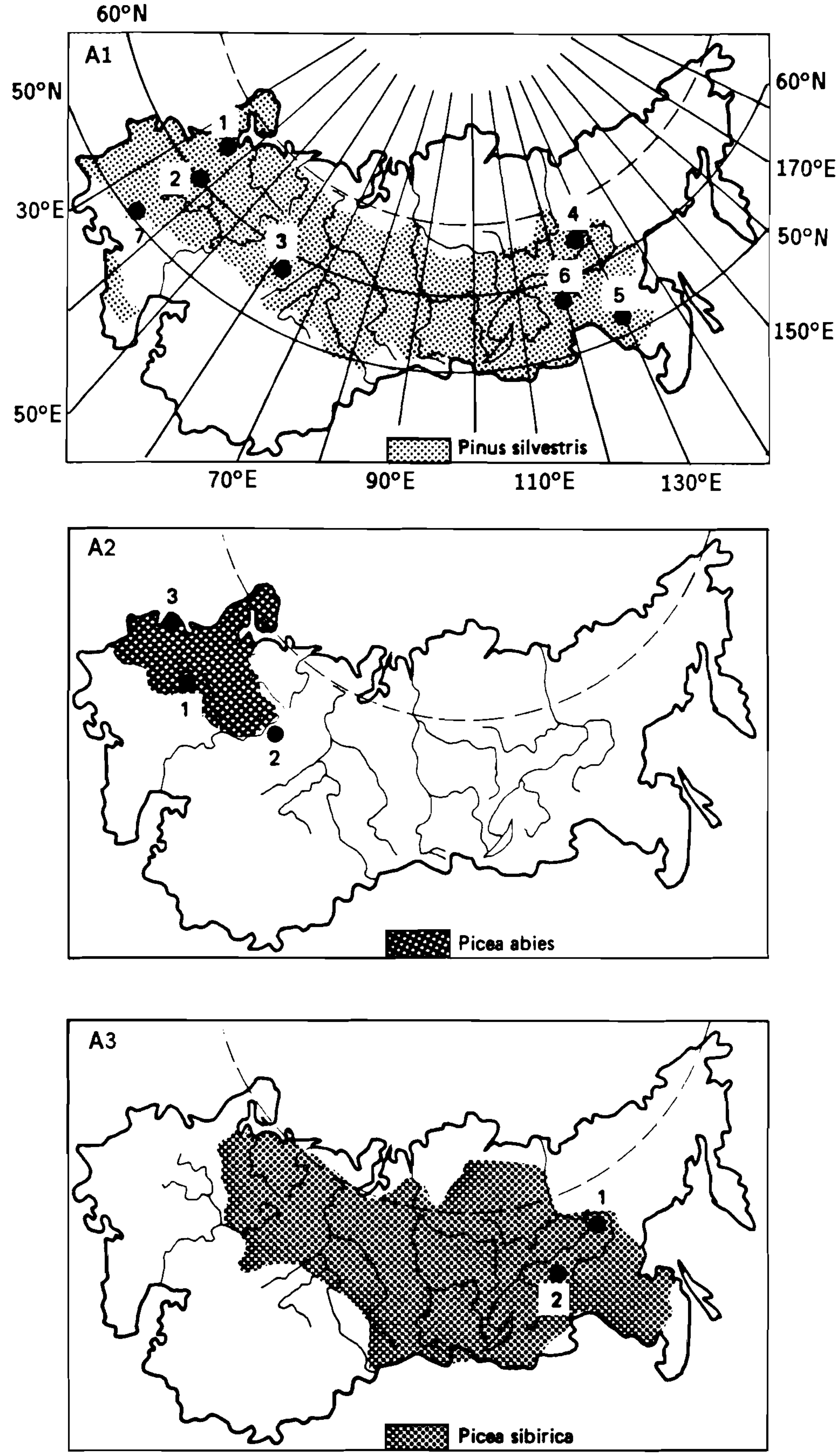
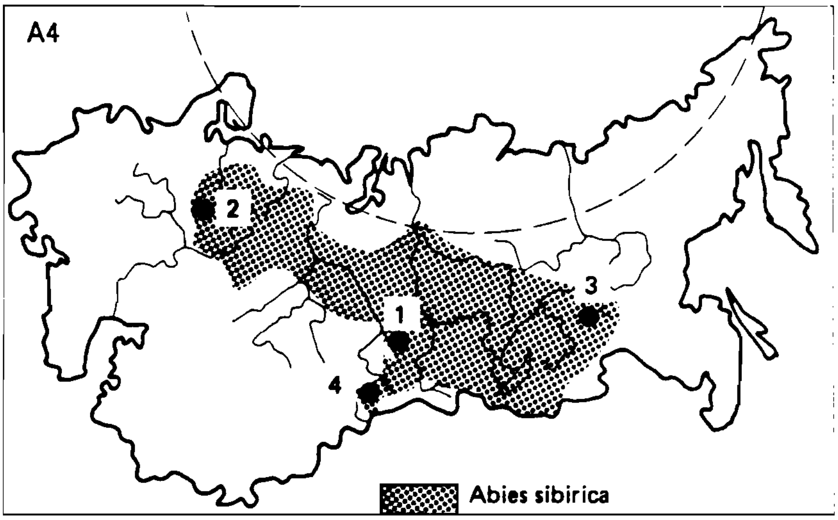


Figure A. Species range maps.

A.1 – *Pinus silvestris* (Anonymous 1977)
A.2 – *Picea abies* (Anonymous 1977)
A.3 – *Picea sibirica* (Anonymous 1977)



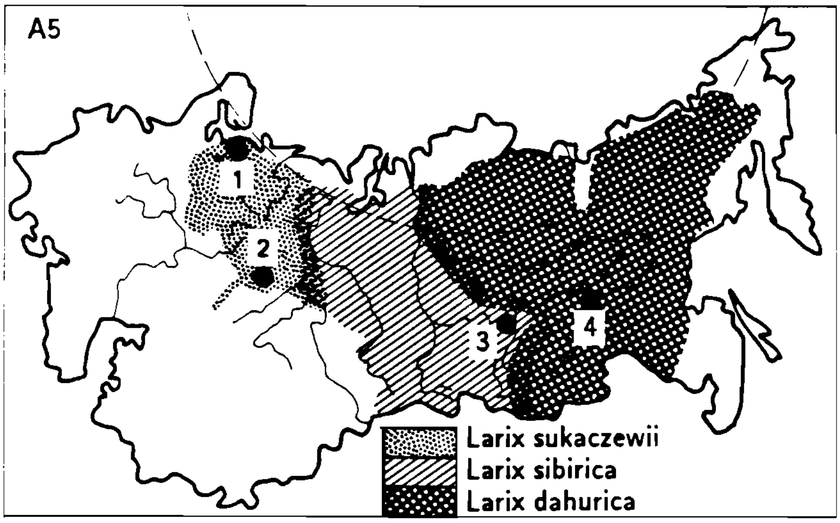
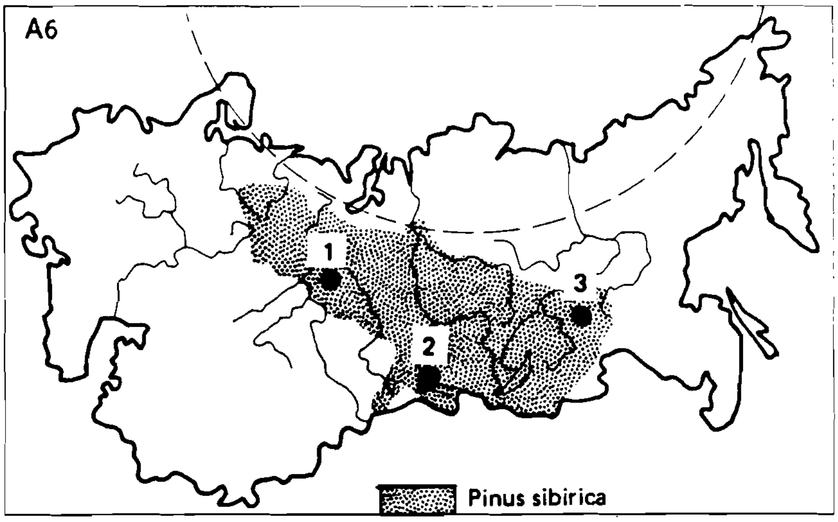
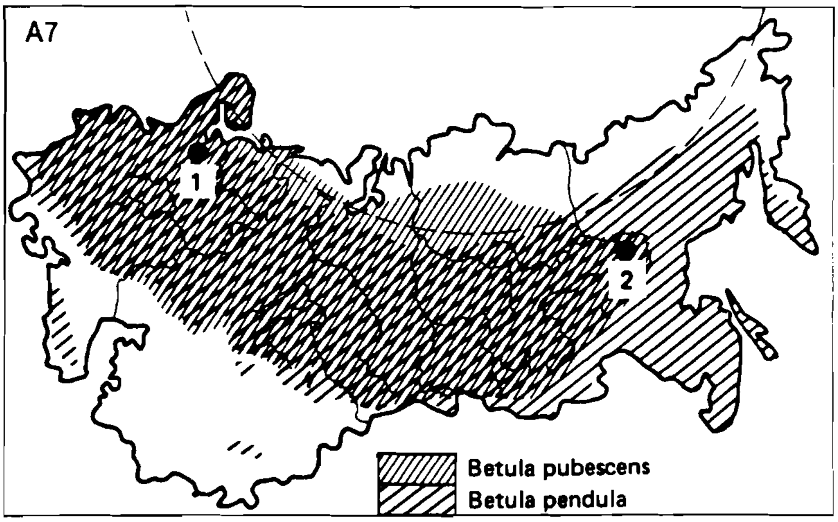


Figure A. Species range maps (continued).

A.4 – *Abies sibirica* (Anonymous 1977)
A.5 – *Larix sukachewii* (Dilis 1981)
– *Larix dahurica* (Dilis 1981)
– *Larix sibirica* (Dilis 1981)





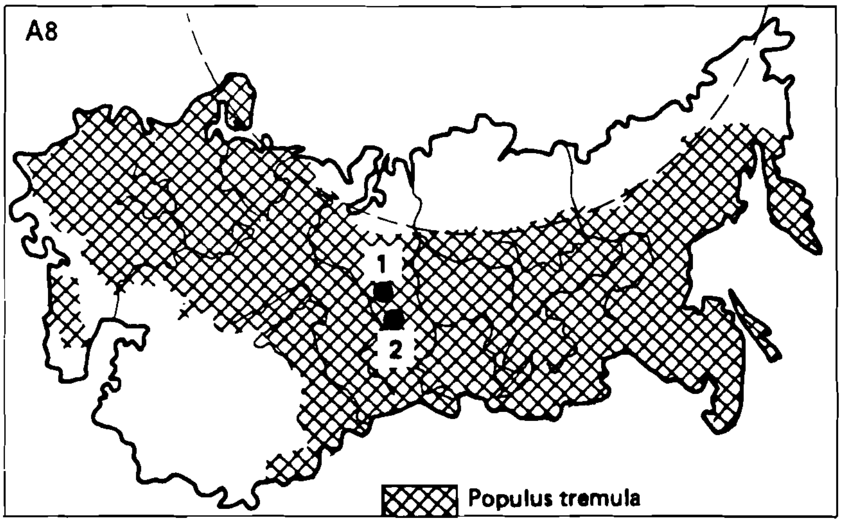


Figure A. Species range maps (continued).

A.6 – *Pinus sibirica* (Bech and Taran 1979; Anonymous 1985)
A.7 – *Betula pubescens and Betula pendula* (Grozdova 1979)
A.8 – *Populus tremula* (Anonymous 1977)

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