Genetic Variation in Frost Tolerance, Juvenile Growth and Timber Production in Russian Larches (*Larix* Mill.)

- Implications for use in Sweden

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Doctoral Thesis
Swedish University of Agricultural Sciences
Umeå 2010

Acta Universitatis Agriculturae Sueciae
2010:30

Cover: Selected tree of *Larix sukaczewii* from Vetluga in the Nizhnij Novgorod region (photo: Valery P. Putenikhin).

ISSN 1652-6880
ISBN 978-91-576-7507-1

Print: Arkitektkopia Umeå 2010

Abstract

Karlman, L. 2010. Genetic Variation in Frost Tolerance, Juvenile Growth and Yield in Russian Larches – Implications for use in Sweden. Doctor's dissertation.

Larch (*Larix* sp Mill.) is an important component in boreal montane and subalpine forests in the northern hemisphere. Macrofossils of larch in the Scandinavian mountains prove the existence of larch in Scandinavia after the last ice age, Siberian or Russian larch is now considered as an indigenous tree species of Sweden. The larches of Russia are of interest for their production potential and wood quality.

The aim of this thesis was to determine frost resistance, juvenile growth, stem straightness and branch traits in a 5-year-old combined provenance/progeny test with *Larix sukaczewii*, *L. sibirica*, *L. gmelinii* and *L. cajanderi* originating from Russia and tested on three sites in Sweden. An evaluation of genetic parameters in this half-sib family material was also made. The yield in 37-86 year old field tests of *L. sukaczewii* and Russian larch hybrids was also evaluated.

The results indicate that larches from western Russia, *L. sukaczewii* were least damaged in the artificial freezing test, had highest survival in the field trials and had the best stem quality. The most northern provenances of this species had, however, poorer growth and lower survival, especially on the southern test site. *L. sibirica* from central Siberia and continental provenances of *L. cajanderi* and *L. gmelinii* were not adapted to any of the sites. Among provenances of *L. gmelinii* and *L. cajanderi* those with more maritime origin showed generally better adaptation than those from more continental areas.

Geographic and climatic variables of provenance origin were important for the performance of the provenances. At the southern test site, provenances from northern latitudes and strongly continental areas in Russia showed poor growth and survival. On the two test sites located in harsh climates, provenances originating in climates similar to the test sites showed best survival. This means a northern transfer of 2-3 latitudes for the most northern site

The yield in 37- 40 year-old *L. sukaczewii* was higher than *Picea abies*, *Pinus sylvestris* and *Betula pendula* on two test sites in central Sweden. In northern Sweden one provenance from Arkhangelsk showed higher yield after 50 years compared to one provenance from the central Ural Mountains. *L. sukaczewii* of Raivola origin demonstrated a wide ecological range with a yield of about 7 m^3/ha/year for 76 years, in a local continental climate in central Sweden and a maritime site in northern Norway. Small test plots with the hybrid *L. decidua* x *L. sukaczewii* had substantially higher production than *L. sukaczewii*.

Keywords: Larix sukaczewii, L. sibirica, L. gmelinii, L. cajanderi, frost tolerance, juvenile growth, stem straightness, Russian larch hybrids, genetic variation, provenance test, progeny test, half-sib families.

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Contents

This thesis is based upon the following papers, referred to by Roman numerals in the text:

I Eysteinsson, T., Karlman, L., Fries, A., Martinsson, O., and Skúlason, B. (2009). Variation in spring and autumn frost tolerance among provenances of Russian larches (*Larix* Mill.). Scan. J. For. Res. 24:100-110.

II Karlman, L., Fries, A., Martinsson, O. and Westin, J. Juvenile growth of provenances and open pollinated families of four Russian larch species (*Larix* Mill.) in Swedish field tests. Silvae Genetica Submitted (August 2009).

III Karlman, L., Fries, A., and Martinsson, O. Stem straightness and branch traits among provenances of Russian larches (*Larix* Mill.) tested in southern Sweden. (Manuscript).

IV Karlman, L., Martinsson, O., Karlsson, C. and Skaaret, G. Yield of *Larix sukaczewii* Dyl. and larch hybrids in northern Scandinavia. (Manuscript).

1 Introduction

The larches (*Larix* sp. Mill.) are a genus of deciduous coniferous tree species belonging to the *Pinaceae* family. They have a wide distribution in the boreal, montane and subalpine forests of Asia, Central Europe and North America. The genus consists of 10-15 more or less distinct species, some considered by botanists as varieties or ecotypes. Larches have their greatest distribution in Asia, especially in Russia where they grow either as pure- or in mixed stands on an area of roughly 280 million ha, constituting 37 % of the forests in Russia (Martinsson and Lesinski 2007). Larches are light demanding and have fast juvenile growth. Their wood is characterised by a high amount of heartwood and resin content, and larches are considered as a valuable timber tree in many regions.

Scandinavia is naturally poor in tree species and especially conifers. There are only two economically important indigenous conifers: Norway spruce (*Picea abies* L. (Karst.) and Scots pine (*Pinus sylvestris* L.). During the 1960's, fear of a shortage in wood supply occurring at the beginning of the 21st century was a reality in Sweden. The shortage of wood was supposed to be covered by introduction of fast growing exotics. Two exotics were of special interest; lodgepole pine (*Pinus contorta* Dougl.) and Siberian larch or Russian larch (*L. sibirica* Ledeb. and *L. sukaczewii* Dyl.). Mainly due to more favourable characteristics in pulp making and administrative difficulties in obtaining larch seeds, *P. contorta* was chosen and was introduced on a large scale during the 1970´s and 1980´s. In total, approximately 600 000 hectares of lodgepole pine have since then been planted in northern Sweden making it the third big conifer in northern Sweden and one of the most extensive planted exotics in the northern boreal forests on the whole (Zobel et al. 1987, Hagner 2005).

The interest in Siberian larch, which had been quite high during the 1950´s and 1960´s in Sweden, dropped and it was not until the 1990´s that interest in the species started again. The Russian-Scandinavian larch project was initiated in 1992 and besides studying the wood quality of the Russian larches, was aimed at sampling different seed sources widely representing large areas of the larch distribution in Russia for establishment of provenance and progeny trials in the 10 participating countries (Martinsson and Lesinski 2007). The main part of this thesis is an early evaluation of the Swedish test series.

1.1 Objectives

The aim of the thesis was to assess genetic variation in adaptive traits of four Russian larch species; *Larix sukaczewii*, *L. sibirica*, *L. gmelinii* and *L. cajanderi*, and find which seed sources that are most suitable for planting in Sweden.

The specific objectives for the different papers were:
I To assess differences in frost tolerance between the Russian larch species and also between provenances within species.

II To make an early evaluation of survival and height growth in the tested material, and its dependence on geographic and climatic variables.

III To reveal differences between species and provenances in stem quality traits like stem straightness and branch traits.

IV To study the yield in older stands of *L. sukaczewii*, the most planted larch species in northern Sweden and to compare the yield of this species with Russian larch hybrids.

An early evaluation of genetic parameters and the potential for breeding has also been done (Paper II and III). The thesis begins with an introduction to the genus *Larix* and especially the larches of Russia. A short review of earlier Swedish research on the genera is included to give more understanding about the peculiarities of the species. As the climate is about to change quite rapidly if global warming theories are realized, this aspect and its implications for growing larch in Sweden are also discussed.

1.2 History of the genus and earlier distribution in Fennoscandia

Larches are evolutionarily one of the youngest conifers. According to Sukachev (1924) and Bobrov (1972), the genus originates from the middle Mesozoic period (251-65.5 million years B.P.) in central Asia in present-day China, where it evolved under mountain conditions and continental climates. The oldest fossils of larch are dated from the Eocene era, some 35-55 million years ago. A species named *L. altoborealis* was found on Axel Heiberg Island, Nunavut, Arctic Canada (Le Page and Basinger 1995).

Interestingly, larch once was a natural component of Fennoscandia. During Pleistocene's (2.6 million-12 000 years B.P.) last two interglacials Holstein and Eem, forests of *Larix* were growing here (Frenzel 1968). Even after the last glaciation, macro fossils of larch in the Scandinavian mountains have proven the existence of larch 8800-7500 years B.P. (Kullman 1998). These new findings have meant that Siberian larch now is considered an indigenous species of Sweden (Skogsstyrelsen 2000). For some reason, however, larch disappeared and was not reintroduced until the 18th century now in the form of European larch. Later in this introduction (Part 10) there will be a discussion about why larch disappeared and the effect global warming will have for the Russian larches will follow.

Two different strains of larch Western (Eurasian) and Eastern (Pacific) appeared at the beginning of the Tertiary period, about 70 million years ago. Sukachev (1924) wrote that the Eurasian larches started to spread westwards "not later than the middle tertiary period" and divided into two separate species, *Larix sibirica* and *L. decidua*. The pacific strain later migrated across the Bering Strait and divided in time into three separate American species.

1.3 Larch species of the world

Larch systematics and geographical distribution

Larches (*Larix* sp Mill.) belong to the family *Pinaceae* (the same family that contains *Abies*, *Picea* and *Pinus*), subfamily *Laricioideae* which comprise three genera; *Larix*, *Pseudolarix* and *Cedrus*.

The genus *Larix* consists of 10 widely accepted species (Ostenfeld and Larsen 1930; Krüssmann 1985; Farjon 1990). Russian and Asian taxonomists, however, divide the Eurasian species further, setting the number of larch species to 13-17. The distribution of the world's more or less recognized larch species is seen in Fig. 1.

The systematics of the Eurasian larch species are complex. There are according to taxonomists at least two species in Russia, Siberian larch (*L. sibirica* Ledeb.) and Dahurian larch (*L. gmelinii* Rupr.) (Milyutin and Vishnevetskaia 1995). Dylis (1981) suggested that the western distributed *L. sukaczewii* Dyl. should be distinguished as a separate species from *L. sibirica*, this based on differences in cone morphology. Later phylogenetic studies (Bashalkhanov *et al*. 2003; Khatab *et al*. 2008), support Dylis, and in this thesis *L. sukaczewii* is therefore treated as a separate species. Bobrov (1972) separates *L. cajanderi* Mayr. from *L. gmelinii* due to differences in ecology and cone morphology, a separation also used in this thesis. The main criterion for the differentiation of species, its reproductive isolation, is weak within the *Larix* genus, the species easily hybridize.

In Russia natural hybrids between *Larix sibirica* and *L. gmelinii* are called *L. x czekanowskii*, and further east, hybrids between *L. gmelinii* and *L. cajanderi* are recognized (Abaimov *et al*. 1998). *L. laricina* in North America and the Russian larches have broad distributions in the boreal taiga, while the other species have smaller specific distributions in mountain areas.

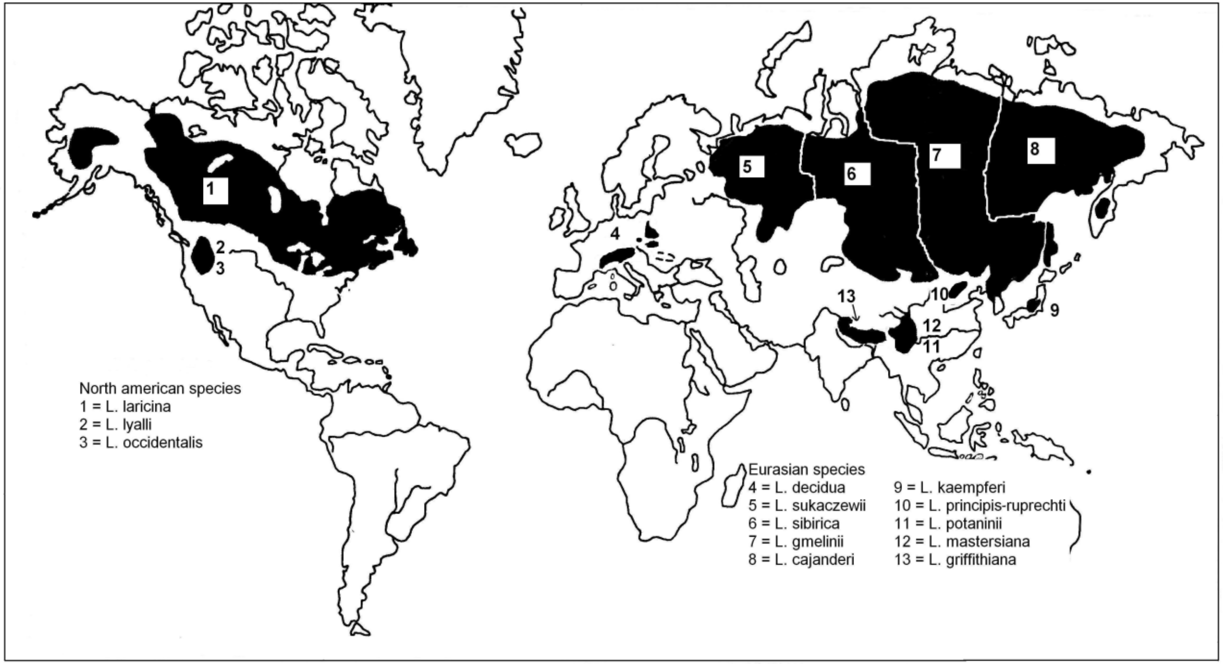


Fig. 1. The world-wide distribution of the genus *Larix* (map from Schmidt 1995).
Species numbers 5, 8, and 10 are not recognized as separate species by Ostenfeld and Larsen (1930) or Farjon (1990). *Larix decidua* distribution according to McComb (1955). Distribution of *L. sukaczewii* according to Putenikhin and Martinsson (1995).

There are two main groups of larches, divided from the length of bracts of female cone: short bracted and long bracted (Fig. 2 and 3, see also Fig. 4). The short-bracted species have generally a northern distribution and have large continuous distribution areas, while the long-bracted species have southern distribution in montane areas (Table 1) (LePage and Basinger 1995).

Table 1. Larch species and their latitudinal range of natural distribution

Short bracted	Used abbreviations	Latitudes ° N	Long bracted	Latitudes ° N
L. laricina		40-68	*L. occidentalis*	43-52
L. decidua	*L. dec.*	43-54	*L. lyalli*	45-52
*L. sukaczewii**	*L. suk.*	52-68	*L. mastersiana*	30-33
L. sibirica	*L. sib.*	45-70	*L. potaninii*	27-35
L. gmelinii	*L. gme.*	35-72	*L. griffithiana*	27-33
*L. prinipis-ruprechti**		36-43		
*L. cajanderi**	*L. caj.*	40-71		
L. kaempferi	*L. kaemp.*	35-38		

* Considered as separate species by some Russian and Chinese botanists (Dylis 1981; Bobrov 1972; Zhang and Xu 1995).

Fig. 2. Short-bracted cone of *Larix sukaczewii* (Photo: Jaap Buitink)

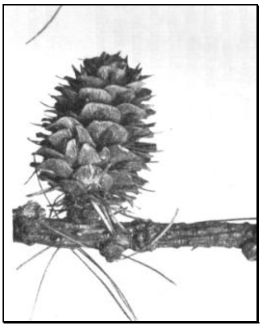


Fig. 3. Long-bracted cone of *Larix occidentalis* (Photo: N. Sylvén)

Larches are the dominating tree species in Russia, especially in eastern Siberia, where it forms vast pure larch forests in the permafrost zone. Total growing stock equals 25 billion m^3, which is ca. 32 % of the total growing stock in Russia. The more or less distinguished species that are found here are Russian larch (*Larix sukaczewii*), Siberian larch (*L. sibirica*), Dahurian larch (*L. gmelinii*), and Cajander’s larch (*L. cajanderi*). Larches cover an area of roughly 280 million ha, about 37 % of the forested area of Russia or almost 7 % of the world's total forested area. Together with Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), birch (*Betula* sp.), and Siberian stone pine (*Pinus sibirica*), these species constitute 89 % of total wood stock in Russia (FAO 2005).

Larch has also a wide distribution in Mongolia and China. In Mongolia, larch is the most common tree species with a growing stock of ca 1 billion m^3. Also in China, larch has a large distribution; it is the fourth most common tree species there with a growing stock of 925 million m3, about 7-8 % of total volume of the Chinese forests (FAO 2005). In North America the Tamarack larch (*L. laricina*) has a very widespread distribution, whereas Western (*L. occidentalis*) and subalpine larch (*L. lyalli*) have small distinct distributions in the mountains of Western United states and Canada. Short descriptions of the most important species are given below.

Eurasia

***Larix decidua* – European larch**

European larch is an important timber tree with its distribution between Lat. 43-54°N mainly in the mountains of central Europe. McComb (1955) distinguished five geographical races of *L. decidua*. 1. Alpine; 2. Sudeten; 3. Tatra (Slovakian); 4. Polish (southern and central Poland); 5. Romanian (Carpathian Mountains) (Fig. 3). European larch was the first larch species that was planted in Sweden. The early plantations were of Scottish seed source, where it had been planted for more than 100 years. The original provenance was probably from the Tyrol. Schotte (1917) described the Scottish larch to have good growth and a strikingly straight stem and considered it to be a separate Scottish race of its own. Later when material from the Alps was tested the stem shape of the trees was often inferior to the Scottish material. Interestingly, the Scottish seed source has grown well in maritime parts of Norway. One explanation could be that the Scottish larch has developed a land race adapted to more maritime conditions. When planted in Sweden – especially in the south-western part and with poorly adapted provenances – *L. decidua* has been severely attacked by larch canker (*Lachnellula willkommii*) and during the two last decades been replaced by hybrid larch (*L. kaempferi* x *L. decidua*) for forestation in southern Sweden. The hybrid has shown resistance to larch canker and has also higher yield (Larsson-Stern 2003a).

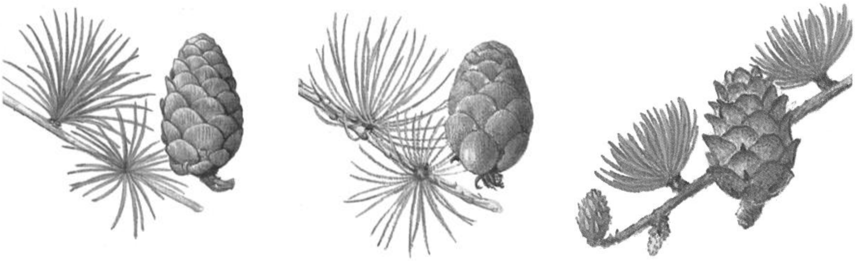


Fig 4. Cones of *L. decidua, L. sibirica* and *L. gmelinii*. European and Siberian larch cones are distinguished by the number of seed scales which are more numerous in European larch and the angle of the upper seed scale which are curled inwards in Siberian larch. Note that the Dahurian larch cone has rather flat angle of seed scales. (Mitchell and Wilkinsson 1995).

***Larix sukaczewii* - Russian larch**

Larix sukaczewii was first distinguished as a separate species by Dylis 1947 (Khatab *et al*. 2008). It is closely related to *L. sibirica* and some taxonomists call it just a variety or subspecies to this species. Their distributions meet east of the Ural Mountains along the River Ob (Fig. 1). *L. sukaczewii* has a scattered distribution in western Russia from Lake Onega in the west to the River Ob in the east, between latitudes 52° N to 68° N. It constitutes less than 1 % of total growing stock in this area (Putenikhin and Martinsson 1995). It grows mostly in mixtures with Norway spruce, Scots pine and birch and the average age of the larch trees is often high. Earlier the distribution area was larger but it has declined during the last century, mainly due to exploitation of the forests and bad management. Also the controlling of wild fires has lead to poor regeneration. It is this species, for the most part, that is planted as ‘Siberian larch’ in Finland, Sweden, Norway, and Iceland. The famous larch stands of Raivola (Lintula) comprise this species. The Raivola larch stand is known for being one of the most impressive cultivated forests in northern Europe with volumes of 1100-1300 m^3 per ha (Redko and Mälkönen 2005). *Larix sukaczewii* grows normally up to 30-35 m tall trees, but in Finland trees up to 46 m have been recorded at Punkaharju research station and at Raivola there are trees reaching over 50 m. It is a species of great ecological adaptability. It tolerates the continental climate of southern Ural as well as the maritime climate in Iceland and north western Norway. In Finland, the seed source Raivola has been used to establish seed orchards that provide planting material for a substantial part of Finland (Simak 1979; Mikola and Vakkari 1995; Abaimov *et al*. 1998).

***Larix sibirica* - Siberian larch**

The Siberian larch has a widespread distribution on the west Siberian taiga, from the River Ob in the west to Lake Baykal in the east. It is adapted to continental climates, more so than *L. sukaczewii*, with great temperature difference between summer and winter. It grows in a variety of different climates but forms the dominating species mainly in two distinct separated areas, one in the northern part of its distribution in the pre-tundra and northern taiga subzone and the second is in the southern taiga and transitional forest steppe subzone (Abaimov *et al*. 1998). It is together with *L. gmelinii* and *L. cajanderi* the dominating tree species in Northeast Russia. Together these species cover more than 40 % of the Siberian forests (Abaimov 1995). Siberian larch has a wide south-north range between Lat. 45°-70° N. The eastern border of *L. sibirica* marks the transition from West to East Siberia. Here it meets the distribution of *L. gmelinii* and forms hybrids with this species, *L x czekanowskii* Szafer (Abaimov *et al*. 1998).

The stem of Siberian larch is generally straight grown and is characterised by an early growth of rough and thick bark, which in a mature tree can constitute 20-30 % of the stem volume. Most of what has been considered Siberian larch plantations in Sweden should with the distinction between the Siberian- and Russian larch species used in this thesis in fact be regarded as *L. sukaczewii*. In 1892, seed material of Siberian larch was brought to Sweden. The origin of seed was the Arkhangelsk district; consequently it belongs to *L. sukaczewii*. In the 1930´s, however, seed materials of *L. sibirica*, from the Altai Mountains were planted in Sweden and in the 1950´s seed from the area around Krasnoyarsk was brought to Sweden. These plantations had generally bad survival and developed poor stem quality and contributed to give Siberian larch a bad reputation in Sweden.

***L. gmelinii* - Dahurian larch**

Dahurian larch has a wide distribution in eastern Siberia, where it forms large pure stands. Dahurian larch is also abundant in Mongolia and Northeast China and has smaller ranges in Kamchatka, Sachalin, and the Sikothe-Alin mountains in Russia. It is divided into several subspecies. In the present thesis are the included varieties *olgensis*, *japonica* or *kurillensis* and *kamchatica*. This species has a wide north-south range between latitudes 35-72°N. *Larix gmelinii* forms the northernmost forests on earth at the Khatanga river basin at Lat. 72° 40´ N in northern Siberia (Abaimov *et al*. 1998). *Larix gmelinii* and *L. cajanderi* form one of the largest homogenous phytogeographical areas in the whole circumboreal zone. The dominance is caused by their tolerance to the severe climatic conditions and permafrost (Krestov 2003). An adaptation to permafrost is the capacity to develop adventitious roots for water and nutrient uptake in the upper thawing layers of the permafrost zone. The seed scales of the cone have moderate angles, which means that seeds could stay in the cone for up to four years. Dahurian larch has developed an interesting adaptation to fires by dropping its lower branches to prevent the fire from reaching the higher parts of the stem (Makoto *et al*. 2007). Dahurian larch was first mentioned in Sweden by Rossander (1879). Rossander found the species to be “peculiar rather than beautiful”. Schotte (1917) found it an interesting species for imperfectly drained mosses in northern Sweden.

***L. cajanderi* – Cajander’s larch**

L. cajanderi has a distribution from latitudes 40°-71° N and between longitudes 125°-170° E in vast areas in north eastern Siberia. It is a close relative to the Dahurian larch, distinguished from this species mainly by cone morphology. The seed scale in a mature cone of Cajander´s larch has a greater angle, often 90 degrees or more. This causes the seed dispersal to take place just 3-5 days after seed ripening. *L. cajanderi* is a species well adapted to continental climates and soil permafrost. An adaptive trait to permafrost is the forming of a shallow root system. As the Dahurian larch it can produce adventitious roots for water and nutrient uptake in the upper thawing layers of permafrost. It tolerates amplitudes of temperature up to 66° C between coldest and warmest month. Regarding soils, it has rather broad tolerance, and it can grow on peaty soils, acid podzolic soils, humus carbonate, and alluvial soils on river valleys. On dry sandy soils in Central Yakutia it becomes outcompeted by *Pinus sylvestris,* however (Abaimov *et al*. 1998).

***L. kaempferi* – Japanese larch**

Japanese larch has a small natural distribution in central Honshu between latitudes 35° and 38° N. It occurs, often in mixed stands with *Abies homolepis, Tsuga diversifolia* and *Abies veithchii,* on mountain slopes at an altitude of 900 to 2800 m. Due to rapid growth and favourable disease and cold resistance it has been widely used in the northern part of Japan from the 1960-70’s (Takata *et al*. 2005). Japanese larch has also been extensively used as an exotic in Western Europe and North America. On the British Isles it has been the most used exotic larch tree species during half a century. Its main advantage compared with European larch is that it has shown great resistance to larch canker, a serious disease that has been damaging the European larch in maritime localities. The stem form is, however, often worse than in European larch. Japanese larch is used as one of the parents in the widely used hybrid larch (*L*. x *eurolepis* Henry), a hybrid between Japanese and European larch, which in recent years has been most planted in Western Europe.

***L. principis-ruprechtii* - Prince Ruprecht´s larch**

This species has a restricted distribution in the mountains of Northern China, between latitudes 36°31´ and 43°30´ N. It grows at altitudes between 1500 and 2800 m. Some taxonomists treat it as a subspecies of *L. gmelinii*, which it is closely related to (Eckenwalder 2009). Prince Ruprecht´s larch is shade intolerant, cold resistant and sensitive to lack of water. It is renowned for its good juvenile growth. Up to 50 years of age, it outgrows the local *Picea* species by 2-3 times both for height and diameter. It is widely adapted to different soil types. Tree improvement started in 1965 and clonal seed orchards have been established. Due to its narrow natural distribution the genetic variation between populations is not that great, and variation among families within a population has been found to be more important (Zhang and Xu 1995).

***L. potaninii* – Chinese larch**

L. potaninii is endemic to China and grows in the mountains of Southwest China on altitudes between 2300 and 4400 meters. It is adapted to grow in cold climates with precipitation varying between 800 and 2000 mm, and is found mainly in the Sichuan and northern Yunnan Provinces (Shimin and Shengxian 1995). It can grow up to 50 m in height and is an important timber tree in the centre of its range in the Sichuan province (Eckenwalder 2009). It was named after the Russian botanist Grigorii N. Potanin and is known in China to be a very beautiful tree.

***L. mastersiana* – Master's larch or Sichuan larch**

This rare, endangered species grows in the high mountains (2000-3500 m altitude) of Western China in a limited area in the Sichuan Province near Guanxian (Shimin and Shengxian 1995). It used to form large pure stands but due to heavy exploitation in the beginning of the 20th century its natural distribution is now restricted to scattered stands in remote locations (Eckenwalder 2009). It is closely related to *L. griffithiana* but its distribution area is more similar to *L. potaninii* (Fig. 3), their distribution meets in western Sichuan. The timber is used for various outdoor constructions and for making furniture. Due to its valuable timber it is to a certain extent used in plantation forestry in China, making it not in immediate danger of extinction (Eckenwalder 2009).

***L. griffithiana* – Himalayan larch or Sikkim larch**

Himalayan larch or Sikkim larch is a high subalpine species. It has its distribution in the mountains of eastern Himalaya: eastern Nepal, Sikkim (India), Western Bhutan, and Southwest China (Xizang Province = Tibet) where it grows at 3000-4100 m altitude. *Larix griffithiana* is the most southern of the *Larix* species, its distribution stretches as far south as Lat. 27° N. It can be distinguished morphologically from other larch species by the size of its cones which is larger than on any other larch species.

North America

Larch immigrated to America from Asia via the former land bridge between Asia and America, which is now the Bering Strait. If not quoted by others, facts about the American larches are from Milan Simak's The American larches (1971).

***Larix laricina* -Tamarack**

The tamarack has a very widespread distribution in the boreal forests of North America. Its southern border is south of the great Lakes (Lat. 40° N) in eastern U.S and it reaches as far north as Lat. 68° 20´ N in the Yukon Territory. It has a very wide ecological niche. It tolerates the continental climate of interior Alaska as well as the maritime climate in eastern North America. It is together with Dahurian larch the only larch species that tolerates bogs and peat lands, where it forms low productive forests, though outgrowing the other native conifers on these types of sites (Johnston 1990). It has, however, its best development in moist but well drained loamy soils along streams, lakes and swamps (Johnston and Carpenter 1985). It grows mostly in mixed stands with black spruce (*Picea mariana*), willows and poplars. Martinsson (1995a) found the tamarack to be a highly productive tree on wet and fertile sites in Sweden. Production of 90-100 m^3 stem wood per hectare during the first 20 years with dominant height up to 14 meters was found on the most productive sites. In North America the wood is mostly used for poles and fence-wood and is appreciated for good strength and rot-resistance. In Alaska, the tamarack has been severely attacked by the eastern larch beetle (*Dendroctonus simplex*) which has killed 3 millions of hectares there (Seybold *et al*. 2002). Serious damage on tamarack has also been caused by the large larch sawfly (*Nematus erichsonii*) and larch sawfly (*Pristiphora erichsoni)* on large scale both in northern United States and Canada (Johnston 1990). If repeated in years, the attacks of the larch sawflies could kill the trees.

***Larix lyallii* – Subalpine larch**

This species forms the tree limit in parts of the Rocky Mountains and the Cascade mountains. It has a small distribution between Lat. 45-52° N on altitudes between 1500 and 3100 m. It is among the smallest of the larches. The tree seldom reaches over 15 m in height and 50 cm in diameter but has a relatively good stem form even on the highest altitudes. Its distribution coincides with the Western larch but the two species seldom grow together, subalpine larch grows most often higher up the mountain side than Western larch. Natural hybrids between the species have been registered (Carlson and Blake 1969). Semerikov and Lascoux (1999) found low genetic variation within this species, a feature which could be explained by the narrow ecological niche of the subalpine larch. Subalpine larch is not an important timber tree, it grows on too high altitudes for being that. It is mostly appreciated for its beautiful autumn colours and is called golden larch by mountain people. It has not been tested in any larger scale in Sweden or in Finland (Martinsson and Winsa 1989; Ruotsalainen 2006). Schotte (1917) suggested trials of this species in the Scandic Mountains.

***Larix occidentalis* – Western larch**

Western larch has a relatively small natural range in the Cascade- and Rocky Mountains in the Northwest USA and British Colombia between latitudes 43° N and 52° N on altitudes between 600 and 2200 m. This species grows tallest of all the larches in the world, heights up to 70 m have been recorded and it is appreciated for its strong durable wood. It grows in dry, cold, high altitude areas often in mixed stands with Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), Engelmann spruce (*Picea engelmanni*) and Lodgepole pine (*Pinus contorta*). Western larch has not been tested in large scale trials in Sweden, but small trials have revealed difficulties in adaptation to climatic conditions. Frost damage and larch canker have caused the poor results (Simak 1971; Martinsson and Winsa 1989). Due to its southern range it might be an alternative only at higher altitudes in southern Sweden, that is, the highlands of the county of Småland.

1.4 Biology and ecology of larch

Larches are one of only five genera of conifers that are deciduous. The other four genera are *Taxodium*, *Pseudolarix, Metasequoia* and *Glybostrobus*. Larches are monoicous in that they have separate male and female flowers existing on the same tree. The female flowers are often located in the upper part of the tree while male flowers are more frequent lower in the crown. Larches (as their subfamily members *Cedrus* and *Pseudolarix*) are characterised by their two forms of shoots. The long shoots have widely spaced needles and the short shoots needles in dense clusters (Nitzelius 1958).

The cones are initiated on the short shoots during summer and overwinter as preformed buds. Pollination occurs in late winter or early spring the following season and cones mature in the late summer (Owens 1995). The cones stay for 2-3 years on the tree before falling off. The pollen has rather high weight and lacks air sacs, a trait that *Larix* and *Pseudotsuga* share. The pollen dispersal is therefore limited compared to most pine and spruce species. The seed in natural stands have generally low germination capacity, often not more than 20-50 %. Seed from seed orchards are larger and have higher germination capacity (Pétursson 1995) than seed from natural stands.

Eriksson *et al*. (1967) studied the seed production in three larch species (European, Japanese, and Siberian larch) when grown in Sweden and found one probable reason for the generally low seed production in larch. The meiosis was found to be sensitive to temperature fluctuations during winter. In *Larix sibirica*, southern located populations had more damaged pollen mother cells than northern due to warmer weather during important stages in pollen development.

Chromosome number in all larch species is n =12. As in Scots pine, (Wang 1992) interspecific hybrids are often fertile.

The deciduous trait makes the larches unique among conifers in the northern boreal forests. Climates with pronounced seasonality should favour a deciduous habit. However, the evergreen conifers dominate much of the boreal forests. Only in the harshest areas in interior Canada and Siberia do the larches prevail over the evergreen conifers. One big advantage that the deciduous larches have over the evergreen conifers is that by shedding their leaves during winter they avoid desiccation (winter drought) which is a concern for the evergreen conifers (Givnish 2002).

Larches are pioneer tree species, adapted to regenerate after fires. The different species have evolved various ways for this adaptation. Some species have unusually thick bark, which can constitute 20-30 % of the stem volume and form an effective protection against fires. Others like *L. cajanderi* have cones that open up and drop their seeds quick after the fire (Abaimov *et al.* 1998).

The light demand is high, even more so than in Scots pine. The Russian larches differ to some extent in their demand for light. *Larix cajanderi* is the most light demanding of the Russian larches. Within species, northern populations have been shown to be more light demanding than southern (Abaimov *et al*. 1998).

The deciduous trait gives some important features to a larch stand. More light and snow reaches the ground compared to an evergreen forest. The thicker snow cover inhibits the ground frost from going so deep and the soil heats up more rapidly in the spring, which favours growth conditions. Larches have impacts on the upper soil horizons and ground flora of the stand that differ from evergreen conifers. Kardell and Lindhagen (1997) found that larch alters the conversion of nutrients in the ground in a way that Norway spruce and Scots pine not do; earthworms were found in the top soil and the mineral soil was mixed with the humus layer. In a small investigation comparing the influences on soil and ground flora of larch and Norway spruce, Ivarsson and Wiklund (1994) showed that the conversion of the humus layer was faster, the pH higher in the soil, and growth faster in the larch stand.

A forest condition that has drawn attention recently is the role of deciduous forests compared to evergreen forests in global warming. During winter when there is snow cover, the albedo is much higher from a broadleaved deciduous or a pure larch stand compared to an evergreen forest, because more solar radiation will be reflected from the snow beneath the leafless deciduous stands and consequently reduces the effects of heat absorption and global warming (Givnish 2002, Kharuk *et al*. 2009).

1.5 Why the larches are of interest to the Swedish forestry

A tree species grown outside its natural range should according to Zobel *et al*. (1987) be defined as an exotic tree species. Given that larch species have not occurred naturally in Scandinavia since just after the last ice age it should according to this definition be regarded as exotic. However, if one takes a longer perspective it has been proven that larch has belonged to the Scandinavian flora both before the last ice age and also in the post-glacial and early Holocene (Kullman 1998, 2002). Ruotsalainen (2006) discussed on the view on what should be regarded a native or an exotic species and underlined that this separation only holds true for a given point of time. In longer perspectives and changing climates it is only an academic question.

Despite the status as non-exotic given by the Swedish forestry commission, the Russian larches are nonetheless influenced to some degree by some of the same problems as other exotic species. When trees are transferred to new environments there are always some risks associated. Adaptation to climate, weather, new pests, and diseases may be involved. As well, some of the pests and diseases of the exotic may inadvertently be introduced and affect native species. We must also mention the possible spread of the exotic larch outside its plantations and influence on the native species and forests. There must be some compelling ecological, and/or economic benefits for an exotic to justify the extra risks of introducing a new species (Ilvessalo 1927; Karlman 1981; Zobel *et al*. 1987).

Potential benefits of Russian larches

Larches and in particular Russian and Siberian larches in northern Fennoscandia are interesting for, among others, the following reasons:

-It has good production rates. According to Hakkila *et al*. (1972), referring to Vuokila's production studies (1960), Siberian larch can on favourable sites produce saw-timber-size trees in half the time required for Scots pine or Norway spruce. Swedish trials have shown a 20-25 % higher yield (m^3 per ha over bark) than Scots pine on more fertile sites. On poor sites, however, the production is lower than Scots pine (Edlund 1966; Martinsson 1995). The thick bark of larch reduces its superiority over Scots pine if volume under bark is considered.

-It has high durability and high density of the wood with its high amount of heartwood. Siberian larch and Russian larch today are used in many outdoor environments instead of chemically treated wood. The amount of heart wood is about 80 % in a mature larch tree compared to 40-50 % in Scots pine. Its wood has a density which is about 20-25 % higher than Scots pine (Rijsdijk and Laming 1994) and holds a higher density with wider year rings than spruce and pine, of which the density declines more rapidly with increasing ring widths. Heartwood in Siberian- and Russian larch with up to 3 mm wide year rings can have a density over 600 kg/m3, which is more than in slow-grown Scots pine. (Karlman *et al*. 2005). Edlund (1966) compared Siberian larch with Scots pine and Norway spruce and found the density of the larch wood, at ring widths between 2-3 mm, to be 30 % higher than in Scots pine and 50 % higher than in Norway spruce.

-It is relatively resistant to pests and diseases. Russian larch has been growing here for more than 150 years. No major pest or disease has hit these plantations yet. Seed sources like Raivola or the Lassinmaa seed orchard seed (*L. sukaczewii*) from Finland (originating also in Raivola) have been showing a remarkably wide ecological niche (Mikola and Vakkari 1995). In our test series in Sweden Lassinmaa seed source survives well in southern Sweden (Lat. 57°N) as well as in northern Sweden at latitude 65°N. It grows well in Finland as well as in a more maritime climate in Iceland.

-It is fairly wind firm. The root system penetrates deeper into the ground compared to Norway spruce. Young stands could, however, be sensitive to storms. Being deciduous, it withstands high snow pressure and is less likely to be damaged by snow breakage (Edlund 1966).

-It is a probably a better choice than spruce on root rot infected land in northern Sweden. This statement is based more on theories than on facts. In theory, larch with an early development of heart wood should withstand the s-form of root rot in the same degree as Scots pine and should as Scots pine be a better alternative than spruce. There is, however, lack of experience in practical trials.

-It has the capacity to produce well in harsh environments. One example is in Tärnaby, Sweden (Lat. 65°43´N, elevation 540 m), where Russian larch (provenance Arkhangelsk region) at a site with a temperature sum of 535 d.d. has produced more than 5 m3 sk/ha (forest cubic meters) per year during 100 years (Martinsson 1995).

-It is resistant to some pests that have infected and in some areas plagued young and middle-aged *Pinus sylvestris* stands. Some examples are *Gremmeniella abietina*, *Melampsora pinitorqua,* and *Endocronartium pini* (Scleroderris canker, pine twist rust and Scots pine blister rust) (Eidmann and Klingström 1990).

-It adds diversity to the species poor forest flora of Fennoscandia and some might say beauty to landscape especially during fall and spring.

-Larches with their fast juvenile growth can be used as shelterwood for secondary, shade tolerant tree species like Norway spruce. In southern Sweden, hybrid larch has been used as a shelter tree for beech (*Fagus sylvatia*) (Larsson-Stern 2003b).

-Each single tree has good height and diameter development, which will mean a cheaper harvesting provided that stems are satisfactory straight (Edlund 1966).

-It gives several options for management to the forest owner. There are many choices of what products you could obtain from larch forests. An early first thinning is possible in which fuel wood could be taken out. One could produce timber and fuel wood. In the future products from bark and extractives could become important.

Potential problems with Russian larches

-Sensitivity to frost during spring and fall. Although very cold tolerant when fully hardened, larch could be sensitive to frost during time of bud burst and bud set when poorly adapted to the site. Also could sudden mild spells during winter break the dormancy and make trees vulnerable for frost (Eysteinsson 1995a).

-Straightness of the tree stem. A curved or sinuous growth form is often seen in larch stems. There is difference between the species but also big differences within species. This characteristic is genetic to some extent, but environment can also have a pronounced effect. Poorly adapted provenances have worse stem shape than climatically well adapted seed sources. Improvements can be made by breeding and selection programs (Stener *et al*. 2002).

-Branch quality traits. The branches of larch are frequent and irregular and can be a problem. The demand for light makes the branches die quite early but the dead branches often remain attached to the stem for a long time (Bergstedt and Lyck 2007).

-Variable wood quality that requires modified methods for treatment. Sawing of larch wood demands a special technique, otherwise the saw blade will glue together by the high resin content (L-Å Falk personal comm., 2005). Drying of larch wood also is more complicated than in Scots pine or spruce. It takes longer time and will therefore be more expensive (Terziev and Zamaratskaia 2007, Heikkonen *et al*. 2007).

-The wood contains lot of water soluble extractives which make it difficult to mix with pine or spruce in the pulp industry (Hakkila *et al*. 1972). In this respect, *Pinus contorta* which can be utilized as pulp without these problems is easier for the pulp industry to deal with. However, Hakkila *et al*. (1972) also found that larch had some good qualities for the pulp industry, namely, higher density of wood compared to Scots pine and Norway spruce and a tearing strength superior to the domestic tree species.

-There is less knowledge available about this tree than for Norway spruce and Scots pine. Although a lot of research on larch has been done in Fennoscandia through the years it can of course not be compared with all research done on Norway spruce and Scots pine.

-Future climate is predicted to become warmer and in Sweden more maritime. Temperature rise will be greater during winters than summers (IPCC 2007). Larch is basically a tree for continental areas even if some areas in Russia have a maritime influence. However, since Russian larch (*L. sukaczewii*) has grown well on Iceland with a much more maritime climate than even the worse prognoses have foreseen for Sweden, correct seed sources may well tolerate warmer winters here. Because of the so called 'genetic aftereffects' that is, that temperatures during seed maturation can affect the phenology of the progeny, an effect which has been shown in several tree species, including within the *Larix* genus (Greenwood and Hutchinson 1996), seed orchards in the semi-maritime climate in Finland produce offspring better suited to maritime conditions than seed collected in natural stands in Russia. Hence, the location of seed orchards could be very important.

1.6 Climate, a comparison between Russia and Sweden

Russia has mostly a strongly continental climate. The great land mass and northern latitudes, more than half of the country is situated above the 60th latitude, create a very harsh continental climate, especially in the interior Siberia. The degree of continentality increases moving eastwards in Russia and reaches a maximum in the Lena river basin, where the difference between mean temperature in January and July is more than 60°C.

The climate in the Russian Far East is more maritime but still with cold winter temperatures even at lower latitudes. On Sakhalin for example, at latitude 50°N at an altitude of 180 m, mean temperature for January is -20.5° C. The influence from the warm currents of the Gulf Stream in the Russian northwest is demonstrated by the relatively warm winters in Murmansk at Lat 68°58´N, where the mean January temperature is -10°C (World survey of Climatology 1977).

The precipitation in Russia is rather low in most areas. The areas in Russia that have a climate most resembling the Swedish climate is the Northwest Russia, with its maritime influence and to a minor degree also the Far Eastern Russia shore bound area around the Sea of Okhotsk, but, with much lower winter temperatures.

The Gulf Stream stretches around the northern point of Scandinavia and parts of the Barents Sea are ice free during winter. Large parts of the White Sea are usually covered with ice from December to April but the last 30 years has witnessed a rapid decline of sea ice in this area (Rodrigues 2008). Since the 1970´s the heating trend in northern Eurasia has been most pronounced during autumn, winter and spring (MacDonald *et al.* 2008).

Comparing the climate at similar latitudes in European Russia and Sweden show this trend:
The mean temperature in July is higher in Russia than in Sweden and the mean temperature in January is lower in Russia (Simak 1979). The transition between the seasons is faster in Russia than in Sweden, this increasingly so as the climate becomes more continental. When transferring provenances from Russia to Sweden, this will have an influence on the timing of growth initiation in spring and to some extent also on the growth cessation in the autumn. What implication this will have for the different provenances and their adaptation to Swedish conditions will be discussed in Paper I below with special reference to frost tolerance.

Sweden, as most of Scandinavia, has a semi-maritime climate with rather mild winters, for being so far north. It is the warm currents of the Gulf Stream that give this effect. The interior parts of Sweden, however, have climates with features that are more continental, and the strongest continental climates are found in the far north.

1.7 Site requirements

Wahlgren (1916) wrote that larch is a tree for the hillsides. Experiences since then confirm Wahlgrens theories. It can not compete with Scots pine on poor dry sites (Edlund 1966; Remröd and Strömberg 1978, Martinsson 1995, Hagman 1995). In Finland, fertile sites are recommended for best possible yield. Slopes with moist and deep mineral soil are considered best possible site conditions there (Viherä-Aarnio and Nikkanen 1995, Hagman 1995). According to Mayr (1909), larch could develop well on poor sites the first decades, but then the growth declined fast.

Sufficient moisture is needed in the soil because of high rate of transpiration of the larches. However, waterlogged sites are not suitable for larches, especially Russian and Siberian larch. In Iceland, *L. sukaczewii* is used on bare volcanic soils and is the species that tolerates this type of sites best (Eysteinsson 1995a). Larch grown in large, pure stands develops a favourable mycorrhiza, and this enables efficient nutrient uptake from soils which are low in nitrogen but rich in minerals.

As a simple rule, larch should be planted on billberry (*Vaccinium myrtillus* L.) and better sites. Availability of moving ground water seems to be more important for the productivity of a larch stand than for spruce or pine. As mentioned above, larch can produce well on high elevations. A prerequisite is that the soils are fertile, on poor sites its production rate is inferior to Scots pine (Martinsson 1995).

Larch should be avoided on sites which are exposed to strong winds. The risk of storm windfall and stem breakage in winter is smaller than for Norway spruce because it then is defoliated. It has in addition a deeper root system. The stem shape of the trees is, however, negatively affected by strong winds (Wahlgren 1916).

It seems that larch has more of an advantage compared to other conifers on eastern, northern and northwest aspects (Rosenberg 2002). This could be an effect of the larches adaptation to harsh environments by an efficient use of nutrients and light (Gower *et al*. 1995). Larch saplings and seedlings could also be sensitive to drought, thus in southern or southwest aspects, drought might be a problem (Schabel *et al*. 1995). The combination coarse sandy soils and southern, southwest exposition should especially be avoided when planting larch.

1.8 Silviculture

Planting in scarified tracks is the most used regeneration method in the Nordic countries (Martinsson and Lesinski 2007). With their high requirement for light, larches are sensitive to shading from vegetation. Planting should be done early in the season before the buds have started to sprout, or alternatively in late autumn when the seedlings have lost leaves and cold-hardened for winter. Planting of 1-year-old, containerized seedlings, works well in northern Sweden. It is important that there is a balance between the size of the root system and the green tissue of the seedling, too much foliage makes the seedling more sensitive to drought. Bigger and older planting material, which is commonly used in southern Sweden, should be replanted in the nursery to allow root system to develop enough. The effect of scarification on the survival of larch seedlings was studied by Oskarsson and Ottósson (1990) in a trial on southern and northeast Iceland. They found a weak positive response of the larches to site preparation. Natural regeneration can work if the mineral soil is exposed. Simak (1979) reported that the procedure in Russia is to leave small groups of larch seed trees, this to achieve cross pollination for better seed quality.

Direct seeding has also been tried with various results. Pétursson (1995) found that microsite preparation, a sowing method in which the seed is put in small inverted pyramidal depressions in the soil (Bergman and Bergsten 1984, Bergsten 1988), significantly increased the number of surviving saplings compared with sowing direct on scarified spots. However, a major disadvantage of direct seeding of larch is that the methods works best on poorer sites where larches generally don't grow so well. On more fertile sites and sites situated in slopes, vegetation and erosion caused by rain or snow melting, could create large problems to using direct seeding. Lastly, at this point in time the larch seed is so expensive that the method has no economic advantage over planting.

All larches are light demanding tree species that need to be pre-commercially thinned and thinned at regular intervals to reach maximum individual growth. The crown of the tree is recommended to be about 50 % of total tree height up to 40-50 years of age (Martinsson and Lesinski 2007). The fast juvenile growth can on the other hand also be a problem in that the branch diameter increases and that the proportion of juvenile wood gets large. The branches of larch generally stay attached for long periods. Pruning is recommended if the desire is to produce valuable timber products. Larches are well suited to be pruned, since the risk of attack by fungi is small and the healing of the stem wound is quick (Rosell 1988). The slower juvenile growth which follows a pruning also increases the quality of the wood.

An interesting result was reported by Parent and Mahoney (2008) who found that by regular thinning the density of Western larch wood actually became higher. The explanation given was that each tree had more space and water supply during the warm period in summer, and hence the growth of the late wood increased making the proportion of latewood greater than in an unthinned stand, thus increasing wood density. A regular thinning regime also increases the wood quality by reducing the variation in growth ring dimensions. This will make the wood more homogenous and the internal tensions decrease in drying and further treatments, making it easier to work with.

Thinning schedules for Siberian larch have been developed by Vuokila *et al.* (1983, see Fig. 5 below):

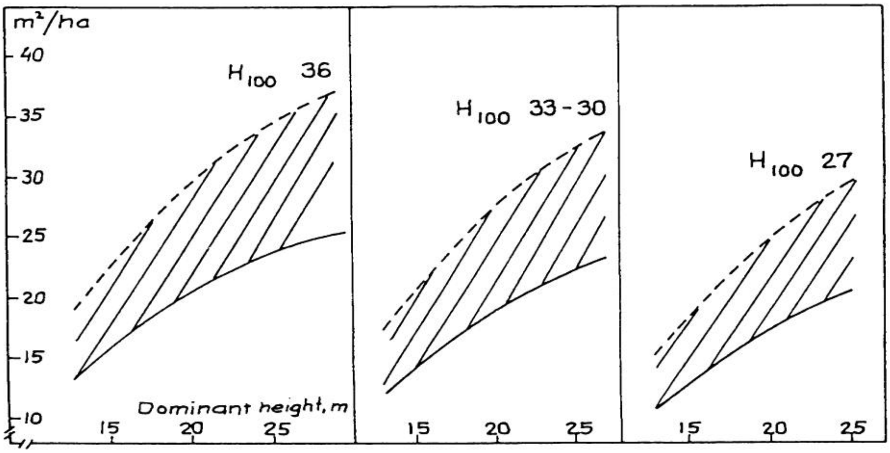


Fig. 5. Thinning schedules for Siberian larch according to Vuokila *et al*. (1983). The figure describes three different larch site indexes, L 27 (dominant height 27 m in 100 years), L 30-33 and L 36. The dashed line indicates the basal area at the latest point of time when thinning should be done.

On the most fertile sites (L 36) the basal area should not pass 30 m^2 when the dominant height is 20 meter, which will be reached at about 35-40 years of total age (Martinsson 1995). On lower site indexes (L 27) the basal area should not pass 18 m^2 at dominant height of 15 meters when total age is about 45 years.

1.9 Damages by insects, pathogens, animals and weather

Insects

The most serious damaging agent in young seedling is the pine weevil (*Hylobius abietis* L.). It probably damages larch at the same scale as Scots pine. Chemical treatment of seedlings is recommended. Gall aphids (*Adelges laricis*) are reported to have caused reduction in growth in larch plantations. In a provenance trial in Stugun in Jämtlands county (Sweden), *Larix sukaczewii* provenances from the southern Ural mountains were heavily attacked by this insect. The insect did not kill the trees, but serious growth reductions were recorded. Provenances of *L. sibirica* and Swedish seed sources of *L. sukaczewii* were not as seriously attacked in the same trial (Simak 1979). Also in Finland attacks of this insect have been causing reduction of growth and death in young Siberian larch plantations, especially in northern Finland (Viherä-Aarnio and Nikkanen 1995).

It seems like resistance to this insect varies a lot between populations and also within populations of larch. Blada (1995) studied the genetic variability in *Adelges* *laricis* resistance in European larch and found great variations in susceptibility between the most resistant and most susceptible clones. The heritability was also high for this trait implying good chances of improvement by breeding.

The larch sawflies (*Pristiphora erichsoni*, *P. laricis* and *P. wesmaeli*) could also damage larch cultures. The heavy attacks on tamarack in North America were mentioned before, but these insects attack also other larch species. Alden (2006) reported attacks by the larch sawfly on *L. sibirica* and *L. sukaczewii* when grown in Alaska. Serious attacks are uncommon, but during warm summers, local mass invasion could occur. Trees growing on more fertile sites generally have better chances to recover and are often not seriously damaged by the larch sawflies (Eidmann and Klingström 1990). Traces of attacks by this insect have been noticed also in the young field trials of Russian larches evaluated in this thesis. No serious damage has occurred, however.

Pathogens

The most serious pathogen on larch is the larch canker (*Lachnellula willkommii* Hartig). This fungus causes severe damage to European larch when planted in south-western Sweden. Scottish nonautochtonus seed sources are according to Schotte (1917) more resistant to this pathogen than other provenances. Japanese larch is resistant to this pathogen and hybrid larch (*L.* x *eurolepis*) has inherited the resistance and is now the most common choice of larch species in southern Sweden (Larsson-Stern 2003a). Russian and Siberian larch are also sensitive to this fungus but serious attacks have not been registered in northern Sweden. In Iceland, Russian larch is considered more resistance to both larch canker and conifer canker than Siberian larch. Eysteinsson and Skúlason (1995) stated that this was probably due to the better tolerance to cool summer conditions that Russian larch has, compared to Siberian larch. Larch canker thrives in moist and cold conditions and it is therefore important to avoid low sites where cold air and fog gathers during night in order to reduce damage by larch canker (Eidmann and Klingström 1990).

Root rot (*Heterobasidion annosum*) can infect larch. Heterobasidion root rot has two different forms in Sweden, the S-type, which attacks Norway spruce and is present in the whole country and the P-type which attacks also Scots pine, larch and several broadleaved trees (Eidmann and Klingström 1990). Kurkela (2000) studied *Heterobasidion* in young Scots pine and Siberian larch plantations in Finland and found Siberian larch to be more susceptible to the P-type than Scots pine. Also European, Japanese and hybrid larch have been seriously attacked by the P-type root rot in experiments in southern Sweden (Vollbrecht *et al.* 1995, Vollbrecht and Stenlid 1999). The P-type does, however, not exist in northern Sweden, its northern boundary is the river Dalälven (Eidmann and Klingström 1990), and thus larch should not be attacked by this P-form when planted in northern Sweden. Whether or not the S-type attacks the Russian- or Siberian larch in northern Sweden is not well known. Research is obviously needed in this field.

Honey fungus (*Armillaria* sp.) can damage young stands of larch. This has been recorded also in the southern most trials included in this thesis. Five-year old trees up to three meters high could die within a year if attacked by this fungus, but only trees with reduced vitality are attacked. Drought, frost injuries, and poor root development are often causes of infection (Eidmann and Klingström 1990).

Animals

Fraying by moose, roe deer, and reindeer may cause damage to young larch plantations. It seems that fraying is a more serious problem than grazing (Edlund 1966). During winter when grazing damage on Scots pine is most frequent, larch is not as attractive fodder, owing to the shedding of its needles, Casual observation suggests that small groups of trees are more sensitive to attacks than large plantations The attacks seem to occur more by chance in focussed sites rather than by systematic grazing on large larch plantations (Martinsson and Lesinski 2007).

Smaller mammals such as hare, voles and even squirrels are reported to have caused damage to larch plantations (Edlund 1966). Voles can cause damage to young seedlings by eating the bark. When the stems reach 5-6 cm in diameter the risks decrease.

Climate and weather

Frost damage is quite common in larch. Compared to Scots pine, the Russian larches are more sensitive to frost. In this respect larch ranks on the same level as Norway spruce. However, when adapted to a site, the larches of Russia are extremely cold tolerant (Sakai and Okada 1971). As mentioned above *L. gmelinii* forms forest stands further north than any other tree species on earth. However, the importance of avoiding frost prone sites when planting larch should be remembered. Wind damage can also injure larch stands, especially younger stands that have been thinned recently. Mature stands are generally wind firm. Zetterberg (2007) compared the effect of the heavy storm "Gudrun" that hit southern Sweden in January 2005 on storm damage in larch (European-, Japanese- and hybrid larch) and Norway spruce. His study showed that larch was less damaged by the storm than spruce, although the difference was not significant. Unlike Norway spruce, in which the risk of storm felling increased with age and height of the stand, no such relationship was seen in larch. Older, shelter trees of larch was not injured at all in this study.

1.10 Global warming and possible effects on the Russian larches

A general opinion among climate researchers is that we are heading for a warmer climate (IPCC 2007). An important question is then how the larches introduced to Sweden will be affected by this. Historically the occurrence of larch has varied and climate changes have definitively contributed to this. As mentioned above, larch was one of the first colonizers in the Scandinavian mountains after the last glaciation. The last known occurrence of larch in Scandinavia is dated to 7500 years B.P (Kullman 1998). It is possible that these findings not represent the temporal limit of larch, but as they coincide with a changing climate, the climate became more oceanic with decreased seasonality, Kullman suggests this as an explanation for the disappearance of larch in the Scandinavian Mountains. The climate of Fennoscandia has become increasingly more continental since then (Giesecke *et al*. 2008) and the climate during the past centuries has probably been more suited for larch than during the oceanic period of the Holocene climatic optimum.

Global warming, if realized according to UN's climate report (IPCC 2007), will have a big impact on the growth and distribution of the northern boreal conifers. Growth will generally increase due to longer growing seasons and species distributions will change. Some species are predicted to expand their distributions and abundance whereas others may suffer reduced ranges and reduced ability to compete.

Predicted climate warming in Sweden during the 21st century

The following predictions are made by the Rossby meteorological science center. They base their models on the IPCC climate report from 2001 (Kjellström 2006). They set up two different scenarios for northern Sweden: a) *Higher emissions* CO_2 *scenario* with winter temperatures increasing with 4-6°C and summer temperatures with 2-4°C and b) the *lower emission* CO_2 *scenario* with winter temperatures 2-4°C higher and summer temperatures 1-2°C higher.

According to these scenarios the future climate of northern Sweden are projected to be more maritime with larger temperature rise in winter than in summer.

Global warming's effect on growth and distribution of trees

The changing climate will have both short term and long term effects on trees and their distribution and growth. In Sweden, Bergh et al. (2007) predicted that growth of pine, spruce and birch generally would increase, especially for spruce and birch in the northern part of the country. On short terms the greatest problems in northern boreal forests will probably be connected to phenology (timing of bud burst in spring and initiation of growth cessation in autumn) and frost damage. Warmer weather during late winter and early spring promotes earlier bud burst and if followed by cold weather the risk of frost damage will increase (Hänninen 1991). The risk of insect damage should also increase. Warm winter temperatures is seen as one of the explanations for the mass invasion of the Mountain pine beetle (Dendroctonus ponderosae) in western North America (Hamann and Wang 2006), killing 13 million hectares of *Pinus contorta* in British Columbia alone (B.C Ministry of Forests and Range 2009).

On longer terms warmer climate will alter the distribution of species. In boreal forests, some species will migrate north but risk to be outcompeted in their southern range of distribution (Chuine *et al.* 2004, Tchebakova *et al*. 2005, Leng *et al.* 2008). Also changes in altitudinal distribution among species are expected. Kharuk *et al*. (2009) studied the response to climate change of *Pinus sibirica* and *Larix sibirica* growing in the Tannu-Ola ridge in southern Siberia and found the growth and regeneration of the former species to be more favored by a warming climate, thus Kharuk *et al*. draw the conclusion that this will be leading to a substitution of larch by Siberian pine as dominating species in the investigated area.

Experiences from Iceland have shown that Siberian larch could be sensitive to warmer winter climates with incoming warm air during the dormant stage. Trees could initiate their bud burst and if weather gets cooler get damaged by frost. Therefore planting Siberian larch in southern Iceland has been avoided. Other species like the Sitka spruce (*Picea sitchensis*) could benefit from milder winter climates (Sigurgeirsson 2006).

In the most southern of the sites studied in this thesis (Österbymo, Paper II), *L. cajanderi* from Magadan, an area in the Russian Far East with a very cold winter climate, started budburst during a sudden warm spell in February 2007. The trees did not die but their top shoot was damaged by frost and the growth the following growing season was inhibited (Martinsson and Lesinski 2007).

Among larch species, European larch (*Larix decidua*) often suffers from autumn frost when planted in northern Sweden (Simak 1969). Temperatures are generally too low during autumn for a complete hardening of top shoots. Warmer climate would in this case probably decrease the risk for autumn frost in European larch. The same pattern would be expected for more southern provenances of Siberian larch adapted to shorter day lengths and warmer climate during maturation of the top shoot.

Global warming - implications for choice of provenances

Rehfeldt *et al*. (1999) studied climate transfer functions for introducing Eurasian larch species into Alberta, Canada. They found five climatic variables most important for a successful introduction:

- mean annual temperature
- degree days <0 °C
- mean temperature in the coldest month
- ratio mean annual temperature/mean annual precipitation mean annual temperature
- annual summer-winter temperature range (continentality)

Survival and growth would, according to their results, be best by matching the provenance climate to the planting site climate.

As the climate of Sweden today generally is semi maritime and if global warming, turning it to be even more maritime, larches from semi-maritime areas are likely to be best suited for the future climate. Raivola larch from the Karelian Isthmus or Finnish and Swedish seed orchard seed sources close to the Baltic Sea or Estonian grown larch should be more suited than larch from strongly continental areas as central Siberia or from areas east of the Ural Mountains.

Provenances from the Arkhangelsk area with its maritime influence from the White Sea could be suitable for northern latitudes in Sweden. Thus material collected in the Russian-Scandinavian larch project will be of importance for future selection and breeding for Siberian larch, especially for harsher sites in Scandinavia.

As a summary of this discussion about the impact of global warming on the performance of the Russian larches in Sweden the following predictions could be made:

- In spite of a longer growing season and an increase in temperature sum which promotes growth there are additional problems connected with an increased temperature. For Eurasian larches this is mainly connected to acclimation to the timing of bud burst in spring. A warming climate will effect trees to start earlier in the spring and the risk for spring frosts increases.

- Future climate will probably favour larch populations adapted to milder winters.

- Larch from strongly continental areas are more likely to be damaged by frost when planted in Sweden.

- A warmer climate may favour more southern Russian larch provenances, including hybrids between Russian larches and European larch or Japanese larch, rather than northern Russian larch provenances.

To prepare for climate change, a wise strategy is probably to maintain a high genetic diversity in the larch material for Sweden. Strains of different provenances, placed in different climatic regions might be one, as well as a range of hybrids of selected species and provenances. The general objective is to preserve a wide range of genetic diversity as a safeguard against devastating losses to unforeseen changes in climate.

1.11 Earlier research on larch in Sweden

Much of useful insight can be obtained from early research on larch in Sweden. In 1754, Carl Linneus in his book “Tankar om nyttiga växters planterande uppå de Lappska fjällen” (Thoughts on useful plants for planting in the Lappish mountains) suggested that larch (*Larix* spp.) from the Alps and Siberia together with Siberian stone pine (*Pinus cembra* v. *sibirica*) should be planted in the mountains of

Lappland. Gunnar Schotte wrote his thesis on larch in 1917. The thesis was titled “Lärken och dess betydelse för svensk skogshushållning” (The larch and its importance in Swedish forest economy) and was written in Swedish with a 26 page English summary. In this thesis of more than 300 pages Schotte included 294 Swedish references on larch and more than 300 references from other countries. Schotte described the species planted in Sweden at that time. The main focus was on European larch but Siberian larch was extensively covered. Japanese and the American larches were also discussed.

Schotte considered Siberian larch suitable for the middle and northern part of Sweden. In southern Sweden attacks of larch canker were common in Siberian larch. Schotte advised against using larch on the poorest sites owing to low production there. On middle rich sites, mixed stands with Scots pine and pruning of larch was considered a good alternative to avoid larch canker. The stem straightness in Siberian larch was considered better than the average European larch provenances, more comparable to the straight growing European larch from Scotland. After this early boost in larch research, the interest declined, and it was not until the 1950’s that research in larch started again on a larger scale. A brief recapitulation of some of the more important findings in addition to those in Schotte’s large monograph follows.

In Fennoscandia, Finland has the most experience in cultivating Siberian larch. Finnish researcher Blomqvist (1881) was the first to discuss the importance of provenance for successful silviculture of Siberian larch. Blomqvist performed comparative sowing experiments at the forestry school in Evois in southern Finland and found different behaviour in three different seed sources of European and Siberian larch. The best development was found in material originating from the Raivola stand.

Hemberg (1899) made several trips to Russia to study larch in its home territory and described the site conditions for natural larch stands. Langlet (1938) considered different behaviour of different larch provenances, Wiksten (1962) studied the production of Siberian larch, and Erik Edlund (1966) wrote a broad study on Siberian larch relative to its adaptation in northern Sweden and suitability as raw material for the forest industry. Remröd and Strömberg (1978) also did production studies of Siberian larch.

Eriksson *et al*. (1967, 1970) studied seed germination and factors disturbing pollen production in European, Japanese, and Siberian larch. Milan Simak (1970) wrote about photoperiodic responses in different larch species, and Simak (1979) was the first to write specifically about *L. sukaczewii* and its suitability for the conditions in northern Sweden. C-L Kiellander (1958, 1965) did important work in European and hybrid larch. Fritz Bergman crossed Russian larch with European and Japanese creating larch hybrids for northern Sweden (Jonsson 1978). These hybrids have now been evaluated after 50 years and show impressive production (Paper IV).

Owe Martinsson (1995a, 1995b), studied the production in *L. sukaczewii* and *L. laricina* and was the initiator of the international Russian-Scandinavian larch project which, among other things, has lead to this thesis and a book about the Russian larches, their history, ecology, silviculture and use in Scandinavia (Martinsson and Lesinski 2007). Marie Larsson-Stern (2003a) presented a thesis on hybrid larch *L. eurolepis* and its performance in southern Sweden and found it to be an interesting complement to Norway spruce on better sites in southern Sweden. Important findings about characteristics of larch wood have been reported by Björkman (1944), Rosell (1988), Bergstedt and Lyck (2007), Terziev and Zamaratskaia (2007), and Gärds and Martinsson (2007).

1.12 Genetics and breeding of larch, larch hybrids

Initial breeding activities

Breeding of larch started in Sweden during the 1940's. Inspired by works from Henry and Flood (1919), describing fast growing larch hybrids between spontaneous crossings between *L. decidua* and *L. kaempferi,* and the Danish Syrach Larsen's (1937) thesis showing examples on the productivity of these hybrids in Denmark, the Swedish Society for Forest Tree Breeding established provenance trials in southern Sweden. Kiellander (1958) summarised the results up to that point of time. Hybrid larch had shown both better height growth and better resistance to larch canker than European and Japanese larch. Later Kiellander and Lindgren (1978) studied resistance to canker in six stands in south-western Sweden and found *L x eurolepis* to resist larch canker almost as well as *L. kaempferi* and much better than the canker prone *L. decidua*.

Kiellander (1958) listed pros and cons considering breeding of larch. Beneficial traits in the genus were:

- Larches have a strong variability in stem quality characters which makes it easy to choose plus tree stands.
- An early production of cones, larch can be fertile as early as 5-6 years of age.
- Vegetative propagation is easily done in larch.
- Its fast juvenile growth will reveal differences in growth between populations at an early age.
  - Larches easily hybridize. The prospects for utilizing hybrid vigour should therefore be good in the species.

Unfavourable traits in the species were:

- A weak pollen production and a high proportion of empty seeds.
- The cones of some of the larch species are hard to extract.
- Saplings and seedlings could be sensitive during transplanting.
- Sensitivity to fraying especially from roe deer. Fencing is often necessary.

Larch seed orchards in Sweden

Selection of larch clones for tree improvement purposes was done during the 1940's and early 1950's. Twenty-one larch seed orchards were established between 1956 and 1964, a majority of them being orchards with different larch hybrids; Crossings between European and Japanese larch being the most common, but also crossings where *L. sukaczewii* is one of the parents (Hannerz *et al*. 1993).

Plus trees were selected in Swedish, Danish and Finnish provenance trials and plantations. Often the origin of the plus trees is not known. Most of the Russian larch material originates from the Arkhangelsk region and the Ural Mountains and also seed sources from the Raivola stand. The design of the larch hybrids seed orchards was done in a special way to maximize the production of hybrid seeds. Only one self sterile clone of one of the species functioned as mother trees. Pollination was done with several different clones of the other species. Seeds were only harvested from the mother clone (Hannerz *et al*. 1993).

The seed orchards have generally given poor results; an exception is the Maglehem seed orchard in south Sweden (Larsson-Stern 2003b). According to Lindgren (1982) a limited interest from the forestry sector to use the produced seed has lead to bad maintenance of the orchards with consequences also for their seed production.

In a series of experiments, Eriksson *et al*. (1967; 1970) searched for explanations for the often poor seed production in larch. They found that the meiosis (cell division during sexual reproduction) which takes place already during autumn in larch was sensitive to both autumn temperatures and during the second stage of meiosis also fluctuations in winter temperatures. European and Japanese larch had greatest risk of damage during autumn while Siberian larch was more sensitive during winter. In southern locations, Siberian larch had greater risk of obtaining damages on the pollen mother cells than in more northern locations.

Hybridization of larches

Other hybrids than between *L. decidua* and *L. kaempferi* for more northern sites in Sweden was suggested by Kiellander (1958). The most promising so far has been the hybrid between *L. sukaczewii* and *L. decidua* (Jonsson 1978). In paper IV, 50 year old hybrids of this type have been evaluated and the wood production potential is promising. Also hybrids between *L. sukaczewii* and *L. kaempferi* have shown good results in northern Sweden (Jonsson 1978) but also in some parts of southern Sweden (Kiellander and Lindgren 1978).

In interspecific hybrids between *L. sukaczewii* and *L. decidua*, experiences from Finland have shown that *L. decidua* should function as mother tree (Lewandowski *et al*. 1994). The pollen production of *L. sukaczewii* is higher than in *L. decidua* and the timing of flowering between the species is difficult to match. When the pollen of European larch is ready the flowering of Siberian larch could already be over. Lewandowski *et al*. (1994) found that the percentage of hybrids produced by the grafts was much higher when European larch was the mother (93 % of the seeds were hybrids) than when Siberian larch was the mother (18 % hybrids).

In Russia, natural hybrids between *L. sibirica* and *L. gmelinii, L x czekanowskii* are widely recognised. Approximately 9.5 million hectares of this hybrid exists in central Russia (Milyutin 2007). In this population reproductive heterosis has been shown. Seed production has been superior compared to the parent species, up to 120 kg/ha. In Far Eastern Russia several hybrids between different varieties of *L. gmelinii* have been given scientific names. *L. x amurensis, L. x lubarski, L x maritima* are among the distinguished larch hybrids in this area.

Breeding of larch in Iceland

Eysteinsson (1995) described the strategy for larch breeding in Iceland. Selection of clones was made in three stages. First step was to select material from plantations in Iceland for both adaptation and growth traits. Resistance against frost and canker injuries, straight growth and height growth better than average trees, and branch traits like fine growth of branches and branch angles as close to 90° angle are important traits to consider. Second stage was directed to fecundity, clones with low fecundity was taken away from the breeding population. The third stage was based on progeny tests. Trees producing the poorest progeny were taken out of the breeding population.

1.13 Growth rhythm - an important factor for frost resistance and growth

As a background to paper I, II and III the importance of growth rhythm of the larches should be discussed. Growth rhythm is closely connected to frost resistance and height and diameter growth.

To understand the different growth rhythm of different populations of trees originating in various climatic types, is essential for choosing planting material that withstands frost injuries and uses the full growing season for growth. Tigerstedt (1993) described four different growth profiles in boreal forests; maritime growth profile, continental growth profile, alpine growth profile and the transitional growth profile. Characteristic for trees with a continental growth profile is a fast start of growth in the spring and high production rate during summer and a quick cessation of growth. Maritime growth profile means a slower drawn out growth in the spring, slower growth during summer and a drawn out longer growth cessation in the autumn. The transitional growth profile is in between.

The different growth profiles are influenced by the climate. Sweden has a semi-maritime climate with unpredictable weather changes depending on large weather front movements. Winters are relatively mild for such northern latitudes and temperature fluctuations around 0° C are common during winter. Other areas having this type of climate in the boreal zone is Finland, parts of eastern Norway, south central Alaska, central British Columbia and minor parts of Russia, mainly in the White Sea region in the north west but also in the Far Eastern Russia close to the Sea of Okhotsk (Tigerstedt 1993). Species that have adapted to this climatic type are relatively tolerant to transfer and some of them, according to Tigerstedt, show an exceptional adaptability to marginal sites in both maritime and continental climates. As mentioned above, Rehfeldt et al. (1999) found that Eurasian larches, when transferred, seemed to develop best in climates most similar to their origin. In semi-maritime Sweden species with the transitional growth profile should be preferred. Most suitable seed sources in Russia for planting in Scandinavia should thus be the Arkhangelsk region, the Russian Far East.

Lukkarinen *et al*. (2009) studied the same provenances as included in this thesis with focus on growth rhythm and height growth. Lukkarinen *et al*. investigated young seedlings growing in greenhouses and studied different variables both geographic and climatic and their influence on growth period and height growth and found growth rhythm mainly be connected with latitudinal origin of seed source. They found southern provenances having longer growth periods than northern, especially an extending growth period during late summer. Latitude explained 74 % of the variation in length of the growing period. Longitude and altitude had generally little effect, except for late summer growth which corresponded well with longitude in that more eastern provenances had longer late summer growth period than more western provenances.

In the boreal forest, frost hardiness in spring and autumn are among the most important adaptational traits to consider when selecting provenances for planting in forestry (Howe et al. 2003). Larches are often damaged by frost if the provenance is poorly adapted to the site where it is planted (Simak 1979, Eysteinsson and Skúlason 1995). The sensitivity to frost among provenances of European larch (*L. decidua*) and Russian larch (*L. sukaczewii*) when planted in Sweden was studied by Simak (1969, 1970, 1979). Major findings were that autumn frost resistance was strongly connected with the growth rhythm-photoperiodic response of the introduced larches.

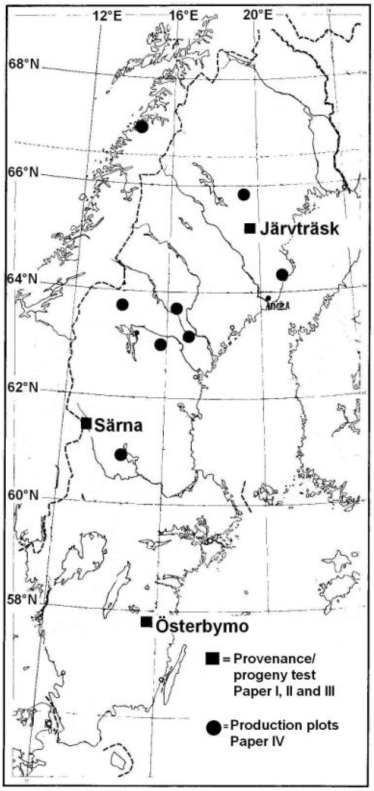
However, frost resistance and survival does not always coincide. Norway spruce, regarded as sensitive to frost, has generally much better survival than the known frost tolerant Scots pine on harsh sites (Fries 1991). Fries (1991) discovered the same pattern for *L. sukaczewii* in a trial at Lat. 67°N. Survival after four growing seasons was 88-91 % in two different facing slopes. At the same time, frost damage was recorded on 75 % of the seedlings. The provenance for *L. sukaczewii* was from Plesetsk from Lat. 63°N. Fries suggested that the transfer of this provenance by four degrees of latitude was the most likely explanation for the frequent frost damages.

2 Material and methods

The thesis is based on two different types of material: a) provenance and progeny trials of four different larch species on three locations in Sweden (Table 3); these trials were planted in 2003 and were 5 years of age at evaluation (**Papers I, II, and III),** and b) 37 to 86 -year-old provenance and production plots of different larch species including Russian larch hybrids (**Paper IV**). Table 2 shows the different species included in each paper.

Paper I-III Evaluation of provenance-progeny test

A combined provenance-progeny test of four Russian larch species was established in May/June 2003 on three locations in Sweden (Fig 6). One-year-old containerized seedlings, consisting of 1005 half-sib families from 29 provenances were planted. Five commercial seed lots were included as reference material (Table 4).



Paper I. Frost tolerance Included species: *L. suk*, *L. sib*, *L. caj*, *L. gme.* Site: Järvträsk
Paper II. Survival and juvenile growth Included species: *L. suk*, *L. sib*, *L. caj*, *L. gme* and *L.* x *eurolepis.* Site: Järvträsk, Särna and Österbymo
Paper III. Stem quality traits Included species: *L. suk*, *L. sib*, *L. caj*, *L. gme* and *L.* x *eurolepis*. Site: Österbymo
Paper IV. Yield study Included species: *L. suk*, different larch hybrids. *L. decidua*, *P. abies*, *P. sylvestris* and *Betula pendula*

Fig.6. Locations of the three combined provenance/progeny test sites (Paper I-III) and the eight production plots evaluated in paper IV. For abbreviations see Table 1.

Table 3. The three locations in Sweden for the provenance-progeny trials of four different larch species. The trials were planted in 2003 and were 5 years of age at evaluation. (Papers I, II, and III).

Loc.	**Lat. N**	**Long. E**	**T-sum dd.** [1]	**Alt. m**	**MAT °C** [2]	**CI** [3]	**TCM °C** [4]	**A-M °C** [5]	**Exp.**	**Soil**
Öst.	57º47’	15º37’	1160	250	5.8	21	-3.4	6.8	Slight S slope	Gravelly morain
Sär.	61º31’	13º00’	725	540	0.8	29	-11.5	3.2	Slight W slope	Stony morain
Jär.	65º11’	19º31’	650	410	0.1	34	-13.4	2.6	Steep E slope	Sandy morain

[1] Temperature sum based on Dag Lindgren´s temperature sum function available on http:www-genfys.slu.se/staff/dagl. (Lindgren 1994) dd = day-degrees (threshold value, +5° C). [2] MAT = Mean annual temperature, [3] CI = continentality index according to Conrad (1946), [4] TCM = Mean temperature for coldest month and [5] A-M = Mean temperatures for April and May.

Paper I. Frost tolerance test

Twigs for the freezing tests were collected at site Järvträsk for test of spring and autumn frost tolerance. The collection took place on 7-8 May 2006 when about half of the provenances buds had started to swell respectively 26-27 November 2006, when the provenances were in various state of autumn hardening. Included provenances were provenance number 1-28 (Table 4). As comparison material two seed stands and the two seed orchard seed sources, Lassinmaa and Östteg, were included (Table 4). Trees were randomly sampled with 5 trees of each provenance in each of the three blocks. In total shoots from 480 trees were tested. Artificial freezing test were done in a freezing test laboratory in Iceland. The twigs were tested at five different minimum temperatures and freezing damage was visually scored using a 12-point scale, where 1 = no damaged tissue and 12 = no undamaged tissue, and the scores in between corresponds to how large proportion of the entire shoot length having damaged cambium, 2 = 1-10 % of tissue damaged, 3 = 10-20 % damaged and so on. This procedure has shown to be appropriate analysing both freezing damage to needles and shoots (Nilsson & Andersson 1987, Lindgren and Nilsson 1992, Eysteinsson and Skúlason 1995).

Paper II. Provenance/progeny test. Growth and survival

The combined provenance and half-sib family test included 29 provenances (1-28 and 34), three commercial Swedish and Finnish seed crops (Nos. 31-33) and four Russian bulk stand collections (29, 30, 101 and 102) (Table 4) and was established in May/June 2003. The total number of half-sib families (progenies from the same mother tree in Russia) planted was 1005 (Table 4). The experiment was designed as a completely randomised block design with three replications. Each 30 x 40 m plots contained 300 seedlings from one or more provenance. The provenances were chosen to have similar regional origin within the plot. Families were completely randomized within the plots, 3-5 seedlings per half-sib family.

Climatic data for test sites and provenance locations were collected from the Climate Research Unit (CRU) database (Ten minute climatology 2002). Monthly mean temperatures for test sites and provenance origin were interpolated from these data. Continentality index was based on Conrad´s (1946) formula:

$$C = \frac{1.7\,A}{\sin(\varphi + 10°)} - 14$$

where C = continentality index, A = the annual monthly temperature range (the difference between warmest and coldest month) and φ = latitude.

The provenance-progeny trials were inventoried in September and October 2007 (after 5 growing seasons) for survival, height growth and damages (fraying, grazing, insect damage).

Paper III. Provenance-progeny test – Quality traits
On the southern site, Österbymo, stem straightness, frequency of trees with sharp branch angle, and frequency of double leaders were measured after five growing seasons. Stem straightness was visually scored in a 4 degree scale where:

1 = perfectly straight stem
2 = slightly crooked stem, one small bend was allowed
3 = crooked stem, both small sinuous bends or at least one severe crook
4 = severely crooked stem. Two ore more severe bends or strong repeated sinuosity

As a general rule trees in class 1 and 2 give a visually good impression while trees belonging to class 3 and 4 look crooked and severely crooked respectively.

All trees were also assessed for branch angles in two classes where 1 = 45-30 degrees and 2 = < 30 degrees (degrees in relation to the vertical stem) and frequency of double leaders where 1 = trees with double leader and 0 = trees with one leader.

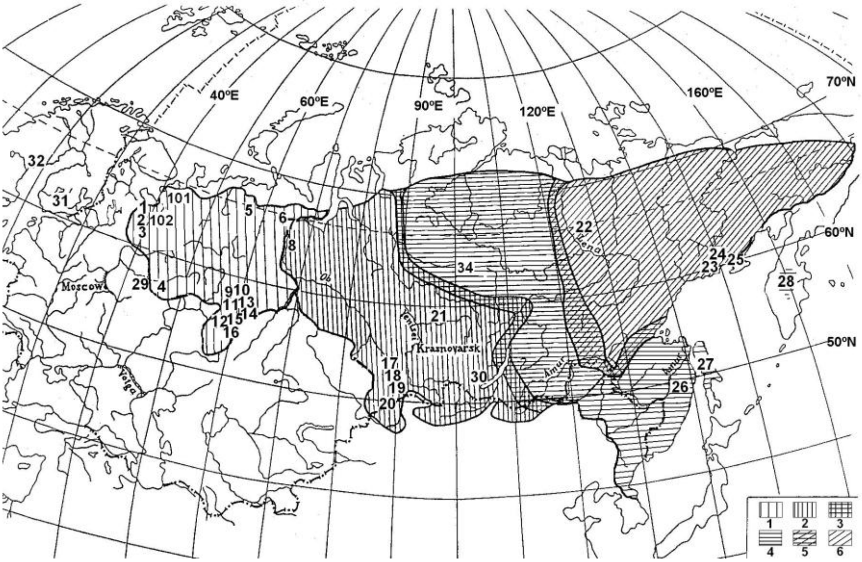


Fig. 7. Location of the 28 provenances (Nos. 1-28), 2 seed stands (29-30) and 2 seed orchards (31-32) as numbered in Table 3. One seed orchard of hybrid larch (No. 33) is not indicated on map. The six different patterns indicate larch species and their hybridization zones 1= *Larix sukaczewii* Dyl., 2=*L. sibirica* Ledeb., 3=*L. x czekanowskii*, 4= *L. gmelinii* Rupr., 5=*L. gmelinii x L. cajanderii*, and 6= *L. cajanderi* Mayr. The map is based on Milyutin and Vishnevetskaya (1995) and modified according to W. Schmidt (1995) and Putenikhin and Martinsson (1995).

Table 4 (see next page). Provenances included in the provenance and progeny trials (Papers I, II, and III).

Footnotes to Table 4:

1) elevations estimated based on map coordinates. *L. suk.* = *Larix sukaczewii*; *L. sib.* = *L. sibirica*; *L .caj.* = *L. cajanderi*; *L. gme.* = *L. gmelinii*; *L. eur.* = *L.* x *eurolepis*; Ru = Russia, Fi = Finland; S = Sweden. 2) MAT = Mean annual temperature, 3) CI = continentality index, 4) TCM = Mean temperature for coldest month, 5) TWM = Mean temperature for warmest month and 6)A-M = Mean temperatures for April and May. Note: * Not included in the freezing tolerance test.

Table 4. Heading, see prev. page

No.	Provenance	Species	Region	Lat. N	Long. E	Elev. m	N Fam.	MAT °C[2)]	TCM °C[3)]	A-M °C[4)]	TWM °C[5)]	CI[6)]
1	Onega	*L. suk.*	Arkhangelsk	64º01'	38º15'	110	7	1.2	-13.7	3.5	15.9	38
2	Emtsa	*L. suk.*	Arkhangelsk	63º00'	40º21-25'	100-120	45	1.2	-14.5	4.1	16.0	40
3	Shalakusha	*L. suk.*	Arkhangelsk	62º09'	40º19'	120	18	1.6	-14.1	4.6	16.3	40
4	Vetluga	*L. suk.*	Niz. Novgorod	57º30'	45º10'	145	66	3.3	-13	8.2	18.4	44
5	Usinsk	*L. suk.*	Komi	66º00'	57º48'	75	64	-3.4	-20.6	-2.1	15.2	49
6	Kharp	*L. suk.*	Yamalia	66º56'	65º45'	130	20	-7.9	-25.7	-7.3	12.6	53
7	Labytnangi	*L. suk.*	Yamalia	66º28'	66º39'	40	20	-6.4	-24.7	-5.6	14.5	54
9	Osa	*L. suk.*	Perm	57º19'	55º27'	160	20	2.6	-14.9	7.8	18.9	48
10	Visim	*L. suk.*	Sverdlovsk	57º30'	59º48'	350	12	0.8	-16.4	6.0	17.1	48
11	Maginsk	*L. suk.*	Ufa	55º45'	56º58'	370	20	2.0	-16.1	7.9	18.5	50
12	Zilair	*L. suk.*	Ufa	52º13'	57º25'	550	10	2.2	-16.8	8.6	19.8	56
13	Nyazepetrovsk	*L. suk.*	Chelyabinsk	56º09'	59º32'	460	20	1.7	-16.0	7.4	18.2	50
14	Kyshtym	*L. suk.*	Chelyabinsk	55º43'	60º27'	480	20	2.2	-15.7	8.0	18.8	50
15	Zlatoust	*L. suk.*	Chelyabinsk	55º07'	59º30'	600	20	0.8	-17.3	6.7	17.6	51
16	Miass	*L. suk.*	Chelyabinsk	54º58'	60º07'	380	20	1.9	-16.3	7.9	18.7	52
8	Beloyarsk	*L. sib.*	Khanti-Mansi	63º41'	66º44'	60	20	-0.9	-22.6	-0.9	16.8	56
17	Antoninovka	*L. sib.*	Kemerovo	54º12'	88º42'	700[1)]	20	-0.8	-18.6	4.2	16.6	52
18	Mezhdurechensk	*L. sib.*	Kemerovo	53º48'	88º00'	400[1)]	20	1.9	-16.5	7.2	19.4	54
19	Kondoma	*L. sib.*	Kemerovo	52º48'	87º24'	600[1)]	20	1.9	-16.1	7.3	19.1	53
20	Aktash	*L. sib.*	Altai	50º12-16'	87º03-54'	1600	78	-2.5	-18.4	2.1	13.0	48
21	Boguchany	*L. sib.*	Krasnoyarsk	58º39'	97º30'	96-158	75	-3.0	-24.8	2.7	17.9	64
22	Zhigansk	*L. caj.*	Sakha	66º45-51'	123º21-22'	70-90	60	-11.5	-39.3	-4.7	16.4	83
23	Motykleyka	*L. caj.*	Magadan	59º30'	148º30'	80	25	-5.2	-21.8	-2.7	11.2	46
24	Sokol	*L. caj.*	Magadan	59º50'	150º40'	60	25	-4.8	-19.8	-2.8	10.5	41
25	Nyurchan	*L. caj.*	Magadan	59º20'	152º30'	100	25	-4.4	-20.0	-2.0	11.2	43
26	Vanino	*L. gme.*	Khabarovsk	49º08-12'	139º00'	90-125	60	-2.7	-20.8	0.2	12.5	52
27	Nogliki	*L. gme.*	Sakhalin	51º48'	143º09'	50	60	0.1	-17.7	2.5	14.8	49
28	Esso	*L. gme.*	Kamchatka	55º48'	158º40'	700[1)]	60	-5.9	-19.2	-5.3	7.0	35
34	Evenkiya	*L. gme.*	Tura	64º17-19'	100º13-16'	270-310	75	-9.6	-36.4	-3.1	15.9	78
	Seed orchards and seed stands											
29	Ivanovo	*L. suk.*	Seed stand (Ru)	57º	41º	130[1)]		4.0	-11.8	8.9	18.4	42
30	Irkutsk	*L. sib.*	Seed stand (Ru)	52º	104º	500[1)]		-0.8	-20.0	4.7	16.6	56
31	Lassinmaa	*L. suk.*	Seed orch (Fi)	62º04'	25º09'	107		2.9	-9.9	5.2	15.9	32
32	Östteg	*L. suk.*	Seed orch (S)	63 º48'	20º16'	10		3.0	-8.2	3.6	15.1	27
33*	Maglehem	*L. eur.*	Seed orch (S)	55º46'	14 º10'	20		7.4	-1.0	7.8	16.2	18
101	Kuloj	*L. suk.*	Seed stand (Ru)	65º	45º	-		-0.3	-15.2	1.6	14.4	38
102	Obozersk	*L. suk.*	Seed stand (Ru)	63º	40º	-		1.2	-14.4	4.1	16.1	40

Paper IV. Yield study

Yield studies were based upon field trials established at nine experimental sites in Sweden and one site in Norway (Table 5). These studies represent three different ages of plantings:

1. Six, 50-year-old field trials in northern Sweden (Lat. 63°00´- 65°42´N) including two provenances of Russian larch (*L. sukaczewii*), Arkhangelsk and Sverdlovsk. In two of these sites hybrids between *L. sukaczewii* and *L. decidua*, *L. kaempferi* x *L. sukaczewii*, and *L. eurolepis* x *L. sukaczewii* were included. (Table 5)

2. Two 37-40-year-old species field trial in Siljansfors (Lat. 60°54´N) comparing the volume production of five tree species; European and Russian larch, Scots pine, Norway spruce, and silver birch (*Betula pendula*) (Table 5).

3. Two 76-86 year-old stands with the same Russian larch seed source, Raivola were tested. One site is located in Breivik, Norway at Lat. 67°04´ N at 100 m altitude. The other site is located in Siljansfors and was 86 year at evaluation. (Table 5).

Table 5. Locations, site conditions, and date of establishment of experimental yield trials (Paper IV).

Trial Category	**Site**	**Site category**	**Field trial established**	**Lat. N**	**Long. E**	**T-sum d.d**	**Elev. m a.s.l.**	**Exp.**
1	Rönnöfors	Farm field	1959	63˚39′	14˚15´	800	330	Gently W
1	Robertsfors	Farm field	1959	64˚10′	21˚51´	1010	40	Even
1	Byom	Farm field	1959	63˚00′	15˚43´	800	375	Gently N
1	Arvidsjaur	*Empetrum* forest	1959	65˚42′	19˚19´	520	515	S
1	Storbränna	Farm field	1960	63˚07′	17˚00´	980	150	Even
1	Sörånäset	Farm field	1960	63˚41′	16˚24´	920	200	Gently S
2	Siljansfors 9229	*Vaccinium* forest	1964-66	60˚54´	14˚22´	1050	230	Gently S
2	Siljansfors 9237	*Vaccinium* forest	1968	60˚54´	14˚22´	960	340	SW slope
3	Siljansfors 9070	*Vaccinium* forest	1926	60˚54´	14˚22´	1050	230	Even
3	Breivik 203	*Vaccinium* forest	1928	67˚04´	14˚28´	790	100	W slope

In the Storbränna and Söränäset field trials (Table 5) plants of hybrid origin were used, and the parent trees of these hybrid progenies are given in Table 6. The crossing scheme for the larch hybrids is given in Table 7.

Table 6. Origin of parent trees and the hybrid progenies they gave rise to. Planted in the Storbränna and Söränäset trials, the material used in Paper IV.

Parent tree number	**Species**	**Latitude N of seed source**	**Elevation, m a.s.l.**
Ld 248	*Larix decidua*	58˚30′ Grensholm (Swe)	63
Ld 4	*L. decidua*	58˚20′ Omberg (Swe)	160
Ls 152	*L. sukaczewii*	61˚50′ Punkaharju (Fin)	80
Ls 69	*L. sukaczewii*	64˚56′ Balstaberg (Swe)	300
Ls 72	*L. sukaczewii*	64˚56′ Balstaberg (Swe)	300
Ls 156	*L. sukaczewii*	64˚56′ Balstaberg (Swe)	300
Ls 489	*L. sukaczewii*	60˚07′ Bjurfors (Swe)	140
Lk 247	*L. kaempferi*	59˚32′ Grimstad (Swe)	110
Lk 488	*L. kaempferi*	58˚30′ Skärsnäs (Swe)	100
Lk 343	*L. kaempferi*	58˚02′ Visingsö (Swe)	120
Le 246	*L. x eurolepis*	60˚21′ Ruotsinkylä (Fin)	50

Hybrids

Progeny No.	**Mother**	**Mother origin**	**Father**	**Father origin**
56-1	*L. decidua*	58˚30′ Grensholm (Swe)	*L. sukaczewii*	64˚56′ Balstaberg (Swe)
56-2	*L. decidua*	58˚30′ Grensholm (Swe)	*L. sukaczewii*	64˚56′ Balstaberg (Swe)
56-3	*L. decidua*	58˚30′ Grensholm (Swe)	*L. sukaczewii*	64˚56′ Balstaberg (Swe)
56-4	*L. kaempferi*	59˚32′ Grimstad (Swe)	*L. sukaczewii*	64˚56′ Balstaberg (Swe)
56-8	*L. eurolepis*	60˚21′ Ruotsinkylä (Fin)	*L. sukaczewii*	61˚50′ Punkaharju (Fin)

Table 7. Crossing scheme for the larch hybrids, material 1, Paper IV. (L s = *Larix sukaczewii*; L d = *L. decidua*; L k = *L. kaempferi*; L e = *L. x eurolepis*)

	L s 69	**L s 72**	**L s 156**	**L s 489**	**L d 4**	**L s 152**
L d 248	56-1	56-2	56-3			
L k 247			56-4			
L k 488				56-8 Eb		
L k 343					56-22 Eb	
L e 246						56-8

Statistical analyses

Statistical analysis for paper I was performed using Sigmastat (Systat Software 2007). The data was not normally distributed, requiring use of non-parametric tests. Friedman repeated-measures ANOVA was used to analyse differences between provenances. Means were compared by use of Tukey test.

To evaluate the effect of geographical variables, multiple linear regression analyses were performed using overall mean damage scores for spring and autumn frost test respectively.
The following multiple regression equation was used: $D = k + a$ x Latitude + b x Longitude + c x Elevation, where D is the spring or autumn damage score, k is a constant and a, b and c are regression coefficients.

For paper II and III the following statistical analyses were performed: SPSS statistical software (SPSS for Windows version 12.0.1.) was used both for paper II and paper III.

In paper II, analyses of provenance height were performed with ANOVA (GLM). Post hoc Tukey test was used to test differences among provenance means. Correlations of geographical and climatic variables to survival and height were done with Pearson correlations test. As the objective of this analysis was to analyse the Russian provenances, seed orchard materials were left out of this analyses and only provenance 1-28 and 34 were included in this analysis. The different species were analysed all together (n = 29) and for *L. sukaczewii* (n = 15) separately and *L. gmelinii* and *L. cajanderi* as one group (n = 8). *L. sibirica* was also analysed separately but due to too few values only unsignificant correlations were obtained and data are not presented.

In paper III correlations between stem straightness, latitude and longitude was calculated. The correlations were based on provenance mean values. As the classification of stem straightness creates data of ordinal character, non parametric, Spearman's rank correlation (Spearman's r) was used to detect correlation between the different variables.

Genetic parameters in paper II and III were calculated with the ASReml 2.0 statistical software (Gilmour *et al*. 2006). Then, the genetic model used was phenotypic effect $P = A + E$, where P is the phenotypic effect, A the additive effect and E the environmental effect. The corresponding variances to be estimated were $\sigma_P^2 = \sigma_A^2 + \sigma_E^2$. In the analyses the additive genetic effect (A) was divided into provenance and family within provenance effects, respectively. In the statistical analysis the following mixed model was fitted:

$$Y_{ijklm} = \mu + bl_i + plant(plot)_j + row(plot)_k + prov_l + fam(prov)_m + e_{ijklm} ,$$

Where

Y_{ijklm}	= individual observation of each trait of the $ijklm^{th}$ plant position,
bl_i	= fixed effect of the i^{th} block,
$plant(plot)_j$	= random effect of the j^{th} plant number within plot,
$row(plot)_k$	= random effect of the k^{th} row number within plot,
$prov_l$	= random effect of the l^{th} provenance material,
$fam(prov)_m$	= random effect of the m^{th} family within provenance,
e_{ijklm}	= random residual (normal independent distribution assumed),

Equations for the narrow-sense heritabilities, defined as the ratio of additive genetic variance to total phenotypic variance, were developed from Falconer (1989) giving following the equations:

Individual heritability: $\hat{h}_i^2 = 4\hat{\sigma}^2_{fam(prov)} / (\hat{\sigma}^2_{fam(prov)} + \hat{\sigma}^2_{prov} + \hat{\sigma}^2_{tot})$,

Provenance+individual heritability:

$\hat{h}^2_{p+i} = (\hat{\sigma}^2_{prov} + 4\hat{\sigma}^2_{fam(prov)}) / (\hat{\sigma}^2_{fam(prov)} + \hat{\sigma}^2_{prov} + \hat{\sigma}^2_{tot})$.

Multiplication with 4 is made since the estimates are based on half-sib families. The additive genetic correlation between trait i and j as

$$\hat{r}_{A_{ij}} = \hat{r}_{A_i A_j} = \frac{\hat{\sigma}_{u_i u_j}}{\hat{\sigma}_{u_i}\hat{\sigma}_{u_j}}$$ (Falconer 1989).

In paper IV one way analysis of variance was used to analyse differences between the tree species in Siljansfors. When the ANOVA revealed a significant difference between the five groups at $P < 0.10$ a multiple comparison was performed using Dunett’s comparison with Russian larch as control.

3 Results and discussion Papers I-IV

Paper I Frost tolerance test

Spring frost tolerance

Provenances from north-western Russia and the Ural region (*L. sukaczewii*) were least damaged in the spring frost test. *L. sibirica* showed intermediate damage while both *L. gmelinii* and *L. cajanderi* were damaged to high degree (Fig. 8). The good results of the north-western provenances, especially the most northern, Nos. 5-7 originating from further north than the test site in Järvträsk, came as a surprise. Earlier research on spruce and larch at high latitudes have generally seen that northern populations are more frost prone in spring than more southern when grown on the same site, owing to a lower heat sum requirement for bud burst (Eriksson *et al.* 2006, Carswell and Morgenstern 1995). An explanation to the good results in the frost tolerance test for the northern provenances of *L. sukaczewii* might be that they originate from areas in Western Russia that are under maritime influence, thus have inbuilt defence against sudden warm spells during late winter and early spring. However, the most northern provenances had poor height growth and did not show higher survival than the more southern provenances (see analysis in paper II). Again frost damage and survival are not always correlated.

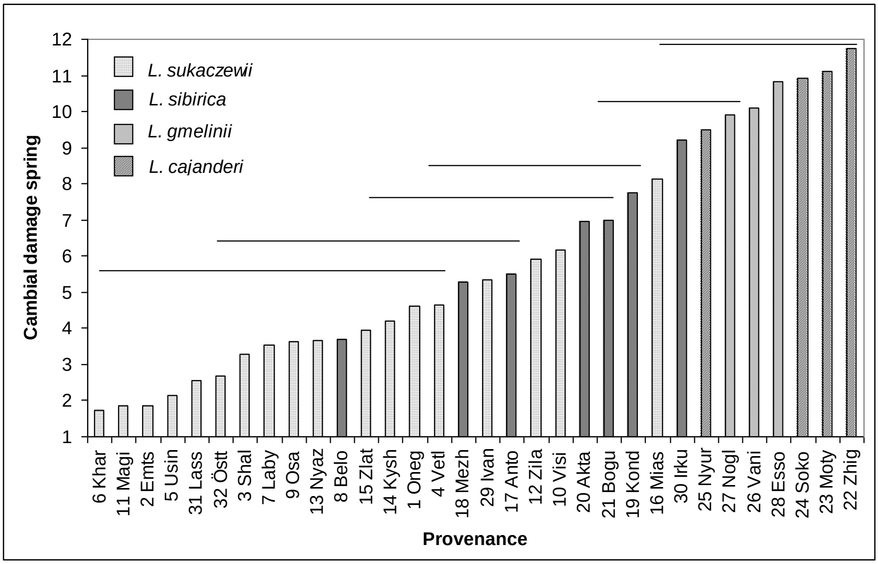


Fig. 8. Spring cambial damage for provenances. Mean values for all five test temperatures combined. (1 = undamaged, 12 = 100% damage). Provenances under each horizontal line did not differ significantly in damage (p<0.05).

Comparing all species, longitudinal origin with eastern provenances showing higher degree of spring frost damages was the only significant (p <0.001) predictor of spring frost damage (Fig. 9).

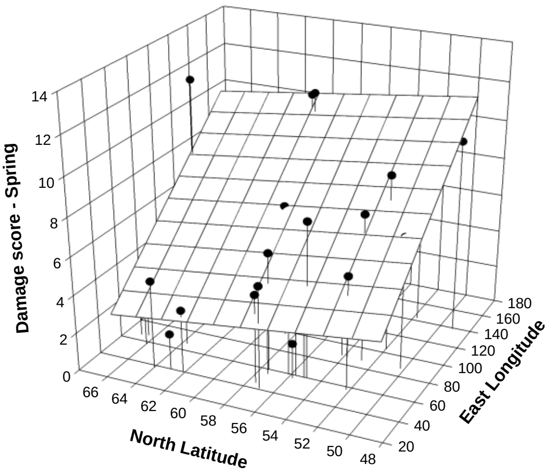


Fig. 9. Spring frost damage for provenances of *L. sukaczewii*, *L. sibirica*, *L. cajanderi* and *L. gmelinii*. Only longitude was a significant (p<0.001) predictor of spring frost damage. Each needle represents one provenance. The plane is a plot of the multiple linear regression equation: Spring damage = 6.039 – (0.0914 x Lat.) + (0.0642 x Long).

Autumn frost tolerance

North-western *L. sukaczewii* provenances had the least severe frost damage (Fig. 10). Latitudinal origin correlated strongest with frost damage with northern provenances having less damage. There was also a significant effect of longitude, where eastern provenances (*L. gmelinii* and *L. cajanderi*) having more damage (Fig. 10). Among *L. sibirica*, the most western provenance (No. 8) from western Siberia (Table 4) was least damaged. Interestingly, this effect of longitude on autumn frost hardiness has also been noticed in Scots pine but with opposite effect. Andersson and Fedorkov (2004) found that Russian populations from more continental climates were clearly more frost resistant than Scandinavian ones. They concluded that not only latitude but also longitude determines autumn frost hardiness in Scots pine. An explanation for the contradictory results in our study could be that the most eastern of the larch provenances originates not far from the Sea of Okhotsk (Fig. 6) and hence are under a certain maritime influence, thus adapted to mild autumns with less autumn hardiness as a consequence.

The risk of serious autumn frost damage, when planting southern material of *L. sukaczewii* at a more northern site was discussed by Simak (1979). Simak warned that a too long northern transfer would mean so large changes in light conditions for the trees that their initiation of growth cessation, which is dependent on a certain critical night length (Dormling *et al.*1968), would appear too late in the season. This should increase the risk for autumn frost damage. So far in Järvträsk, this has not been the case for a southern provenance like Ivanovo, which has been transferred 7-8 latitudes north and has not seriously been injured by frost so far. There is, however, a trend that more southern provenances of *L. sukaczewii* (Nos. 9-16) have lower survival than the Arkhangelsk provenances at this site, and the long northern transfer and changed light conditions might be the reason for that.

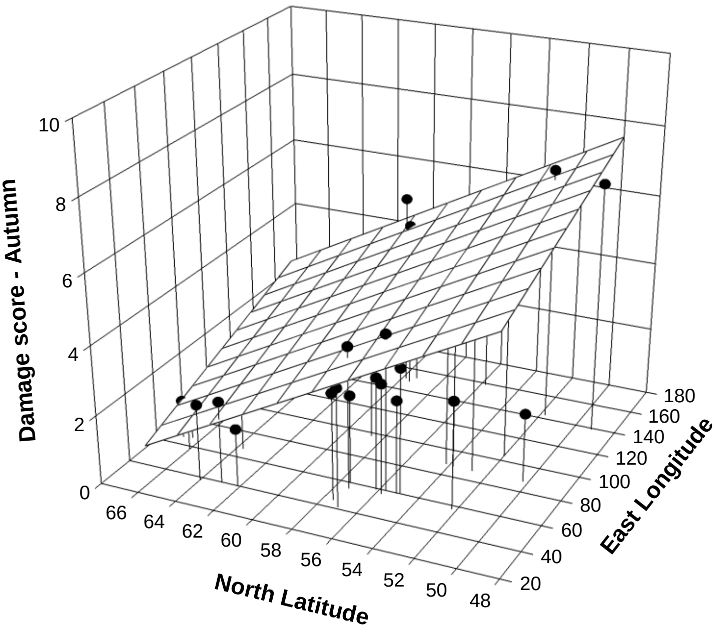


Fig. 10. Autumn frost damage for provenances of *L. sukaczewii*, *L. sibirica*, *L. cajanderi* and *L. gmelinii* by latitude and longitude. Each needle represents the damage score for a provenance. Southern provenances show more damage than northern, and eastern provenances were more damaged than western. Both latitude and longitude were significant ($p<0.001$) predictors of autumn frost damage.

Paper II Juvenile growth and survival

Survival at the test sites

Both the Särna and the Järvträsk sites are located in harsh climate. The temperature sums are 725 and 650 degree days, respectively, for the two sites. The severity index, defined in Eriksson *et al*. (1980) as the mortality of the local Scots pine provenance at a site after 20 years, is about 65 % for Järvträsk and about 55 % for Särna. Although the trees are only 5 years old, and the majorities of young trees have been protected in the snow for much of the winter and therefore are not fully tested for their hardiness, the survival is satisfactory for many of the tested provenances (Table 8). Initial survival after the first two growing seasons was 90.9 % on the most southern site, (Österbymo) and 69.4 and 84.9 % respectively in Särna and Järvträsk (Martinsson and Takata 2005). The poor initial survival at Särna might have been influences by a very stony soil and occasional planting outside of the scarified tracks. The mortality has between the years 2004 and 2007 decreased at Särna and was during these years more in agreement with that at Järvträsk.

Table 8. Survival of provenances at the three test sites. Figures in bold text show the 10 provenances with the highest survival on each site.

No.	Name	Origin Latitude ºN	Species	Survival Järvträsk %	Järvträsk SE	Särna %	Särna SE	Österbymo %	Österbymo SE	Ave. %
Half-sib family stands										
1	Onega	64º01'	*L. suk.*	**85**	3.5	**79**	4.0	74	4.3	**79**
2	Emtsa	63º00'	*L. suk.*	79	1.5	70	1.8	**88**	1.2	**79**
3	Shalakusha	62º09'	*L. suk.*	**87**	2.3	**72**	3.1	83	2.6	**81**
4	Vetluga	57º30'	*L. suk.*	76	1.4	56	1.7	**89**	1.1	74
5	Usinsk	66º00'	*L. suk.*	78	1.4	**74**	1.5	16	1.2	56
6	Kharp	66º56'	*L. suk.*	76	2.7	62	3.1	0	-	46
7	Labytnangi	66º28'	*L. suk.*	78	2.4	57	2.8	2	0.8	46
9	Osa	57º19'	*L. suk.*	77	2.6	67	2.9	**89**	1.8	**78**
10	Visim	57º30'	*L. suk.*	**81**	3.8	**71**	4.5	**92**	2.6	**82**
11	Maginsk	55º45'	*L. suk.*	72	3.0	62	3.3	**87**	2.2	74
12	Zilair	52º13'	*L. suk.*	77	2.9	70	3.0	**86**	2.3	**78**
13	Nyazepetro.	56º09'	*L. suk.*	70	2.8	60	3.1	81	2.4	71
14	Kyshtym	55º43'	*L. suk.*	62	3.0	56	3.0	80	2.5	66
15	Zlatoust	55º07'	*L. suk.*	71	3.1	60	3.3	**86**	2.4	72
16	Miass	54º58'	*L. suk.*	78	2.7	64	3.3	**88**	2.2	77
8	Beloyarsk	63º41'	*L. sib.*	**83**	2.0	**73**	2.4	33	2.6	63
17	Antoninov.	54º12'	*L. sib.*	65	2.7	58	2.8	45	2.8	56
18	Mezhdur.	53º48'	*L. sib.*	70	2.5	60	2.7	52	2.8	61
19	Kondoma	52º48'	*L. sib.*	62	3.0	64	2.9	56	3.0	61
20	Aktash	50º12-16'	*L. sib.*	42	1.6	47	1.7	2	0.5	30
21	Boguchany	58º39'	*L. sib.*	46	1.7	60	1.6	28	1.5	45
22	Zhigansk	66º45-51'	*L. caj.*	6	0.8	16	1.2	0	-	7
23	Motykleyka	59º30'	*L. caj.*	**84**	2.2	63	2.8	75	2.6	74
24	Sokol	59º50'	*L. caj.*	78	2.4	64	2.9	70	2.7	71
25	Nyurchan	59º20'	*L. caj.*	**89**	1.8	62	2.8	75	2.5	76
26	Vanino	49º08-12'	*L. gme.*	74	1.5	36	1.6	85	1.2	65
27	Nogliki	51º48'	*L. gme.*	79	1.4	65	1.6	84	1.2	76
28	Esso	55º48'	*L. gme.*	75	1.4	**72**	1.5	52	1.7	66
34	Evenkiya	64º17-19'	*L. gme*	-		24	1.9	-		24
Seed orchards and seed stands										
29	Ivanovo	57º	*L. suk.*	**81**	1.3	**72**	1.5	**91**	1.0	**81**
30	Irkutsk	52º	*L. sib.*	47	2.4	41	2.3	20	1.3	32
31	Lassinmaa	62º04'	*L. suk.*	**82**	1.3	**85**	1.2	85	1.2	**84**
32	Östteg	63 º48'	*L. suk.*	79	1.4	58	1.6	81	1.3	73
33	Maglehem	55º46'	*L. eur*	54	2.4	22	2.0	81	1.3	60
101	Kuloj	65º	*L. suk.*	**84**	2.7	**79**	3.0	76	3.2	**80**
102	Obozersk	63º	*L. suk.*	**83**	2.5	**77**	2.7	**87**	2.1	**82**
Averages for the sites				68		58		59		
Averages among species			*L. suk.*	78		66		73		
			L. sib.	59		58		34		
			L. caj.	64		51		55		
			L. gme.	76		58		74		

Survival among species

Larix sukaczewii demonstrated the best survival on the two northern sites, whereas *L. gmelinii* had highest survival on the southern site, where northern provenances of *L. sukaczewii* had low survival (Fig 11, Table 8). *L. sibirica* had lower survival than *L. sukaczewii* on all three sites. The very low survival of *L. cajanderi* is influenced by the high mortality of provenance 22 from interior Siberia (Fig. 7, Table 8). The good performance of *L. sukaczewii* and *L. gmelinii* might be explained by that a majority of the provenances tested in these species originate from areas in Russia that have a climate most resembling the climate of Sweden. Both the northern part of European Russia and the Russian Far East are under a certain amount of maritime influence. As Rehfeldt *et al*. (1999) showed, best acclimation in Eurasian larch populations was obtained when transferred to a climate similar to their origins.

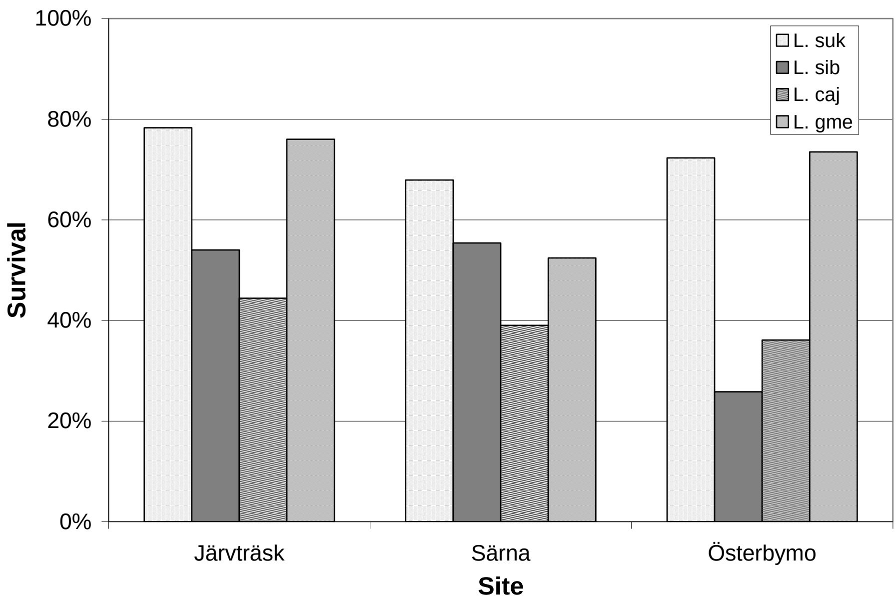


Fig. 11. Survival for species at the different sites, the bars from left to right represents *L. sukaczewii*, *L. sibirica*, *L. cajanderi* and *L. gmelinii.* Altitude for the sites, Järvträsk 410 m, Särna 540 m and Österbymo 250 m a. s. l.

Survival among provenances

Within *L. sukaczewii*, an interesting difference between the more western provenances and the more eastern from the northern Urals was noticed. In

Österbymo at Lat. 57°47´ N, the western provenances from latitude 64° N and 65° N (Nos. 1, 101) showed survival between 74 and 76 %, whereas the northern Ural provenances from latitude 66°N (Nos. 5-7) had very low survival, 0-15 % (Fig. 7, Table 8). Also *L. sibirica* from its most western distribution area, provenance No. 8 originating from latitude 63°41´N, showed considerably lower survivals than the more western provenances of *L. sukaczewii*. This big difference in performance cannot be explained by differences in frost resistance only, as it was shown in Paper I that the northern Ural provenances actually had good spring frost tolerance. A probable explanation to the poor performance of the northern interior provenances is that their growth rhythm is not adapted to the southern site in Österbymo. Lukkarinen et al. (2009) compared growth rhythm in one-year old seedlings grown in greenhouse, the same provenances as tested in this thesis, and showed that northern provenances of *L. sukaczewii* had the shortest growing period of the compared material. Northern provenances stopped their growth early in the summer with poor height growth as a result, and this might have implications also for their survival. Competition from vegetation could increase the mortality of these northern provenances. The more maritime influenced western provenances had better growth and also survival.

The Lassinmaa seed orchard material shows a remarkably uniform performance on the three sites with survivals between 82-85 % (Table 8). The southern Ural provenances (Nos. 9-16) have all high survivals on the southern site.

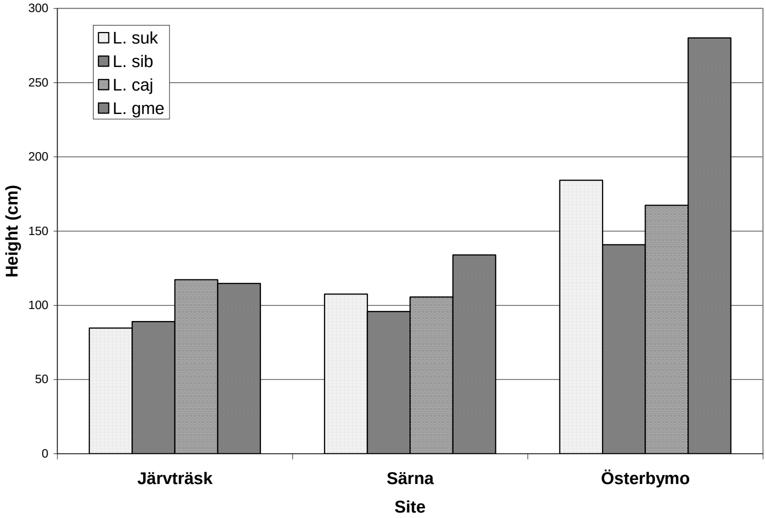
Among the *L. sibirica* provenances the survival is higher in the two northern sites (Table 8). The survival in Österbymo varies between 2-55 % for the seven provenances; the corresponding figures for Särna and Järvträsk are 40-72 % and 42-82 %, respectively. The northern Ural provenance (No. 8) from the farthest western collection of the species has the highest survival in Järvträsk and Särna. On the southern site provenances No. 17-19 from the Novokuznetsk area has highest survival. Among provenances of Siberian larch, the provenance from the high altitude site in the Altai Mountains had lowest survival on all three sites.

L. cajanderi provenance No. 22 from Zhigansk (northern interior Siberia) does not survive well on any of the three sites in Sweden. On the southern site, the mortality was 100 % after five growing seasons. However, provenances Nos. 23-25, all from an area near Magadan, show better survival (Table 8). These three provenances are among the best on the most northern site and perform satisfactory well also on the two other sites. At Österbymo, however, they were, as mentioned earlier, starting bud burst as early as February one year and their adaptation to this southern site must be questioned.

Among the *L. gmelinii* provenances Nos. 26 and 27 show similar good survivals on the southern site and 75-78 % survival on the two northern sites. In Särna the Khabarovsk provenance (No. 26) more or less fails however, with below 40 % survival. The Sachalin provenance (No. 27) has a somewhat better performance. The more northern provenance No. 28 from Kamchatka has low survival on the southern site whereas it survives better further north. Hybrid larch (No. 33 Maglehem) is well adapted to the southern site but suffers badly in the north, especially in Särna.

Height growth

The height growth was best on the most southern site, Österbymo with an overall mean height of 2 m after five growing seasons. Corresponding figures for Särna and Järvträsk was 1.1 m and 0.95 m. The mean height for the four species was ranging between 1.4 and 2.8 m at Österbymo. The corresponding figures for Särna and Järvträsk were 0.95-1.3 m and 0.85-1.2 m (Fig 12).



Fig, 12. Height growth for the included Russian larches at the three different sites.

Detailed results for the different provenances are seen in Paper II. The results showed that at this early evaluation, growth was positively correlated to the temperature sum of the sites (Table 3). Growth differences between Särna and Järvträsk were small. It will be interesting to follow the development of the growth in these trials in the future. The yield of larch has been shown to be sensitive to site conditions. On more fertile sites, good production rates have been obtained also in harsh climates (Martinsson 1995). In paper IV it was shown that the Raivola provenance of *L. sukaczewii* had almost the same yield after 76 years in two sites with large differences in temperature climate. The site in central Sweden had a temperature sum of 1050 day-degrees (dd) and the one in northern Norway 790 dd, and both had produced about 7 m^3 $ha^{-1}year^{-1}$.

Fig. 13 a-c show the ten best (based on height x survival) provenances and seed sources at each site. On the most northern site (Fig 13a), *L. gmelinii* from Sakhalin (No. 27) and *L. cajanderi* from Magadan had the best height growth. Of the *L.*

sukaczewii provenances origins from the Arkhangelsk region produced best. Among the comparison material, Ivanovo (no 29) and Lassinmaa seed orchard seed source has produced best. At site Särna (Fig. 13b), *L. gmelinii* from Sakhalin had the best height growth. The survival was, however, below 70 % and *L. sukaczewii* seems as a safer choice on this site, especially the Lassinmaa seed orchard seed source, which had a survival of 85 %. Within *L. sukaczewii* both Arkhangelsk provenances (provenance No. 2, 3 and 102) and provenances originating in Central Ural (No 9, 10 and 12) showed good initial adaptation to the site. Provenance No. 12 from southern Ural originates from rather high elevation in the Urals, 550 m a. s. l. and this might explain this provenance good production at this site. At Österbymo (Fig. 13c), the production rate in the *L. gmelinii* provenances No 26 and 27 is worth noticing. Hybrid larch of Maglehem seed source (No 33) has earlier been shown to have very fast juvenile growth (Stener 2007) but are outgrown at this early stage by both provenance 26 (Khabarovsk) and 27 (Sakhalin). Of the *L. sukaczewii* provenances, material from more southern latitudes 52-57°N demonstrated the best production. Below, the influence of geographic and climatic variables on survival and growth will be discussed.

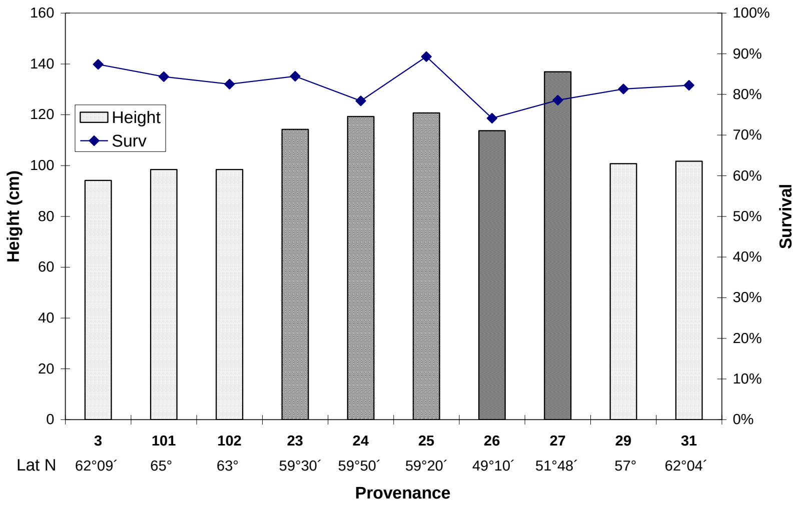


Fig. 13a. The ten best producing (based on height x survival) provenances and seed sources at site Järvträsk (Lat. 65°11´ N, altitude 410 m). The different patterns indicate various larch species, from left, *L. sukaczewii*, *L. cajanderi*, *L. gmelinii*, Seed source 29 Ivanovo and 31 Lassinmaa of are from a Russian seed stand and the Finnish seed orchard stand of *L. sukaczewii*.

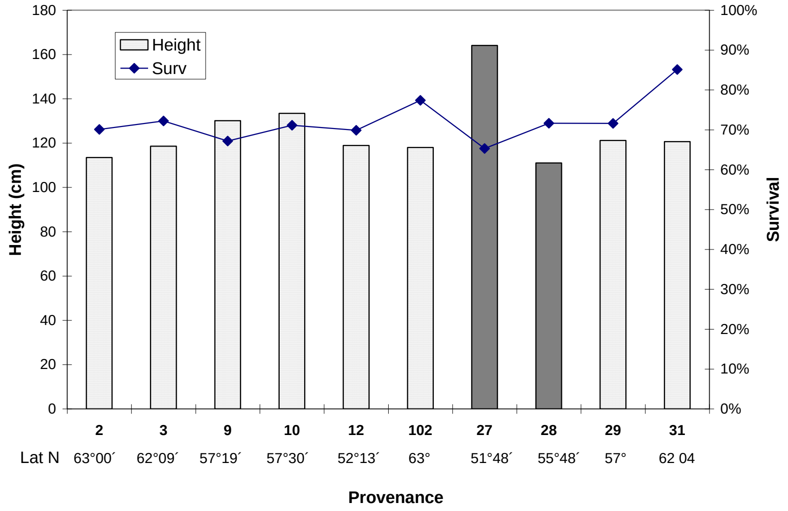


Fig. 13b. Ten best producing provenances and seed sources at site Särna Lat 61°31´ N, altitude 540 m. The different patterns indicate from left *L. sukaczewii*, *L. gmelinii*. Prov 29 and 31 are from a Russian seed stand respectively the Finnish seed orchard stand of *Larix sukaczewii*.

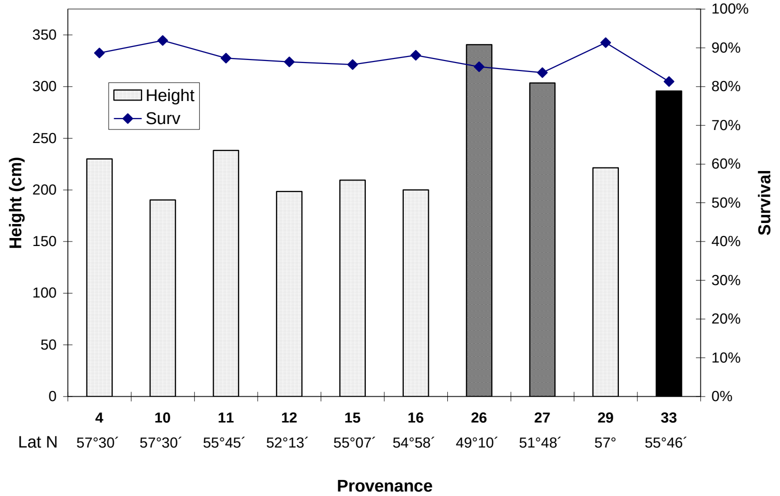


Fig. 13c. Ten best producing provenances and seed sources at site Österbymo (Lat 57°47´ N, altitude 250 m). The different patterns indicate from left *L. sukaczewii*, *L. gmelinii*. Provenance 29 is from a Russian seed stand of *L. sukaczewii* and 33 is *L.* x *eurolepis*.

Correlations with geographic and climatic variables

In Järvträsk and Särna, survival for *Larix sukaczewii* was weakly correlated to geographic and climatic variables, while height growth was under stronger influence (Table 9). Provenances from more continental areas (high continentality index) generally had lower survival than provenances originating in more maritime regions. The continentality index (CI) at the test sites varies between 21 (Österbymo) to 34 in Järvträsk (Table 3). The Arkhangelsk provenances have CI of 38-40 while the very northern and southern Ural provenances have CI of 48-56 (Table 4). Provenances from more continental areas are thus transferred to sites with a more maritime climate and this might explain the poor performance of the more continental provenances. However, the southern Ural provenances also originate from continental climates and these provenances show good adaptation to the southern test site. At this southern site, latitude origin plays a more pronounced role for the survival of the different provenances. In the southern test site, Österbymo, northern provenances showed low survival and poor height growth.

Table 9. *Larix sukaczewii (n=15*), correlations between geographical and climatic variables with survival and height growth, respectively. TCM = Mean temperature coldest month, MAT = Mean annual temperature, CI = Continentality index, A-M = mean temperature for April and May.

Variable	**Survival**			**Height**		
	Österbymo	Särna	Järvträsk	Österbymo	Särna	Järvträsk
Lat.°N	-0.78 **	0.28	0.45	-0.86 **	-0.82 **	-0.27
Long.°E	-0.45	-0.53 *	-0.55 *	0.06	-0.30	-0.74 **
TCM, °C	0.91 **	0.23	0.09	0.54 *	0.82 **	0.81 **
MAT, °C	0.96 **	0.08	-0.10	0.76 **	0.91 **	0.71 **
CI	-0.34	-0.51	-0.52 *	0.18	-0.19	-0.70 **
A-M, °C	0.96 **	-0.06	-0.24	0.87 **	0.94 **	0.59 *

* Significant at $p < 0.05$. ** = significant at $p < 0.01$.

For *L. gmelinii* and *L. cajanderi*, latitudinal origin of provenances was negatively correlated to survival and height at two of the sites (Table 10). Also longitudinal origin of provenances had great effect with eastern populations having higher survival than more eastern provenances from interior Siberia. Continentality index was negatively correlated with both survival and height growth in Järvträsk and Särna, while height growth was positively correlated with continentality index in Österbymo, where in addition temperature climate was important for survival.

Table 10. *Larix gmelinii* and *L. cajanderi* (n=8). Correlations between geographical and climatic variables with survival and height growth. For abbreviations see table 9.

Variable	**Survival**			**Height**		
	Österbymo	Särna	Järvträsk	Österbymo	Särna	Järvträsk
Lat. °N	-0.77 *	-0.47	-0.60	-0.89 *	-0.91 **	-0.63
Long. °E	0.59	0.86 **	0.84 *	-0.92 *	0.57	0.49
TCM°C	0.91 **	0.89 *	0.96 **	0.13	0.87 **	0.84 *
MAT°C	0.92 **	0.68	0.79 *	0.82 *	0.98 **	0.92 **
CI	-0.75	-0.94 **	-0.92 **	0.89 *	-0.70	-0.64
A-M, °C	0.68	0.17	0.40	0.86 *	0.78 *	0.77 *

* Significant at $p < 0.05$. ** = significant at $p < 0.01$.

Correlation between survival and frost damage in freezing test

For *L. sukaczewii* and *L. sibirica* the correlation between both the spring and autumn frost damage in the freezing test (Paper I) and the survival in the field was generally low (Table 11). Only at site Järvträsk a significant correlation between the frost damage and survival is apparent. Southern Ural provenances have lower survival than northern provenances and they are less frost tolerant in the autumn freezing test.

Table 11. Correlations between frost damage in freezing test and survival at the three sites.

Variable	**Survival**		
	Österbymo	Särna	Järvträsk
L. suk. and *L. sib*. (n=25)			
Cambial damage spring	0.006	-0.312	-0.412 *
Cambial damage autumn	0.352	-0.251	-0.463 *
L. caj. and *L. gme*. (n=7)			
Cambial damage spring	-0.714	-0.250	-0.500
Cambial damage autumn	0.679	0.357	-0.107

* Significant at $p < 0.05$.

It was suggested in paper I that the good spring frost tolerance of the most northern provenances might be explained by the maritime influence these provenances are exposed to. It does, however, not show as better survival. It seems that the high mortality of the most northern provenances of *Larix sukaczewii* (Nos. 5, 6, 7) at site Österbymo could not be explained by frost damage. It suggests that other factors than spring frost tolerance influence the high mortality of the northernmost provenances. These provenances have an early growth cessation, the height growth is poor, and shading from competing vegetation might increase their mortality. Drought could also be an explanation for their high mortality. According to Hagman (1995), drought could have a big impact on survival for larches that has been transferred long distances south.

For the eastern species, *L. gmelinii* and *L. cajanderi* correlations were generally higher but due to only seven observations the significance were low. At Österbymo, spring frost tolerance seems more important for survival than autumn frost tolerance. The positive correlation between autumn frost damage and survival is explained by that northern provenances with good autumn frost tolerance have an early growth cessation and although tolerant to autumn frost, are not adapted to the site at Österbymo. Other factors like spring frost, a too early growth cessation, or maybe drought explain their poor results on this site.

Skogforsk's test series with Russian larches

The same provenances as included in this thesis were also tested on ten smaller sites in Sweden with 55-60 seedlings of each region (Table 4) planted per site. Approximately 1000 trees were planted per site. These field trials were established by Skogforsk (the Forestry Research Institute of Sweden) in 2003 and were evaluated in 2006 after four growing seasons by Dumanskaya and Karlova (2006). The location of the sites stretches from Svalöv (Lat. 55°56´N, Alt. 105 m.) in the very south of Sweden to Dokkas in the north (Lat. 67°08´N, Alt. 360 m).

The following main results were found: The survival was generally good on nine of the sites. The tenth site, located in southern Sweden, had high mortality owing to spring frost and heavy damage by wild bore. *Larix sukaczewii* had the highest mean survival over all sites (86 %). The survival for *L. sibirica* was 75 %, *L. cajanderi* 58 %, and *L. gmelinii* 70 %.

The survival averaged 82 % (range 52-95 % for the provenances) on the northern sites (Lat. 64-67°N), 66 % (5-94 %) on the southern sites (Lat 55-60°N). Northern provenances and the high mountain provenance from Altai failed more or less on the four southern sites, whereas southern provenances survived satisfactorily on the northern sites. The highest survival in the five northern sites was shown by *L. sukaczewii* from the Plesetsk region, south of Arkhangelsk at Lat. N 62°-63°N. High initial survival was shown by *L. sibirica* from the Boguchany region, somewhat surprising compared to our results. On the four southern sites *L. sukaczewii* from the Nishnij Novgorod region and southern Ural Mountains had the highest survival.

Comparing the results from these nine remaining sites to our results, strengthen the conclusion that material from far northern latitudes and high mountain areas in south Siberia are not adapted to the test sites in Sweden. It should however, be noted that none of the sites are located at really high altitudes and it is possible that in the most severe climates in Sweden these provenances could have better survival. As in our study (Paper II), the southern provenances of *L. sukaczewii* grow well in southern Sweden and survive satisfactory even in the most northern sites. Studying the seven sites located in northern Sweden (above Lat. 61°N), the highest survival has been shown by *L. sukaczewii* from the southern part of the Arkhangelsk area or seed orchard material from Finland (at Lat. 62°N) originating in the Raivola forest.

Norwegian trials

Experiences from Norway (Öyen *et al*. 2007), where the same material as included in this thesis have been tested on a site 15 km south of Bergen (at Lat 60°N), with a pronounced maritime climate found the Far Eastern provenance Khabarovsk (*L. gmelinii* var. *olgensis*) to have the best survival and growth after three growing seasons. Finnish seed orchard material showed best adaptation of the *L. sukaczewii* provenances. Not surprisingly did the material from central Siberia, both northern and southern provenances, fail completely. Southern material had generally better growth than northern provenances. In this part of Norway, west of the mountains, Öyen *et al*. (2007) concludes, that Japanese, Hybrid or European larch of Scottish seed sources seem like a better choice.

Genetic parameters

The estimated genetic parameters did not show any clear genetic pattern neither for survival nor height on the family level. Instead, those traits showed only a few significant individual heritabilities (h^2_i), and they were most often very low (below 0.10). The combined family+provenance heritabilities (h^2_{p+i}) were for both height and survival on the whole considerably higher than the individual heritabilities: h^2_{p+i} =0.25, 0.25 and 0.45 for Järvträsk, Särna and Österbymo, respectively compared to h^2_i=0.04, 0.06 and 0.08 for the sites. Still, the combined family+provenance heritabilities were with one exception non-significant. There were no significant genetic correlations between height and survival. One probable reason for the low heritabilities, is the early age at measurement (five years from seed). It is likely that the immediate non-genetic effects of seed weight still dominate in plant growth. Thus, the trial with the highest trees, Österbymo (average height 1.4-2.8 m compared to 0.95 m respectively 1.1 m in the other test sites, had higher heritabilities; average h^2_{p+i} = 0.45 in Österbymo compared to average h^2_{p+i} = 0.25 both in Järvträsk and Särna. Lack of genetic correlation may have similar reasons. The establishment phase in regenerations is a sensitive phase in northern Sweden and harsh climate on the whole (Eriksson et al. 1980). Thus, materials with fast early growth can either grow high or die due to spring or autumn frost damages, and materials with poor adaptation may grow slowly and have high mortality.

Paper III Stem quality of provenances at Österbymo

This paper describes stem straightness, branch angle and frequency of double leaders at the site of Österbymo. This site was chosen as the trees had the best height growth on this site. The mean height for the site was 1.5 meters after five growing seasons, with 12 provenances out of 29 with mean heights equal or above 1.9 m (Fig. 14).

As one of the objectives for growing larch is to produce high quality timber, the stem quality of the different species needs to be investigated. An evaluation after five years will not give the definite answer on which seed source to use. It can, however, give an early indication if there are species specific differences at this early stage.

The results indicate that stem quality varies a lot between the compared species. Russian larch (*L. sukaczewii*) has the best stem shape (Fig. 14) and lowest frequency of trees with sharp branch angles.

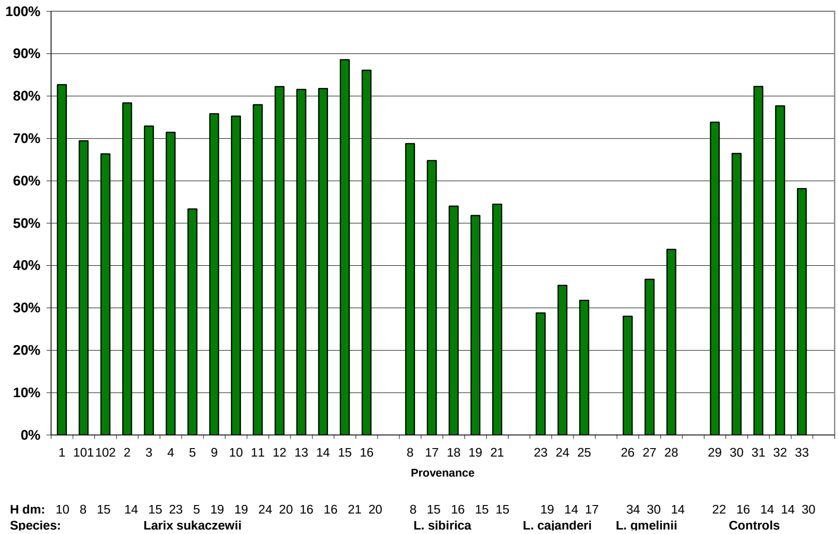


Fig. 14. Percentage of trees with satisfactory stem straightness (Class 1 and 2). Regional origin for provenances: 1-3 = Arkhangelsk; 4-5 N Ural; 9-16 S Ural; 8= W Siberia; 17-19=S Siberia; 21= central Siberia; 23-28=Russian Far East. In the figure the mean height for each provenance is also presented.

Both *L. cajanderi* and *L. gmelinii* suffer from high proportions of trees with poor stem shape. *Larix sibirica* is intermediate in this respect.

L. sukaczewii had the lowest frequency of trees with sharp (0-30°) branch angles (12%). Corresponding frequencies for *L. sibirica*, *L. cajanderi* and *L. gmelinii* were 25%, 27% and 29% respectively (Paper III). Among the control provenances (Nos. 29-33), *L. sukaczewii* had clearly lower amount of trees with sharp branch angle, 12-14% compared to *L. sibirica* 21% and *L. x eurolepis* 22%.

The frequency of double leaders was generally quite high (Paper III). Within *L. sukaczewii* it varied considerably. The provenances that had the best height growth on the site had also the lowest frequencies of double leaders. Northern provenances had generally slow height growth and high frequencies of double leaders. The development of double leaders in larch is mainly connected with frost injuries. Within *L. sukaczewii*, the least amount of double leaders is found in the provenances originating from roughly the same latitudes as the test site. Provenance No. 4 from Lat. 57°N and the southern Ural provenances Nos. 9, 10, and 13-16 from latitudes 54-57°N all have lower frequency than the Arkhangelsk and northern Ural provenances.

The negative correlation between height growth and double leaders is also found in *L. gmelinii* where the slow-growing northern provenance from Kamchatka has 4-6 times more double leaders than the faster growing provenances from Khabarovsk and Sakhalin (Nos. 26, 27). The explanation for this correlation between good height growth and lower frequency of double leaders ought to be that well-adapted provenances with their growth rhythm in harmony with the new site suffer less frost damage. This can be connected to the frost tolerance of the different provenances. However, this negative correlation does not hold for the stem shape, where the fast growing *L. gmelinii* provenances are among the worst for stem shape. An explanation for this negative correlation between growth and stem straightness was suggested by Bastien *et al.* (1995). They found in European larch that trees that extended shoot elongation long into the summer could develop an unstable tissue if the lignification rate was slow after growth had ceased. Also Kiellander (2001) was of this opinion.

Generally, quality traits such as stem straightness and branch angle are considered as inheritable traits (Andersson and Hattemer 1978; Codesido and Fernández-López 2008; Wu et al. 2008). In the present study, individual heritabilities for stem straightness were rather low to intermediate for *L. sukaczewii*, *L. sibirica* and *L. gmelinii* respectively (0.10, 0.31 and 0.15, $p < 0.05$). For *L. cajanderi* it was very low (0.01), and not significant. The Prov+Fam heritabilities were of similar sizes. Relevant heritabilities for branch angle could generally not be estimated. One exception was individual heritability for *L. gmelinii* (h^2_i =0.12, $p < 0.05$).

There were no genetic correlations between stem straightness and branch angle. The genetic correlations for height with stem straightness and with branch angle that were possible to estimate were generally positive, but most often connected to large standard errors and based on non-significant variance components. The low genetic parameters for branch angle might be explained by the early age for evaluation as also indicated by low levels for genetic variation within species was low with CV_A values 4-10% for stem straightness. One factor behind the low genetic influence here may be that the trait at low age not is fully expressed due to that the thin branches are sensitive to environmental factors (snow, rain, wind, soil vegetation etc).

Paper IV Yield of *L. sukaczewii* and larch hybrids in northern Scandinavia

The results from the six 49-53 year old provenance trials show that the Arkhangelsk provenance produces more volume per hectare than the Sverdlovsk provenance on five of the six sites (Table 12). There were big differences in production between the sites. On the most fertile sites, the mean annual volume production for the first 50 years, reaches 9-11 m^3 ha^{-1} yr^{-1} for the Arkhangelsk provenance.

The Russian larch hybrids with European and Japanese larch mothers 56-1, 56-2, 56-3 and 56-4 exceed the two Russian larch provenances in yield, basal area, and dominant height. The volume production per hectare from the four larch hybrids are 33-66 % superior to that of the Arkhangelsk provenance and 95-143 % superior to the Sverdlovsk provenance (Table 12). The dominant height (Fig. 15) is also superior in the hybrids compared to the pure species. In Söränäset a difference of four meters in favour of the hybrids is visible. Compared to Norway spruce grown on the most productive farmland in northern Sweden, the dominant height of the best Russian larch hybrids is 5-6 m taller than in spruce. As the edge effect does not influence the height growth in the same way as volume growth, it is probably the development of the dominant height and mean height that is the most impressive result in these hybrids.

The small plots, especially in Söränäset, make it difficult to draw any certain conclusions about the production capacity of the tested material. Although edge trees are present, except for the plots of hybrids in Storbränna, edge effects surely influence the results. Within the sites the uneven results between the tested provenances gives edge effects, if a plot is surrounded by other weaker growing provenances. Elfving (2005) recommend 1000 m^2 plots for yield plots.

However, the results of the Russian larch hybrids are anyway interesting. On these two test sites, they outgrow the Russian larches both in height growth and in volume per hectare. Together with older yield studies that have shown that *L. sukaczewii* produces more than Scots pine on medium to fertile sites in northern Sweden (Edlund 1966, Martinsson 1995) it gives an indication of a very high volume production capacity in these Russian larch hybrids.

Table 12. Results of the 49 to 53-year-old provenance test. SV = Standing volume, MAI = Mean annual increment. Bold figures are for hybrids. [1] = Thinned volume not included in the results

Experimental site	Provenance or hybrid	No. of trees and trees/ha	Tot. Age	Mean dbh, cm	Mean tree height, m	Dominant height, m	Tree vol. $m^3 tree^{-1}$	SV $m^3 ha^{-1}$	MAI $m^3 ha^{-1} yr^{-1}$
Rönnöfors[1]	Arkhangelsk	161 (1006)	50	23.7	16.7	19.1	0.304	306	6.1
	Sverdlovsk	138 (863)	50	24.1	13.6	17.9	0.155	134	2.7
Robertsfors[1]	Arkhangelsk	144 (625)	50	25.6	20.7	23.2	0.453	283	5.7
	Sverdlovsk	156 (677)	50	26.4	20.3	22.7	0.470	318	6.4
Byom[1]	Arkhangelsk	194 (842)	49	25.3	18.9	21.7	0.372	313	6.4
	Sverdlovsk	187 (812)	49	25	16.8	20.7	0.306	248	5.1
Arvidsjaur	Arkhangelsk	158 (686)	51	19.4	9.5	13.7	0.101	69	1.4
	Sverdlovsk	139 (603)	51	16.8	8.1	12.2	0.061	37	0.7
Storbränna[1]	**56-1 *L. dec×L. suk***	**22 (714)**	**52**	**34.5**	**29.0**	**30.5**	**1.267**	**905**	**17.4**
	56-8Eb *L. kae×L. suk*	**16 (519)**	**52**	**33.8**	**26.3**	**28.8**	**1.078**	**560**	**10.8**
	Arkhangelsk	109 (681)	53	27.2	25.1	28.0	0.715	487	9.2
	Sverdlovsk	100 (625)	53	29.1	25.5	27.1	0.669	418	7.9
Söränäset	**56-1 *L. dec×L. suk***	**60 (960)**	**51**	**31.3**	**28.0**	**28.9**	**0.996**	**956**	**18.7**
	56-2 *L. dec×L. suk*	**69 (1104)**	**51**	**25.5**	**25.0**	**25.8**	**0.629**	**694**	**13.6**
	56-3 *L. dec×L. suk*	**66 (1056)**	**51**	**28.3**	**26.4**	**28.0**	**0.785**	**829**	**16.2**
	56-4 *L. kae×L. suk*	**61 (976)**	**51**	**27.6**	**26.9**	**27.7**	**0.766**	**748**	**14.7**
	56-8 *L. eur×L. suk*	**25 (400)**	**51**	**30.7**	**25.2**	**26.9**	**0.875**	**350**	**6.9**
	56-8Eb *L. kae×L. suk*	**12 (192)**	**51**	**30.1**	**23.0**	**29.5**	**0.958**	**184**	**3.6**
	56-22 Eb *L. eur*[2]	**2 (32)**	**51**				**0.625**	**20**	**0.4**
	Arkhangelsk	71 (1136)	51	24.3	22.6	24.7	0.493	560	11.0
	Sverdlovsk	62 (992)	51	22.5	19.9	22.0	0.389	386	7.6

Jonsson (1978) studied growth, survival, and stem quality of the Russian larch hybrids in Söråbäset and Storbränna after 20 years, and found the Russian larch hybrids to have superior juvenile growth compared to the pure *L. sukaczewii* provenances. The hybrid between *L. decidua* and *L. sibirica* was the best hybrid at this time of evaluation. The most common defects were twisted growth, forking, and double stems. In quality the hybrid between Russian larch and the European mother tree was better than with the Japanese larch as mother tree.

In Arvidsjaur the site index is low and has resulted in the lowest volume production. The production was as low as 0.8 to 1.5 m^3 ha^{-1} $year^{-1}$ for the Sverdlovsk and Arkhangelsk provenances, respectively. This site is the only one of the six sites that was originally a forest site, and the site was in addition burned in 1933 and treated with herbicides in 1954 to kill broadleaved vegetation before establishment of the larch experiment. These treatments may have had an influence on the fertility of the site.

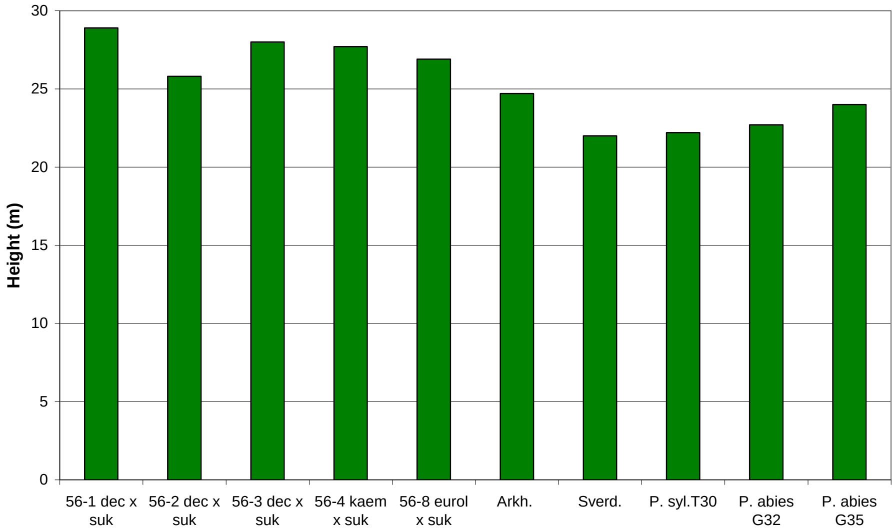


Fig. 15. Dominant height of five different larch hybrids and two provenances of Russian larch (*Larix sukaczewii*) in Söråbäset, at the total age of 51 years. As comparison the estimated dominant height at similar age of Scots pine and Norway spruce at the most fertile sites on forest land in northern Sweden is presented. Site index T30 in Scots pine corresponds to a dominant height of 30 m at the total age of 100 years. Norway spruce G35 shows the dominant height of the most productive spruce stand on abandoned farm land in northern Sweden (Johansson 1996). Parents of hybrids are defined in Table 6 and 7.

The hybrid 56-8 is a crossing in which hybrid larch (*L. eurolepis*) has been used as mother and *L. sukaczewii* as father and is evidently inferior to the other larch hybrids (Table 12). The low production in this hybrid is due to high mortality. If the trees survives the first crucial years, the height development is quite good (Fig. 15). The hybrids 56-8Eb and 56-22Eb having Japanese mothers are not adapted to the site in Sörånäset and are outcompeted. It is also interesting that the tallest and biggest tree in the whole experiment (height 31 m, dbh 55 cm) is found in the hybrid 56-4, an offspring of the Japanese larch mother (L k 247) and Siberian larch father (L s 156).

The reason for the superiority in growth in the hybrids is probably a combination of several factors. The seed of the two Russian provenances, Arkhangelsk and Sverdlovsk, was collected as bulk, most likely in connection to forest operations. Therefore the seed trees were not selected and the seed collection represents an average of trees in the stand in contrast to the hybrids, where the parent trees were selected plus trees. Unfortunately it is not possible to separate the effect of individual parent tree selection and the hybrid effect between two larch species. Probably a part of the superiority of the hybrids is related to the selection of the parent trees.

Another explanation could be hybrid vigour or heterosis, a common term used to explain the superiority of interspecific hybrids compared to the pure species. Research in hybrid larch (*L. eurolepis*) has revealed a positive correlation between genetic distances of parents and growth in the F1 hybrid (Arcade *et al*. (1996). The high level of heterozygosity in the hybrid was suggested as the explanation for the better growth of the hybrid compared to the parental species.

A third explanation could be the different growth rhythm of the hybrids. Compared to pure Russian larch, the hybrids have a longer growing season in the fall and should therefore also produce more, if not damaged by autumn frost.

The yield of *L. sukaczewii* in Sweden has been described by various researchers. Wiksten (1962) found that provenances of Russian larch from Arkhangelsk, Raivola, and the southern Ural mountains to have higher yields than Scots pine in northern Sweden on more fertile sites during the first 50-60 years. In the southern and middle part of Sweden, larch was equal to Scots pine during the same time span. Remröd and Strömberg (1977) found that after 50 years height growth declines more rapidly in larch than in pine, that larch does not tolerate denser stands, and that the areal volume production therefore can not compete with Scots pine or Norway spruce. Martinsson (1995), however, found that the height growth did continue longer than Remröd and Strömberg suggested, and that the volume production per hectare was 20-25 % higher for larch on more fertile sites at a rotation period of 100 years. The larch production on lower site indexes, however, has in all production studies in Sweden been found to be inferior to Scots pine (Wiksten 1962; Edlund 1966; Remröd and Strömberg 1978; Martinsson 1995).

Strand (1963) studied European and Siberian larch and their production when planted in Norway and compared it to Schober's (1949) results on European larch grown in Germany. Strand concluded that larch in Norway, both Siberian and European, had a total growth in basal area, in the first 50 years as high as European larch has in Central Europe. According to Strand the increment probably had an early maximum at 50-70 years.

Russian larch compared to European larch, Scots pine, Norway spruce and silver birch

The tree species trials in Siljansfors are the youngest of the three trial categories and established on the most southern locality, but at a relatively high elevation (230-360 m). The high production of the two different provenances of European larch (*Larix decidua*), one Polish and one from high altitude (1400 m a.s.l.) in the Tatra Mountains (Slovakia) gives an illustration on the broad adaptability of this species. The interest for growing European larch has been very low in Sweden, since serious attacks of larch canker (*Lachnellula willkomii*) mainly in maritime localities in southern Sweden (Martinsson and Winsa 1989). In the middle part of Sweden, however, it is possible that European larch could be a good alternative on high altitudes on more fertile sites. The results from this investigation suggest that. Further north in Sweden, there is lack of experience on the adaptation of European larch. However, Lähde *et al*. (1984), reported good hardiness of European larch in major parts of Finland, although the quality of stems was inferior to Siberian larch (Martinsson and Winsa 1989).

Although situated on a climatically more favourable site the Russian larch at site 9229 has lower mean annual increment than at site 9237 (Table 13 and 14). The general result that all species have shown better growth at trial 9229, might be influenced by its location in a slope. Although not indicated in differences in ground vegetation, both sites belong to the *Vaccinium* forest type, site 9237 is situated in a slope and is probably a better site for the larches, which growth is positively affected by moving groundwater (Schotte 1917, Edlund 1966, Martinsson 1995). The different seed sources of Russian larch used, in site 9237 seed orchard seeds from Domsjöänget (SWE), while at trial 9229 the Russian provenance Onega also could play a role in the better production at site 9237.

Table 13. Siljansfors, trial 9237, Central Sweden. Trial established 1968.

Tree species	No. of trees/ha after last thinning	Total age years	Mean dbh, cm	Mean tree height, m	Dom. height m	Basal area m^2/ha	Standing Volume m^3 /ha	Total prod. m^3/ha	Tree vol. $m^3 tree^{-1}$	Mean annual Increment from birth m^3/ha and year	Mean annual increment 1994-2004 m^3/ha and year
L. sukaczewii	553	40	24.5	21.3	22.3	18.5	184	375	0.502	9.4	12.3
L. decidua	608	40	25.9	23.4	24.4	18.3	201	406	0.586	10.2	15.7
Pinus sylvestris	1295	40	18.7	15.6	16.4	22.0	170	324	0.212	8.1	11.7
Picea abies	2040	40	12.2	12.4	15.2	20.6	134	156	0.079	3.9	9.2
Betula pendula	786	38	18.5	19.7	20.5	16.0	143	242	0.242	6.4	7.8

Table 14. Siljansfors trial 9229, Central Sweden. Established 1964-1966.

Tree species	No. of trees/ha after last thinning	Total Age Years	Mean dbh, cm	Mean tree height, m	Dom. height m	Basal area m^2/ha	Standing Volume m^3/ha	Total prod. m^3/ha	Tree vol. $m^3 tree^{-1}$	Mean annual Increment from birth m^3/ha^{-1} $year^{-1}$	Mean annual increment 1992-1999 m^3/ha^{-1} $year^{-1}$
L. sukaczewii	592	37	19.8	17.4	18.2	18.2	150	267	0.254	7.2	13.3
L. decidua	466	37	22.8	21.7	22.9	18.4	189	320	0.428	8.6	15.4
Pinus sylvestris	1192	38	15.7	14.5	15.6	23.1	166	259	0.139	6.8	9.6
Picea abies	2405	38	8.4	8.9	11.1	13.4	63	64	0.026	1.7	4.4
Betula pendula	699	37	14.0	17.3	18.0	10.7	86	151	0.125	4.1	5.1

The higher production of Russian larch compared to Scots pine on this type of site is in accordance with earlier research (Wiksten 1962, Edlund 1966, Martinsson 1995). Site index for Scots pine on the two sites is T28 (dominant height of 28 m at 100 years total age) which represents a rather fertile site in this area. Martinsson (1995), studying the production of *L. sukaczewii* in northern Sweden, found that with increasing site index the superiority of larch compared to Scots pine increased. The significant superiority in yield (317 % respectively 140 % on the two sites) of Russian larch compared to Norway spruce could partly be explained by the low age of the stand. Norway spruce has a low production rate the first half of the rotation time. It is shown in Table 13 that the current increment of spruce is increasing fast between 30 and 40 years of age. The annual increment of Russian larch is, however, still considerable higher than in Norway spruce during the last 10 years period. It will be interesting to see how long this superiority lasts.

Table 15. Results of field trial 9071 Siljansfors, Central Sweden and 201 Breivik, Norway. Established year 1926 respectively 1928.

Exp. site	Tree species	Prov.	N trees at inv.	Total age years	Mean dbh, cm	Mean tree height, m	Dom. height, m	Bas-al area, m^2	Total prod. m^3/ ha	Mean annual incr., m^3 ha^{-1} $year^{-1}$
Siljans-fors 9071	*L.suk*	Raivola	30	86	35.8	28.5	29.7	24.9	604	7.0
Breivik 201	*L.suk*	Raivola	59	76	32.0	26.1	29.2	36.3	516	6.8

The two older stands in Breivik and at Siljansfors are of interest because of that the same seed source, Raivola, could be compared at two sites with two different types of climates. Breivik is located close to the coast in northern Norway (Lat 67° 04´N) with a strong maritime influence, temperature fluctuations around 0°C are common during winter, while Siljansfors has a local continental climate. The winters are milder and summers cooler in Breivik and the precipitation much higher. Temperature sum is 260 d.d. higher in Siljansfors, therefore a superiority in growth would be expected. The results after 76 respectively 86 years, however, show almost identical mean annual productions between the two sites (Table 15).

Raivola larch forest, a man made plantation of *L. sukaczewii* with seeds originating from the Arkhangelsk district is situated on the Karelian Isthmus 63 km north-west of St Petersburg (Redko and Mälkönen 2005). The stand is situated within 15 km from the coast of the Baltic Sea and is under a certain maritime influence. The Raivola seed source has been widely used in Finland, Sweden and Iceland and has been shown to have a very wide ecological niche (Mikola & Vakkari 1995). It tolerates the climate in major parts of Finland. They found the main reason for this to be due to its high individual physiological plasticity. If climate change will progress according to IPCC's scenarios (IPCC 2007), the climate in northern Sweden will become more maritime, with higher temperature rises in the winter than in summer. It is therefore of interest to use provenances that are adapted to sudden mild spells during winter. Raivola seed source seem as a good alternative in this perspective.

Reports from Alaska (Alden 2006), show that the Raivola larch seed source also are adapted well there. Growth is clearly superior to the indigenous White spruce (*Picea glauca*). Mean heights of 20.7 m after 36 growing season has been recorded. *L. sukaczewii* and *L. sibirica* was considered as among the most promising exotic species there.

An advantage of using larch is its ability to develop merchantable timber in a shorter time than the indigenous conifer tree species (Hakkila *et al.*1972). This was clearly shown in the Siljansfors trial, where Russian larch had mean volumes per tree between 2.3 to 6.7 times greater than Scots pine and Norway spruce respectively (Table 13 and 14).

Considering the small plots, comparing height growth gives more reliable indication of production potential, and in the tests with Siberian larch hybrids, Scots pine, and Norway spruce grown on abandoned farmland, the larch hybrids were 5-6 meters higher than pine and spruce at 50 years age.

Stem quality traits were not scored during the assessment of this material. However, all provenances and hybrids demonstrated heavy branchiness. This is often the case in larch growing in pure stands, particularly in larch stands established by planting. Hybrid larch as well as pure Siberian larch develops thinner branches and better self pruning in a mixed stand.

Considering the growth potential in Russian larch hybrids, future research on these hybrids is of great interest. Frost resistance, site requirements and silvicultural methods need to be investigated. Individual plus tree selection and establishment of seed orchards for Russian larch hybrids would also be of great interest.

4 Conclusions

- Among the four Eurasian larch species compared, Russian larch (*Larix sukaczewii*) seems best adapted to northern Sweden. It has the highest survival on the two northern sites, a trend that is confirmed by the results from five smaller test sites located north of Lat. 64° N., which includes the same provenances and where *L. sukaczewii* also had the highest survival of the four compared species.

- *L. sukaczewii* showed best spring and autumn frost hardiness in the frost tolerance test, where the *L. gmelinii* and *L. cajanderi* provenances had high degree of frost injuries.

- From stem quality aspects *L. sukaczewii* seems also as the best choice, since many of the Far Eastern provenances of *L. gmelinii* and *L. cajanderi* having seriously crooked stems.

- Within, *L. sukaczewii* the highest survival on the northern sites is shown by provenances originating in north western Russia, south of Arkhangelsk. The most northern provenances did not show better hardiness and had slower growth.

- *L. sibirica* shows bad adaptation, especially on the southern site. On the two northern sites its survival increases but is still inferior to both *L. sukaczewii* and *L. gmelinii*.

- On all three sites, the juvenile growth of *L. gmelinii* was superior to the other species. It was especially provenances from Khabarovsk and Sakhalin that showed superior growth. The Khabarovsk provenance had, however, high mortality on one of the northern sites.

- The most northern provenances and provenances originating from strong continental areas grew slow and had low survival, especially on the southern test site.

- Strong influence from both geographic and climatic variables was observed for all tested species, both on survival and growth. Within *L.*

sukaczewii survival was most dependent on latitudinal origin and temperature climate of provenance origin. On the two northern sites longitude and continentality were most important with eastern more continental provenances having lower survival.

- The results of the provenance-progeny tests, together with older provenance and production trials, give an indication of good adaptation of *L. sukaczewii* to Swedish conditions. How global warming will affect the suitability of this and the other species is uncertain.

- The early age of the present progeny tests (5 years) is most likely one reason for the low or absent significant genetic information at the family level. Still, heritabilities, especially provenance plus individual heritabilities, indicate that breeding improvement for height and stem straightness could be possible. Evaluations at higher ages should more safely reveal breeding possibilities, as also in a later stage establishing well-designed second generation progeny tests with the present material.

5 Future research

The large provenance/progeny trials should be followed up and evaluated for genetic parameters in about 5-10 years. Local adaptation to the test sites and growth characteristics will become more pronounced in the future. Selection of families and individuals within families should be done. Larch seed orchards could be built upon the selected material. Hybridization may be one option for such seed orchards. International cooperation between the Nordic countries and Russia may become relevant. The genetic material in the three test sites could function as breeding populations for future selection and function as a genetic base for seed orchards.

Bearing in mind the changing climate, and the potential for development of after effects, land races, or hybrids, seed material from southern plantations and seed orchards could have the most promising future in less harsh environments in Sweden. For far northern latitudes and high altitude sites, Russian larch (*L. sukaczewii*) is probably the safest choice, thus for these purposes, the big field trials have an important usage in the future.

Bio-fuels will get increasing importance in future forestry as fossil fuels become limited and are being replaced by alternative forms of energy. Trees with the production potential as the Russian larch hybrids have shown (Paper IV) will become increasingly interesting. In the past, when pulp was the only market for wood of small dimensions from thinning, there were problems to find markets to sell small dimension larch wood, owing to higher costs for pulping. Now and within the foreseeable future, production of bio-fuels from thinnings of larch stands is becoming economically feasible, although producing high quality timber will continue to be the main focus when planting larch. The wood quality of these fast-growing hybrids will continue to be an important management and research issue. The special characteristics of larch wood, with its high density and high content of water soluble extractives are of interest in respect to alternative use of wood products.

With respect to the good juvenile growth and hardiness of some of the provenances from the Russian Far East and their rather bad stem straightness, breeding for better stem shape in these provenances is also an important issue for future research.

Also within the field of silviculture, there are questions concerning the Russian larches that need to be investigated more. The yield in mixed stands, together with Norway spruce for example, should be compared with the yield in pure larch stands. The influence of different planting densities and pre-commercial thinning and thinning regimes on quality and growth could also be investigated further. The often seen big variability in growth within larch plantations and what factors that influences this, what micro stands conditions that favour larch, need also to be investigated more. Effect of mycorrhiza fungus for growth of larch stand and if growth and survival in young plantations would be favoured if mycorrhiza was inoculated at the seedling stage is also interesting research areas. The susceptibility of the different Russian larches to root rot in northern Sweden is not well known, also this is an important future research project.

The Russian larch hybrids have been showing exceptional growth in northern Sweden. In the 1960s seed orchards with hybrids were established but only two, Maglehem (*L. decidua* x *L. kaempferi*) and Långtora (L. *kaempferi* x L. *sibirica*) have produced seeds of any significant quantity. New seed orchards would be of interest, and are recommended.

6 Acknowledgements

First I would like to express my gratitude to my supervisors; my main supervisor Owe Martinsson, and co-supervisors Anders Fries, Björn Hånell and Dag Lindgren for help and support during the work of the thesis. Owe initiated the Russian-Scandinavian larch project after long and stubborn struggle and much thanks to his initiative. Russian larches are now being tested in ten different countries around the world. Thanks for your encouragement and guidance through the years. Anders, thank you for your dedication in reading manuscripts and always give quick replies whatever the question. Invaluable your contributions have been.

Dag and Björn, thanks for constructive discussions during our meetings and help with financial support during the last tough months.

Furthermore I would like to thank all the people that have been working together with me in the field, measuring the larches; Tom Gärds, Lena Helin, Joel Kelloniemi, Lidia Kovler, Kurt Olsson, Håkan Schüberg and Nicole Suty, your help was also invaluable. It was the best part of the whole experience, through drought and snow and rain measuring larches day by day. Rikard Jakobsson, Pelle Mattsson and Mozosi Rugerinyange, Tamara Dumanskaya and Ludmila Karlova, also contributed to the project by field work.

Participants in the Russian-Scandinavian larch project, among them, Leonid Milyutin, Vladimir Barzut, Alexandra Berkutenko Aleksey Fedorkov, Valery Putenikhin, organizing the collection of seed from all over Russia, must be mentioned, without your work my thesis would not have written. Natalia Demidova, Boris Mochalov and Vladimir Barzut, Jaap Buitink and Gisle Skaret, Teijjo Nikkanen, Seppo Ruotsalainen among others, organized Siblarch meetings and field trips that brought us to various exotic places in northern Russia and Norway and also to the famous Raivola larch forest.

Susan Jeglum revised the language of the manuscripts, which was needed and much appreciated.

Bispgården colleagues, Gabriella Gärds, P-O Nilsson, Håkan Schüberg, Micke Rein, Robert Nygård, Tom Gärds and Nils-Erik Jonsson, thanks for help, good company, astonishing stories from Africa, fierce badminton matches, interesting sport discussions, various other discussions and good food.

Other persons at Bispgården that have been helpful are KA-Driftteknik (Kent Andersson, Sören Olsson, Roland, Micke) They have solved computer problems, irritating flickering lights, printer problems, heating problems at Brynet and so on, thanks to you too. Älggårdsberget (Therese Moe, Ulrika Sjöbom, Kicki, Carola, Tuula, Katharina) for having probably the best lunch restaurant in this part of the country. Thanks also Anders Jönsson for welcoming us all to Bispgården.

Thanks also Erik Andersson, our head chief at JiLU, for showing interest and belief in our larch project, Bengt Andersson for valuable discussions about the evaluation of the progeny trials and Berit Gregorsson for help with background material for the Skogforsk's production plots.

I also want to thank Tore Ericsson, Sören Holm, Jan-Erik Nilsson and Robert Nygård for guidance in statistics.

Furthermore, I thank Ann-Kathrin Persson for help with administrative questions.

The cooperation with co- writers has been good education. Thröstur Eysteinsson, Brynjar Skúlason, Gisle Skaret, Johan Westin, Christer Karlsson, thanks.

Thanks also to the staff at Skogisbiblioteket for help in finding old larch articles and books and Jim Wallgren, Arkitektkopia for editing and printing the thesis.

Financial support from the Kempe foundation and Interreg project Siblarch is also gratefully acknowledged.

Finally I would like to thank my parents for support and encouragement during these years. Your search for facts has been a good inspiration to me. Kaisa and Marc, for your company, friendship and support.

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