

# The Growth Rhythm and Height Growth of Seedlings of Siberian (*Larix sibirica* Ledeb.) and Dahurian (*Larix gmelinii* Rupr.) Larch Provenances in Greenhouse Conditions

Antti J. Lukkarinen, Seppo Ruotsalainen, Teijo Nikkanen and Heli Peltola

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The aim of this study was to determine whether the growth rhythm and height growth differ between various larch provenances grown in greenhouse conditions. We also investigated whether the geographic and climatic conditions at the origin of the provenance could explain the possible differences between the provenances. The study material consisted of 16 Russian Siberian (*Larix sibirica* Ledeb.) and Dahurian larch (*Larix gmelinii* Rupr.) provenances and four seed sources from Finland as comparison lots. The growth rhythm differences were clearest between the southern and northern provenances; the southern provenances grew for a longer period and the proportion of late summer height growth was larger. Autumn colouration also developed later in these provenances. In the Russian larch material the provenances with a longer growing period had greater height growth. In the whole material the relationship was not so linear due to the deviating behaviour of the comparison material. Several of the Russian larch provenances were taller than the Finnish comparison seed lots, although the difference was not statistically significant. However, the growth of these provenances must be followed for a much longer period in field trials before any conclusions can be drawn about their usability in practical forestry.

**Keywords** larch, *Larix*, provenance, growth rhythm, height growth

**Addresses** Lukkarinen and Peltola, University of Joensuu, Faculty of Forest Sciences, P.O. Box 111, FI-80101 Joensuu, Finland; Ruotsalainen and Nikkanen, Finnish Forest Research Institute, Punkaharju Research Unit, Finlandiantie 18, FI-58450 Punkaharju, Finland

**E-mail** antti.lukkarinen@pp.inet.fi

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## 1 Introduction

A species with a wide geographical range can have several differing populations and, thus, a relatively large natural variation (Hagman 1993). The variation in individual trees and tree populations is caused by adaptation to the prevailing climate and growing site conditions and, therefore, the growth, quality and hardiness differ between provenances when grown in the same conditions (Eriksson et al. 2006). As a whole, the growth rhythm of a tree is defined by its genotype and environmental factors such as photoperiod and temperature (Partanen and Beuker 1999, Partanen 2004), to which the adaptation of the species is essential (Sarvas 1972, 1974). In order to survive in boreal conditions, trees have to develop adequate cold hardiness before the onset of winter (Partanen and Beuker 1999).

The size of the geographical range and the distribution of the species in different vegetation zones are the principal factors affecting the amount of geographic variability (Wright 1976). Provenance tests with species of the north temperate zone have revealed some common trends. Southern provenances usually start to grow later in the spring than northern provenances, and they also grow later in the autumn. As a result, they are less susceptible to late spring frost, but less resistant to extreme winter cold. They also have less intense autumn colouration (Wright 1976).

Similarly to latitude, altitude also affects the adaptation of tree species, because temperature decreases on moving upwards (Hämet-Ahti et al. 1992). In the troposphere the average temperature drop per hundred meters of increasing elevation is 0.65 °C (Liljeqvist 1962), which corresponds to a transition of approximately one degree latitude to the north (Laaksonen 1976). The continentality of the climate, which increases on moving inland, also affects the performance of tree species, in addition to the local microclimate, due to the larger annual temperature range compared to that of an oceanic climate (Heikinheimo 1956, Tuhkanen 1984).

In order to find a suitable exotic species for the Finnish climate, for example, the provenance should originate from an area with similar climatic conditions (Ilvessalo 1920, Hämet-Ahti et al. 1992, Sarvas 2002). Adaptation can be affected through the selection of growing site,

but the climate cannot be changed (Hämet-Ahti et al. 1992). Failure in the selection of origin has often been the cause of poor success of an exotic tree species (Reinikainen 1997). However, areas having similar climatic conditions to Finland are very limited in number.

As far as Russian larches (*Larix* Miller) are concerned, regions that are climatically similar to Finland are found in northwest Russia and eastern Asia (Cajander 1917, Hämet-Ahti et al. 1992). Similar areas in Asia are situated in the coastal areas of the Okhotsk Sea (Hämet-Ahti et al. 1992), e.g. in the eastern and southern parts of Sakhalin, north-eastern parts of Hokkaido, Kurile Islands and along the eastern shoreline of the Kamchatka Peninsula (Cajander 1917).

The natural range of larch mainly covers the boreal zone of the northern hemisphere, and especially its coldest parts, reaching alpine and polar regions (Schmidt 1995, Sarvas 2002). Most larch species have, however, only rather small distribution areas that are limited to mountainous areas. Of the ten species commonly recognized in the larch genus, only the Siberian (*Larix sibirica* Ledeb.) and Dahurian larches (*Larix gmelinii* (Rupr.) Rupr.) in Eurasia and the North-American tamarack (*Larix laricina* (Du Roi) C. Koch) have a large natural range (Farjon 1990).

In Finland, the Siberian larch can be considered as a returnee species, which has formerly belonged to the Finnish flora (Robertsson 1971, Mäkinen 1982, Hirvas 1991). Nowadays, the range of Siberian larch covers an area extending from the northern parts of European Russia to the central parts of Siberia, south to the Altai Mountains and into north Mongolia and northwest China. Siberian larch grows on variable sites as pure or mixed stands, but it thrives the best on well-drained sandy or rocky soils. In comparison, Dahurian larch with its many varieties has spread throughout vast areas in eastern Siberia (Farjon 1990, Sarvas 2002). The main variety (*Larix gmelinii* var. *gmelinii* (Rupr.) Rupr.) occurs throughout most of the species distribution area in north-eastern Asia, whereas other varieties grow on the south-eastern edges of the range (Hämet-Ahti et al. 1992). On the western edge of its range Dahurian larch forms mixed stands with Siberian larch (Sarvas 2002), and in the north it forms the timberline (Cajander 1917). Dahurian larch grows on a range of sites and it is

undoubtedly the most heterogeneous of the larch species (Farjon 1990).

The first larch plantations in the Nordic countries originate from the 19th century in Finland and from the 18th century in Sweden and Norway (Martinsson and Lesinski 2007). The famous Raivola stand established in 1738 on the Karelian Isthmus has played a crucial role in Nordic larch research (Sarvas 2002, Redko and Mälkönen 2005). The approximate area of larch stands in Finland is currently about 30 000 hectares and 500–1000 hectares are planted annually. Only Siberian larch (*Larix sibirica* Ledeb.) of Raivola seed source is used. Seed is also sold by several seed orchards to other Nordic countries, especially to Iceland. The larch stands in Iceland consist of 1000 hectares of older stands and 5000 hectares of young stands established since the 1990's. The area of larch stands in Norway is about 3500 hectares and in Sweden 4000 hectares. An average of 170 hectares of larch is planted annually in Sweden. Most commonly the Nordic larch cultivations originate from the European part of Russia, but other origins and species have also been used. Most of the larch in Sweden are hybrid larch (*Larix* × *eurolepis* Henry) plantations established in the 1960's in the southern parts of the country. The majority of the Nordic larch plantations are sapling stands and young stands of first thinning age (Martinsson and Lesinski 2007). In Finland, for instance, there is not much larch timber on the market and little specialised industry that uses it. Harvesting opportunities will increase over time, but imports of larch timber from Russia are still needed if the industry plans to expand (Verkasalo 2001).

Already at the seedling stage, the climatic adaptation and hardiness of the trees can be predicted on the basis of their genetically determined growth rhythm. The development of the terminal bud describes well the growth rhythm of provenances and their adaptation to climate. For example, the northern provenances of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karsten) and lodgepole pine (*Pinus contorta* Douglas ex Loudon) cease their height growth and form terminal buds earlier in the autumn than the more southerly ones (Hagner 1970a, 1970b, Mikola 1980, 1982, Nilsson and Åman 1986). This relationship between origin

and growth rhythm has been studied less in Russian species of larch, but studies with tamarack show similar results as for the other conifers (Simak 1970, Joyce 1987).

The aim of this study was to compare the growth rhythm and height growth of seedlings representing 16 Russian larch provenances and four Finnish larch comparison lots in greenhouse conditions during the first growing season. The growth rhythm describes the adaptation and the height growth potential of the trees. Specifically, the study investigated whether the geographic and climatic variables of the origin of the provenances could explain the differences between the provenances. This study is a part of a larger international larch provenance test series, covering most of the range of the Russian larches. Provenance test sites with the same material have been established in Sweden, Norway, Iceland, Russia, France, Japan, China, Canada and the United States (Martinsson and Lesinski 2007).

Most of the larch material used so far in Finnish forestry originates from the Raivola stand and its descendants on the Karelian Isthmus (Reinikainen 1997, Redko and Mälkönen 2005). This study could help to identify alternatives for these provenances. No comprehensive provenance tests or broad investigations on the geographical variation of larches have so far been carried out in Finland to determine the most suitable provenances for forestry (Viherä-Aarnio 1993, Ruotsalainen 2006).

## 2 Material and Methods

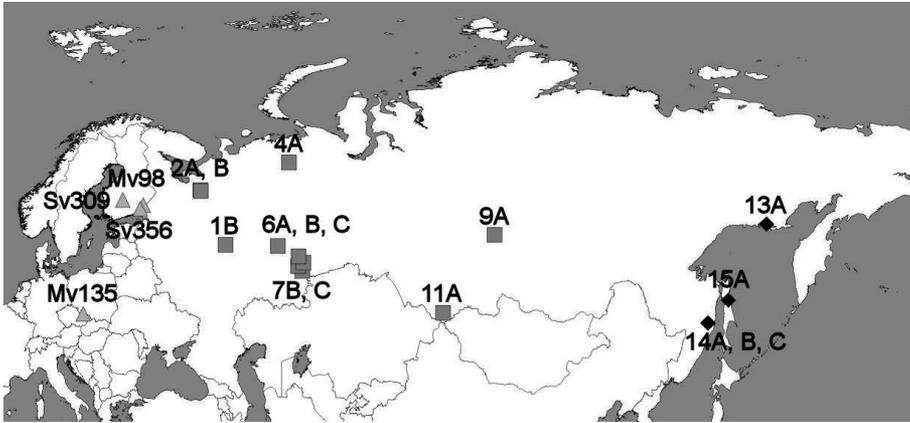
### 2.1 Locations and Climate of the Provenances and Stands

The seed material was collected in Russia during 1996–1999 (Abaimov et al. 2002). The material used in this study consisted of eleven Siberian larch (*Larix sibirica* Ledeb.) and five Dahurian larch (*Larix gmelinii* (Rupr.) Rupr.) provenances (Table 1), which cover most of the range of Russian larch (Fig. 1). The 16 Russian provenances were chosen from a slightly larger set of provenances by rejecting those that had weak germination or less than ten seed trees (a small number of seed trees was believed to weaken

**Table 1.** Geographic and climatic information and seed weight of the different provenances. Siberian larches (top), Dahurian larches (middle) and the comparison lots (bottom) are separated from each other with a horizontal line. The same grouping is also used in the figures.

Provenance Name of region	Nearest village/town	Geographical location and elevation			Annual mean temperature, °C	Continentality index	Seed weight, g/1000 seeds
		Latitude, N°	Longitude, E°	Elevation, m			
1B Nishnij Novgorod	Vetluga	57°30′	45°10′	145	3.3	43	9.4
2A Plesetsk	Ermisa	63°05′	40°21′	100	1.2	39	8.2
2B Plesetsk	Korasi	63°00′	40°25′	120	1.1	39	8.5
4A Petchora	Usinsk	66°00′	57°48′	75	-3.3	47	8.1
6A Perm	Okhansk, Yugo-Kamsky	57°19′	55°27′	160	2.7	47	9.6
6B Perm	Nyazepetrovsk, Uzaim	56°09′	59°32′	460	1.3	49	12.9
6C Perm	Kyshtym	55°43′	60°27′	480	1.4	49	13.5
7B Ufa	Miass	54°58′	60°07′	380	2.1	51	15.1
7C Ufa	Zlatoust	55°07′	59°30′	600	0.7	50	13.4
9A Boguchany	Boguchany	58°39′	97°30′	158	-2.3	63	9.7
11A Altai	Kosh-Agash	50°16′	87°54′	1630	-0.7	48	7.5
13A Magadan	Splavnaya	59°50′	150°40′	60	-2.8	41	2.6
14A Chabarovsk	Vaninskyi	49°09′	139°00′	100	1.5	53	3.1
14B Chabarovsk	Vaninskyi	49°12′	139°00′	125	1.3	53	3.2
14C Chabarovsk	Vaninskyi	49°08′	139°00′	90	1.3	53	3.2
15A Sachalin	Nogliki	51°50′	143°00′	50	-0.0	49	2.4
Mv98 Punkaharju <sup>a), b)</sup>	Punkaharju, Finland	61°48′	29°19′	95	3.1	34	9.2
Sv309 Lassimaa <sup>a)</sup>	Jämsänkoski, Finland	62°04′	25°09′	107	3.2	31	12.3
Sv356 Neitsytmiemi <sup>a)</sup>	Imatra, Finland	61°12′	28°48′	70	3.7	33	11.2
Mv135 Punkaharju <sup>b), c)</sup>	Krnov, Czech Republic <sup>d)</sup>	50°05′ <sup>d)</sup>	17°40′ <sup>d)</sup>	330 <sup>d)</sup>	8.2 <sup>d)</sup>	23 <sup>d)</sup>	5.9

<sup>a)</sup> Raivola origin, seed orchard or stand. <sup>b)</sup> Seed from Metla Punkaharju research forest. <sup>c)</sup> European larch (*Larix decciana* Miller). <sup>d)</sup> Values for origin.



**Fig. 1.** Provenance origins. Symbols: ■ Siberian larch provenances, ◆ Dahurian larches, ▲ comparison lots. Detailed information about the provenances is given in Table 1.

the representation of the provenance). Two of the four comparison lots originate from Finnish seed orchards and the other two from the cultivations of the Finnish Forest Research Institute in Punkaharju. One of the comparison seed lots (Mv135) from Punkaharju was European larch (*Larix decidua* Miller) and the other three were Siberian larch (*Larix sibirica* Ledeb.).

The species concept and nomenclature used in this study are according to Farjon (1990) and Hämet-Ahti et al. (1992), which differs from that used in Russia (Abaimov 2002). The Siberian larch (*Larix sibirica* Ledeb.) provenances 1B–7C and comparison lots Mv98, Sv309 and Sv356 are considered in Russian nomenclature as *Larix sukaczewii* Dyl. The Dahurian larch (*Larix gmelinii* var. *gmelinii* (Rupr.) Rupr.) provenance is considered in Russia as *Larix cajanderi* Mayr.

The geographical information about the provenance origins was mainly obtained from the literature and available databases (for example, see Martinsson and Takata 2000). However, clear inaccuracies in this information were corrected and missing information added. The average seed weight for the provenances (mass of thousand seeds) were calculated from single tree seed weights. The climatic data were interpolated from the high-resolution surface climate data provided by the Climatic Research Unit (Ten minute climatology 2002, New et al. 2002). Based on the above information, monthly mean temperatures for the

provenance origins were obtained by interpolating the temperature from the nearest value point (if deviation < 0.05 degrees, nearest value was used). An approximate annual temperature sum (d.d. degree days) was calculated from these monthly mean temperatures. In addition, altitude correction for the temperature value (and temperature sum) was also applied based on the difference between the interpolated altitude and the value provided by the seed collectors (a temperature drop of 0.65 °C for every 100 m in elevation was applied, see Liljeqvist 1962). The temperature sums calculated in this way were found to be consistent with the temperature sum map published by Tuhkanen (1984).

The following variables were used to describe the climatic properties of the seed collection sites: temperature sum with +5 °C threshold value, annual mean temperature, mean temperature of the coldest month (minimum temperature), mean temperature of the warmest month (maximum temperature), annual range of the monthly mean temperatures (minimum – maximum temperature), latitude (N°), longitude (E°), altitude above sea level and continentality index according to Tuhkanen (1980) (Eq. 1),

$$C = \frac{1,7A}{\sin(\varphi + 10^\circ)} - 14 \quad (1)$$

where *A* is the annual monthly temperature range and  $\varphi$  is the latitude (Tuhkanen 1980).

## 2.2 Layout of the Greenhouse Experiment and the Seedling Measurements

The experiment was set up in April 2005 at the Punkaharju Research Unit (61°48' N, 29°20' E, 81 m), Finnish Forests Research Institute, when the seeds were sown in greenhouse. Seven weeks after sowing, seedlings representing the individual provenances were transplanted to Plantek PL-64F seedling trays (115 cm<sup>3</sup>). At the same time, the seedlings were grouped into five different blocks, each block consisting of one seedling tray for each provenance (total of 64 seedlings per seedling tray). The growth dynamics was followed on eight seedlings growing at the centre of the tray in order to avoid the edge effect caused by the deviating growing conditions (i.e. a total of 20 provenances × 5 blocks × 8 seedlings = 800 seedlings). Autumn colouring was, however, observed on all the seedlings in the tray.

The seedlings were grown in typical greenhouse conditions. The temperature in the greenhouse varied generally between +20–30 °C, but no precise temperature monitoring was conducted. Overheating was avoided by opening the roof windows and by forced air circulation when the temperature exceeded +20 °C. Manual (by hand) watering and fertilization, applied as evenly as possible, were performed frequently. After transplanting, the seedlings were fertilised five times at one-week intervals (starting 20th June) with 0.2% concentration *Turve-Superex* liquid fertilizer (NPK fertilizer with micronutrients designed for peat cultivation).

The height growth of the seedlings was measured on July 5–6 and on October 5. The end of height growth was determined by observing the formation of terminal buds based on classification of the bud development into three different stages: 1. no bud, 2. bud formation started and bud greenish in colour, and 3. terminal bud formed and bud brownish in colour. Terminal bud observation was started on 6th of September and continued weekly up until 4th of October. The autumn colouring of the seedlings was recorded at seven-day intervals from the weeks 40–42 (6th, 13th and 20th of October) and classified into four different stages: 1. approximately 76–100 percent of green needles, 2. 51–75 percent, 3. 26–50 percent and 4. 0–25 percent.

## 2.3 Statistical Analysis

The measured seedling data and the geographical and climatic data were processed with Microsoft Excel 2002 SP3 spreadsheet software. For the statistical analyses, the length of the growing period was defined as the time from sowing to the time when 90 percent of all the seedlings measured in each provenance (5 blocks × 8 seedlings = 40 seedlings) had formed their terminal bud. The growth rhythm was divided into height growth during the early (height growth before July 6) and the late (height growth on October 5) growing period, and the development of autumn colouring.

Statistical analyses were performed with SPSS statistical program package 13.0 (SPSS for Windows, version 13.0; SPSS, Chicago, III). Abnormal values were removed if they were considered to be outliers. Differences between provenance means were tested with two-way analysis of variance with provenance and block as fixed factors. However, because the variances for the terminal bud formation, autumn colouring and height growth variables were unequal according to the Levene's test, the differences between provenances were also tested with Kruskal-Wallis non-parametric one way analysis of variance. Pair-wise analyses (with the Tukey post hoc test,  $p < 0.05$ ) were also used to test the differences between provenances.

The dependences between different variables were studied with Pearson correlation analysis and linear regression analysis. Regression analyses were used to explain the variation in measured variables on the basis of climatic and geographic data and with seed weight. The explanatory variables used were statistically significant with a probability of at least 0.05. Transformations of the data (square root, power, and logarithmic) were also performed for most of the geographical and climatic variables in order to study nonlinear relationships. In the above context, the Siberian larch provenance 4A Petchora was excluded from most of the statistical analyses because it was regarded as an outlier. The Siberian larch comparison lots were also excluded from the analyses when geographic or climatic variables were used as explanatory variables because the origin of these Raivola descendants is uncertain.

### 3 Results

#### 3.1 Differences between the Provenances

##### *Growth Rhythm*

The average length of the growing period of the provenances was 166 days from sowing to 90% bud formation. The European larch (*Larix decidua* Miller) comparison lot Mv135 had the longest growing period (190 days). The southern Olga Bay larches (*Larix gmelinii* var. *olgensis* (Henry) Ostenf. & Syrach Larsen) 14A, 14B and 14C Chabarovsk and Kurile larch (*Larix gmelinii* var. *japonica* (Regel) Pilger) 15A Sachalin also had relatively long growing periods. The shortest growing period was found in Siberian larch 2A Plesetsk (147 days), when 4A Petchora was excluded (all of its seedlings had formed terminal buds before the onset of the measurement).

The differences in bud formation between the provenances were statistically significant (Table 2). The Siberian larches differed significantly from the Dahurian larches (except for provenance 13A Magadan (*Larix gmelinii* var. *gmelinii*)) and from the European larch comparison lot Mv135 (Table 3).

The differences between the provenances in autumn colouring were statistically significant (Table 2). The development of autumn colouration was fastest in the Siberian larch comparison

lots and provenances 2A and 2B Plesetsk, 9A Boguchany and Dahurian larch 13A Magadan, which differed clearly from the more southern varieties. The European larch Mv135 was the last to develop full autumn colouration. Unlike the other provenances, uneven autumn colouration of the blocks was observed in Siberian larch comparison lots Mv98 and Sv309 (Table 3).

On the average, 78% of the total height growth occurred during late summer (after 6th of July). The differences between the provenances were statistically significant (Table 2). The proportion of late summer growth was over 80 percent in all the Dahurian larch provenances and the European larch comparison lot Mv135, whereas it was close to the average for the Siberian larch comparison lots. The lowest proportion of late summer growth occurred in provenances 4A Petchora (67%) and 7C Ufa (74%) (Table 3).

##### *Height Growth*

The average total height was 31 cm (Table 2). The differences between the provenances were relatively small, except for the Siberian larch provenance 4A Petchora (Fig. 2). The heights of the Dahurian larches were above the average. Of the Siberian larches, 1B Nishnij Novgorod and 6A and 6C Perm were the tallest, and also taller on the average than the Finnish comparison lots.

**Table 2.** Means and standard deviations (stdev) of the growth rhythm and growth variables and the two-way analysis of variances F-test and statistical significance of the differences between provenance and the coefficient of determination for the whole model.

Variable	n	Mean ± stdev	Analysis of variance	
			F	R <sup>2</sup>
Terminal buds, week 36 <sup>a)</sup>	19	2.0 ± 0.73	83.91 (<0.001)	0.96
Terminal buds, week 37 <sup>a)</sup>	19	2.2 ± 0.73	69.17 (<0.001)	0.95
Autumn colouring, week 40 <sup>b)</sup>	19	2.1 ± 0.78	194.52 (<0.001)	0.98
Autumn colouring, week 41 <sup>b)</sup>	19	2.9 ± 0.89	126.09 (<0.001)	0.97
Late summer growth, %	20	78.4 ± 5.08	3.94 (<0.001)	0.54
Early summer growth, cm	19	6.6 ± 1.13	4.10 (<0.001)	0.53
Late summer growth, cm	19	24.7 ± 2.82	3.94 (<0.001)	0.56
Total height growth, cm	19	31.2 ± 3.14	3.41 (<0.001)	0.51

<sup>a)</sup> Bud development stages: 1) no bud, 2) bud formation started and bud greenish in colour, and 3) terminal bud formed and bud brownish in colour.

<sup>b)</sup> The autumn colouring stages: 1) approximately 76–100 percent of green needles, 2) 51–75 percent, 3) 26–50 percent and 4) 0–25 percent.

**Table 3.** Means and standard deviations of the terminal bud<sup>1)</sup> and autumn colouring<sup>2)</sup> stages and proportion of late summer growth for the different provenances. Means in column with different letters are statistically significantly different (Tukey's test,  $p < 0.05$ ).

Provenance	Terminal buds, week 36	Terminal buds, week 37	Autumn colouring, week 40	Autumn colouring, week 41	Late summer growth, % <sup>3)</sup>
1B Nishnij Novgorod	1.88±0.27 <sup>b</sup>	2.33±0.40 <sup>b</sup>	2.00±0.00 <sup>b</sup>	3.00±0.00 <sup>c</sup>	78.46±3.45 <sup>b</sup>
2A Plesetsk	2.90±0.14 <sup>e</sup>	2.95±0.11 <sup>d</sup>	3.00±0.00 <sup>d</sup>	4.00±0.00 <sup>e</sup>	76.69±6.46 <sup>ab</sup>
2B Plesetsk	2.85±0.20 <sup>e</sup>	2.98±0.05 <sup>d</sup>	3.00±0.00 <sup>d</sup>	4.00±0.00 <sup>e</sup>	80.28±2.35 <sup>b</sup>
4A Petchora	3.00±0.00 <sup>-</sup>	3.00±0.00 <sup>-</sup>	4.00±0.00 <sup>-</sup>	4.00±0.00 <sup>-</sup>	67.34±13.93 <sup>a</sup>
6A Perm	1.98±0.10 <sup>bc</sup>	2.28±0.28 <sup>b</sup>	2.00±0.00 <sup>b</sup>	3.00±0.00 <sup>c</sup>	77.95±2.33 <sup>b</sup>
6B Perm	2.13±0.13 <sup>bc</sup>	2.74±0.22 <sup>bcd</sup>	2.00±0.00 <sup>b</sup>	3.00±0.00 <sup>c</sup>	74.82±2.84 <sup>ab</sup>
6C Perm	1.85±0.21 <sup>b</sup>	2.25±0.18 <sup>b</sup>	2.00±0.00 <sup>b</sup>	3.00±0.00 <sup>c</sup>	76.79±1.98 <sup>ab</sup>
7B Ufa	1.70±0.19 <sup>b</sup>	2.27±0.27 <sup>b</sup>	2.00±0.00 <sup>b</sup>	3.00±0.00 <sup>c</sup>	77.21±4.70 <sup>b</sup>
7C Ufa	1.93±0.22 <sup>b</sup>	2.38±0.43 <sup>b</sup>	2.00±0.00 <sup>b</sup>	3.00±0.00 <sup>c</sup>	74.40±2.66 <sup>ab</sup>
9A Boguchany	2.85±0.16 <sup>e</sup>	2.93±0.11 <sup>cd</sup>	3.00±0.00 <sup>d</sup>	4.00±0.00 <sup>e</sup>	79.01±2.28 <sup>b</sup>
11A Altai	2.40±0.35 <sup>cd</sup>	2.50±0.36 <sup>bcd</sup>	2.00±0.00 <sup>b</sup>	2.00±0.00 <sup>b</sup>	78.65±2.13 <sup>b</sup>
13A Magadan	1.74±0.32 <sup>b</sup>	2.44±0.25 <sup>bc</sup>	3.00±0.00 <sup>d</sup>	4.00±0.00 <sup>e</sup>	80.60±2.16 <sup>b</sup>
14A Chabarovsk	1.00±0.00 <sup>a</sup>	1.08±0.17 <sup>a</sup>	1.00±0.00 <sup>a</sup>	2.00±0.00 <sup>b</sup>	80.35±1.88 <sup>b</sup>
14B Chabarovsk	1.00±0.00 <sup>a</sup>	1.00±0.00 <sup>a</sup>	1.00±0.00 <sup>a</sup>	2.00±0.00 <sup>b</sup>	83.09±0.41 <sup>b</sup>
14C Chabarovsk	1.03±0.06 <sup>a</sup>	1.20±0.17 <sup>a</sup>	1.00±0.00 <sup>a</sup>	2.00±0.00 <sup>b</sup>	81.79±1.89 <sup>b</sup>
15A Sachalin	1.03±0.06 <sup>a</sup>	1.41±0.16 <sup>a</sup>	1.00±0.00 <sup>a</sup>	2.00±0.00 <sup>b</sup>	80.84±2.86 <sup>b</sup>
Mv98 Punkaharju	2.82±0.21 <sup>de</sup>	2.92±0.07 <sup>cd</sup>	2.40±0.55 <sup>c</sup>	3.40±0.55 <sup>cd</sup>	77.41±2.68 <sup>b</sup>
Sv309 Lassinnmaa	2.81±0.17 <sup>de</sup>	2.95±0.07 <sup>d</sup>	3.00±0.00 <sup>d</sup>	3.60±0.55 <sup>de</sup>	79.32±1.91 <sup>b</sup>
Sv356 Neitsytniemi	2.75±0.20 <sup>de</sup>	2.98±0.05 <sup>d</sup>	3.00±0.00 <sup>d</sup>	4.00±0.00 <sup>e</sup>	79.63±2.58 <sup>b</sup>
Mv135 Punkaharju	1.03±0.06 <sup>a</sup>	1.10±0.11 <sup>a</sup>	1.00±0.00 <sup>a</sup>	1.00±0.00 <sup>a</sup>	82.54±1.56 <sup>b</sup>

<sup>1)</sup> Bud development stages: 1) no bud, 2) bud formation started and bud greenish in colour, and 3) terminal bud formed and bud brownish in colour.

<sup>2)</sup> Autumn colouring stages: 1) approximately 76–100 percent of green needles, 2) 51–75 percent, 3) 26–50 percent and 4) 0–25 percent.

<sup>3)</sup> n=20

However, only the Siberian larch provenance 2A Plesetsk differed statistically significantly from the tallest provenances (Fig. 2).

### 3.2 Explanations for the Differences between Provenances

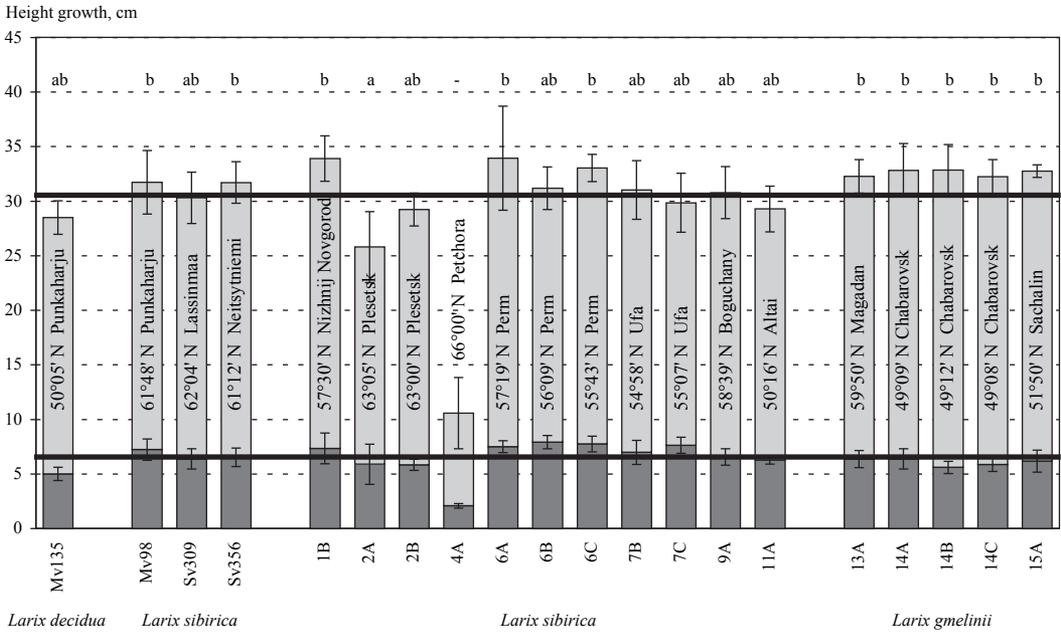
#### *Growth Rhythm*

There was a strong correlation between some of the measured growth rhythm variables and the geographic variables of the provenance origin (Table 4). A strong negative correlation was observed especially between the latitude and the duration of height growth. Also strong positive correlation was observed between the latitude and the autumn colouring, the northern provenances developing their autumn colouring first. The latitude and proportion of late summer height growth correlated negatively. In most cases neither the

longitude nor the altitude correlated with any of the measured variables. However, positive correlation was observed between the longitude and the late summer height growth.

The seed weight correlated negatively with the length of the growing period and the proportion of late summer growth (Table 4). Positive correlation was observed between the seed weight and the autumn colouration. However, it should be noted that Dahurian larch has, in general, distinctly smaller seed than Siberian larch. Thus, when only Siberian larches were used in the correlation analysis (n=13), none of the growth rhythm variables correlated with the seed weight.

In general, the climatic variables correlated poorly with the measured variables. The annual mean temperature of the origin showed corresponding, but weaker, and usually statistically non-significant correlation with growth rhythm, than latitude, i.e. provenances from northern, cold sites had faster development (Table 4). The only



**Fig. 2.** Average height growth and standard deviations of the different provenances. The two horizontal lines represent the early summer average height growth and the total average height growth. Means with different letters are statistically significantly different (Tukey's test,  $p < 0.05$ ).

**Table 4.** Pearson correlation coefficients between growth rhythm variables and geographic and climatic variables of the provenances. Statistically significant values ( $p < 0.05$ ) are highlighted in bold and the significance is shown in parentheses.

Variable	n	Latitude, N°	Longitude, E°	Annual mean temperature °C	Continental index	Seed weight, g/1000 seeds
Length of growing period	16	<b>-0.86</b> (<0.001)	0.37 (0.163)	0.48 (0.061)	-0.13 (0.622)	<b>-0.54</b> (0.017) <sup>a</sup> )
Autumn colouring, week 40	16	<b>0.91</b> (<0.001)	-0.32 (0.228)	-0.49 (0.056)	-0.02 (0.939)	<b>0.46</b> (0.050) <sup>a</sup> )
Autumn colouring, week 41	16	<b>0.93</b> (<0.001)	-0.17 (0.528)	<b>-0.56</b> (0.024)	0.42 (0.103)	0.44 (0.057) <sup>a</sup> )
Late summer growth, %	17	<b>-0.63</b> (0.007)	0.42 (0.090)	0.42 (0.098)	-0.13 (0.620)	<b>-0.50</b> (0.026) <sup>b</sup> )
Early summer growth, cm	16	0.25 (0.350)	-0.22 (0.420)	-0.20 (0.468)	0.48 (0.060)	<b>0.66</b> (0.002) <sup>a</sup> )
Late summer growth, cm	16	-0.45 (0.079)	<b>0.62</b> (0.011)	-0.04 (0.898)	0.18 (0.517)	<b>-0.47</b> (0.043) <sup>a</sup> )
Total height growth, cm	16	-0.32 (0.230)	-0.28 (0.301)	-0.11 (0.694)	0.34 (0.193)	-0.17 (0.476) <sup>a</sup> )

<sup>a</sup>) n = 19, <sup>b</sup>) n = 20

statistically significant correlation was observed between the annual mean temperature and autumn colouring in week 41.

Several of the measured growth rhythm variables also correlated with each other (Table 5). Provenances with a long growing period had late autumn colouration and high, relatively late summer height growth. Autumn colouration also correlated negatively with the proportion of late

summer height growth, although this was not statistically significant.

Geographic variables also proved to be the best explaining variables for the length of the growing period (*LGrPe*). Latitude (*Lati*) explained 74 percent of the variation in the length of the growing period (Eq. 2, Fig. 3). According to Eq. 2, an increase of one degree in latitude shortens the length of the growing period by 2.2 days.

**Table 5.** Pearson correlation coefficients between the measured variables (n = 19).

Variable	Autumn colouring, week 40	Autumn colouring, week 41	Late summer growth, %	Early summer growth, cm	Late summer growth, cm	Total height growth, cm
Length of growing period	<b>-0.90</b> (<0.001)	<b>-0.88</b> (<0.001)	<b>0.51</b> (0.027)	-0.29 (0.223)	<b>0.53</b> (0.021)	0.37 (0.122)
Autumn colouring, week 40		<b>0.94</b> (<0.001)	-0.36 (0.133)	0.17 (0.489)	<b>-0.47</b> (0.041)	-0.37 (0.123)
Autumn colouring, week 41			-0.39 (0.098)	0.29 (0.228)	-0.31 (0.190)	-0.18 (0.474)
Late summer growth, %				<b>-0.82</b> (<0.001)	<b>0.54</b> (0.017)	0.18 (0.470)
Early summer growth, cm					0.02 (0.926)	0.41 (0.083)
Late summer growth, cm						<b>0.92</b> (<0.001)

$$LGrPe = 291.345 - 2.238 \times Lati \quad (2)$$

$$R^2 = 0.737, F = 39.161 (p < 0.001), n = 16$$

When the altitude (*Alti*) and continentality index (*Cont*) were added as explanatory variables to the equation, the coefficient of determination rose to 92.7 percent (Eq. 3). An increase in altitude and continentality decreased the length of the growing period.

$$LGrPe = 333.925 - 2.602 \times Lati - 0.011 \times Alti - 0.407 \times Cont \quad (3)$$

$$R^2 = 0.927, F = 50.915 (p < 0.001), n = 16$$

The autumn colouration at week 40 (*Colw40*) was also the stronger the more northern and the higher the altitude of the origin of the provenance and the lower the annual mean temperature (*MTYr*) (Eq. 4).

$$Colw40 = -6.322 + 0.149 \times Lati + 0.00046 \times Alti - 0.067 \times MTYr \quad (4)$$

$$R^2 = 0.943, F = 66.401 (p < 0.001), n = 16$$

At week 41, the degree of autumn colouration (*Colw41*) increased with latitude and decreasing annual mean temperature (Eq. 5).

$$Colw41 = -5.826 + 0.160 \times Lati - 0.122 \times MTYr \quad (5)$$

$$R^2 = 0.956, F = 138.894 (p < 0.001), n = 16$$

Latitude also explained 39 percent of the variation between the provenances in the proportion of late summer height growth (*LSGr%*) (Eq. 6).

$$LSGr\% = 103.046 - 0.445 \times Lati \quad (6)$$

$$R^2 = 0.393, F = 9.697 (p = 0.007), n = 17$$

### Height Growth

None of the geographic or climatic variables explained well the total height growth, although the late summer height growth correlated with longitude. It must be noted, however, that all the eastern provenances were also southern (except Magadan 13A) and well growing provenances of Dahurian larches, which explains this result. The seed weight (*SeedW*) explained 43 percent of the early summer height growth (*ESGr*), the height growth being greater in provenances with heavy seeds (Eq. 7).

$$ESGr = 5.499 + 0.128 \times SeedW \quad (7)$$

$$R^2 = 0.431, F = 12.856 (p = 0.002), n = 19$$

The early summer height growth correlated negatively with the proportion of late summer growth (Table 5). The late summer growth also clearly correlated with the length of the growing period, proportion of late summer growth and total height growth as well as with autumn colouration at week 40. The total height growth (*TotGr*) was best explained by a combination of transformations of the length of the growing period (Eq. 8). The relationship was curvilinear: with a long growing period the total growth started to decrease, although in the shorter growing periods the correlation was positive (Fig. 4).

$$TotGr = -312.203 + 35.424 \times \sqrt{LGrPe} - 4.061 \times \frac{LGrPe^2}{1000} \quad (8)$$

$$R^2 = 0.556, F = 10.008 (p = 0.002), n = 19$$

Relatively similar results were obtained when

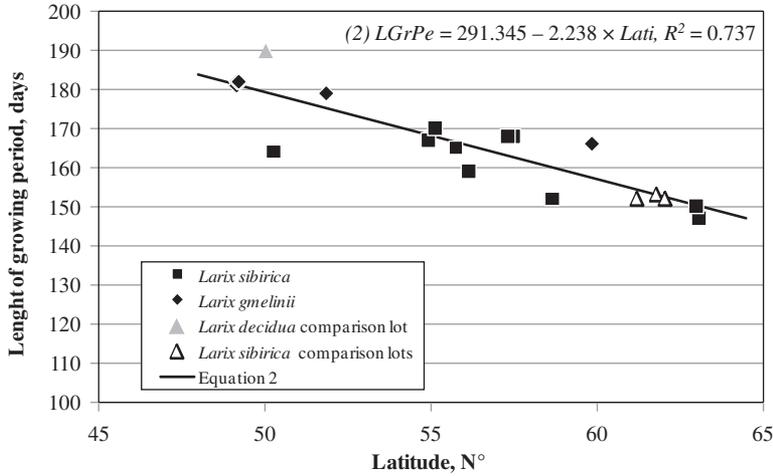


Fig. 3. Length of the growing period (in days) in relation to latitude (n = 16).

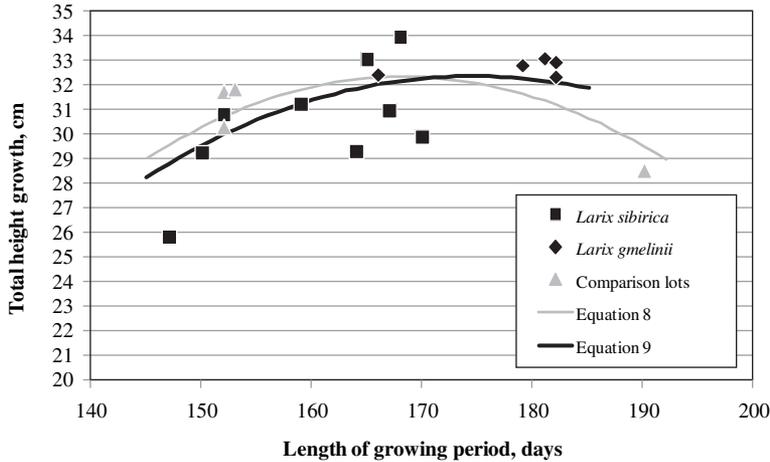


Fig. 4. Relationship between the total height and the length of the growing period. Graphs representing the whole material (Eq. 8) and the Russian larch provenances (Eq. 9) are shown.

the total growth was studied in the Russian provenance material, without the comparison lots but the decrease in the total growth with longer growing periods was not as strong as in the whole material (Eq. 9, Fig. 4).

$$TotGr = -249.871 + 28.486 \times \sqrt{LGrPe} - 3.089 \times \frac{LGrPe^2}{1000} \quad (9)$$

$R^2 = 0.650$ ,  $F = 11.157$  ( $p = 0.002$ ),  $n = 15$

## 4 Discussion and Conclusions

The average length of the growing period, 166 days, is far longer than that observed in natural conditions, and especially in later growing seasons. It was caused by the early onset of the growing period and favourable growing conditions in the greenhouse. It must also be borne in mind that the growing period as defined in this study also included the time between sowing

and germination. The range in the length of the growing period between the provenances was 43 days. In fact, the difference was even larger because the height growth of provenance 4A Petchora had already ended before the measurements were started. It should be also noted that transplantation of the seedlings may have caused some error in the results, especially in the case of early summer growth.

The differences between the provenances in all the growth rhythm variables were clear and statistically significant, and they could be explained on the basis of the geographical variables, of which latitude was the most important. The clear decrease in the length of the growing period with increasing latitude has earlier been demonstrated by Mikola (1982) for Scots pine, and is in line with the general geographical variation of forest trees (Wright 1976). In this study, latitude explained 74 percent of the length of the growing period (Eq. 2). According to Simak (1970), the growth processes of larch are highly regulated by photoperiod and temperature. A shorter day length could explain the poor height growth and early growth cessation of the northernmost provenance from Petchora.

The latitudinal variation between the provenances in autumn colouration was in line with earlier findings, as summarised by Wright (1976), i.e. northern provenances have earlier colour development than southern ones.

There was a curvilinear relationship between total height and the length of the growing period; with an extremely long growing period the total height started to decrease. This was partly caused by the European larch comparison lot, which formed its buds late in the autumn. However, the results were similar when only the experimental material proper was included (Eqs. 8 and 9, Fig. 4). Even though the length of the growing period of the Dahurian larches was very long, the rate of height growth declined towards the end of the growing period and could not match the best performing Siberian larches with shorter growing periods.

Similar to the findings of this work, the length of the growing period and the total height growth have been found to correlate well in Scots pine and Norway spruce provenances already at the seedling stage (Mikola 1980). Although the differ-

ences in total height after the first growing season in the greenhouse were small, it is expected that the differences between provenances will become more pronounced in field conditions.

The seed weight correlated with the length of the growing period and the proportion of late summer height growth (Table 4). However, these parameters should be regarded as indications of the indirect influence of provenance or species differences. As the Dahurian larches had small seeds and late growth cessation in the autumn, it is mainly this dependence which was reflected by these correlations. The seed weight and the length of the growing period of trees are genetically determined properties, and are linked to the geographic origin of the provenances (Wright 1976, Mikola 1980, 1982). Seed weight itself does not, however, affect the length of the growing period or its timing, for example in Scots pine or Norway spruce (Mikola 1980).

The seed weight also correlated strongly and positively with early summer height growth (Table 4), and it explained well the differences between the provenances (Eq. 7). This dependence was caused by the species and provenance differences in a similar way as for the growth rhythm. Southern provenances of Siberian larch had larger seeds and better early summer height growth than northern Siberian larches or the Dahurian larches. However, the late summer growth was negatively correlated with the seed weight, because in this situation the genetically determined height growth properties of the small-seeded Dahurian larches started to manifest themselves. This change in the seed weight – height growth relationship is in good agreement with the findings of Mikola (1980) for Scots pine and Norway spruce.

In general, the geographical variables of the provenance origin also better explained the variation between the provenances than the climatic variables. These results must, however, be interpreted such that these geographical variables describe the climate of the provenance. The only climatic variables that could be used to explain the growth rhythm were continentality (used to explain the length of the growing period, see Eq. 3), and the annual mean temperature (used to explain autumn colouration, see Eqs. 4 and 5). Increased continentality shortened the growing period and a higher temperature retarded the

development of autumn colouration. The effect of continentality is in line with the reported trends in Scots pine autumn colouration (Wright and Bull 1963) and freezing tolerance (Andersson and Fedorkov 2004), and the effect of temperature corresponds to the general trends described above.

It is possible that there were some inaccuracies in the climatic data that subsequently affected their usability in the statistical analysis (e.g. altitude information for provenances from mountainous areas). In mountainous areas, climatic data representing a larger area than the precise location of the stand from which the seed material originates could perhaps also better describe the environment to which the seed material is adapted. Due to long-distance pollen flight, the fathers of the seed can represent a larger climatic area than that occupied by the stand from which the seed was collected. In addition, the dependences between different variables could also have an impact on the observed results.

In three field experiments with the same material in Sweden, provenances from Chabarovsk and Sachalin have had the highest height growth, but provenances from Nishnij Novgorod, Plesetsk, Ufa and Perm have also performed well (Martinsson and Takata 2005, Karlman and Martinsson 2005, 2007). This is in agreement with our results obtained in the greenhouse. However, the growth dynamics of these provenances should be followed for a longer time period in field trials with different environmental conditions (climate, site) in order to be able to draw more general conclusions about the growth and success of certain provenances relative to others. In Finnish long-term field experiments established in the 1920's and 1930's, Siberian larch has proved to compete with Norway spruce as regards height growth and stem volume. In fact, in the 70-year-old experiments in Punkaharju, too, Dahurian larch has performed almost as well as Siberian larch, reaching 30 metres in height although the latter has had a higher stem volume growth (Silander et al. 2000).

When looking for the most suitable larch provenances for Finnish conditions, the most important factors are hardiness and suitability to the relatively short growing season. The Raivola origin comparison lots seem to be well suited

to the climatic conditions in Finland. Almost all of the Siberian larch provenances compared in this study had a longer growing period than the comparison lots. Only the northernmost Petchora and Plesetsk provenances and the very continental 9A Boguchany had a shorter growing period. If the height growth continues very late in the autumn, the risk of early frost increases, because the hardening process may not be completed (Christersson and von Fircks 1990). However, the European larch comparison lot Mv135, which had the longest growing period in this study, has succeeded well in Finland (Silander et al. 2000). Among the Dahurian larches, the northern provenance 13A Magadan proved interesting because it had only a slightly longer height growth period than the Siberian larch comparison lots, and its height growth was at the same high level as the other Dahurian larches (Fig. 2).

To conclude, the broad provenance material used in this work and in the corresponding new field experiments cited above, could offer proper regeneration material for practical forestry in Finland in the future. It will also facilitate the study of climatic adaptation in respect to the expected climate change (see e.g. Parry 2000, Carter et al. 2002, IPCC 2007), which is expected to affect the growth of trees in the long run and cause adaptation difficulties that might have a significant impact on forestry. In fact, the use of more southern provenances to adapt to changing environmental conditions has already been proposed earlier (Partanen and Beuker 1999, Marttila et al. 2005), with some reservations (Beuker 1996, Koski 1996), as well as the use of exotic tree species (Ruotsalainen 2006).

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