Variation in the Leader Shoot Elongation Patterns in *Larix* Species and Provenances in the North-West of Russia

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Abstract

A phenological study of seven Russian larch (*Larix* Miller) provenances was performed in a field trial located in the Komi Republic (north-west Russia) (61°39'N, 50°41'E, alt. 160 m a.s.l) at the age of five years. The provenance origin had a significant (p<0.001) effect on the leader shoot growth characteristics. The average undamaged leader shoot length was 27 cm and varied considerably over the provenances: 38 cm for Plesetsk and 14 cm for Yakutia. The average growth rate was 5.2 mm day-1 and means varied from 8.5 mm day-1 for Plesetsk and to 3.4 mm day-1 for Yakutia provenances. The earliest time for onset and cessation of shoot elongation was for Yakutia provenance and the latest one for Ufa provenance. The range of these provenances was 28 days for start and 46 days for cessation of the growth. The onset of growth correlated positively with the latitude and longitude of the provenance origin but negatively with annual elongation. A positive correlation was observed between rate of shoot elongation and annual shoot growth.

Key words cessation of growth, onset of growth, phenology, Russian larch, shoot length.

Introduction

Larch (*Larix* Miller) is an economically and ecologically important group of tree species in the boreal forests of the northern hemisphere. Most of larch forests of the world, considering both distribution area and wood stock is in Eurasia (Schmidt 1995). Larch has been widely acknowledged as a fast-growing tree species producing high quality timber (Chubinski et al. 1990). Larch timber is suitable as material for outdoor constructions, owing to its high mechanical strength and decay resistance (Polubojarinov et al. 2000). In Finland, larch wood is considered as good as Scots pine when it comes to decay resistance (Venäläinen et al. 2001). Larch is the most common tree species in Russia. More than 280 million ha in Russia, which makes up 37% of the forest area and 30.7% of the wood stock, is dominated by larch (Martinsson and Lesinski 2007).

The nomenclature of the Eurasian larch species are complex and varies in different countries (Eystensson and Skślason 1995, Abaimov et al. 2002, Lukkarinen et al. 2009, Karlman 2010). According to Farjon (1990), two larch species are recognized in Russia: Siberian larch (*Larix sibirica* Ledeb.) and Dahurian larch (*L. gmelinii* Rupr.). Earlier Dylis (1947) suggested to distinguish *L. sukaczewii* Dyl. as a separate species in the European part of Russia. But according to Bobrov (1978), *L. sukaczewii* cannot be distinguished from *L. sibirica* Ledeb., which occupies the central part of Siberia. Later the phylogenetic studies (Bashalkhanov et al 2003, Khatab et al 2008, Newton et al 2008) supported the idea of Dylis, and in this study *L. sukaczewii* is treated as a separate species. Bobrov (1972) suggested to separate *L. cajanderi* Mayr. from *L. gmelinii* due to differences in ecology and cone morphology, this separation is also used in this study.

Tree growth is a complex trait that may be described by the growth rate and duration of the growth period (Eriksson et al. 2006). To survive in northern latitudes the growth rhythm of forest trees has to synchronize with the local climate. Onset of growth in spring and growth cessation in autumn is strongly related to the risk of frost damage (see review in Hannerz 1998, Aitken and Hannerz 2001). It is also known that there is a positive correlation between frost resistance and the growth on the one hand and stem form in young larch seedlings on the other hand (Eystensson and Skúlason 1995).

The series of field trials with *L. sukaczewii* Dyl., *L. sibirica* Ledeb., *L. cajanderi* Mayr., and *L. gmelinii* Rupr. was established in Canada, China, Finland, France, Iceland, Japan, Norway, Russia, Sweden and the United States (Martinsson and Takata 2005). The growth rhythm and height growth of one-year-old seedlings representing this material were studied in greenhouse condition (Lukkarinen et al. 2009). The parameters that describe the annual growth cycle are the most informative to predict the effects of climatic changes on tree growth and survival (Hänninen 1990, Beuker 1994, Beuker and Koski 1997).

The main objective of this study was to compare growth onset and cessation, growth rate as well as annual shoot elongation of seedlings representing *L. sukaczewii* Dyl., *L. sibirica* Ledeb., and *L. cajanderi* Mayr. in a field condition. The growth rhythm describes the adaptation and the height growth potential of the trees. The other goal was to calculate the relationships between growth rhythm traits and climatic and geographic variables. It is also important for a proper selection of provenances for commercial planting

Material and methods

Field trial and material

The study was performed in a field trial located in the Komi Republic (NW Russia) (61°39’N, 50°41’E, alt. 160 m a.s.l). Seed collections were done within the frame of Russian-Scandinavian Larch Project in 1994–2000 (Abaimov et al. 2002) (Fig.1, Table 1). The planting of the seedlings was carried out in September 2007 with two-year-old potted seedlings with a spacing of 3×1 m. Seeds were sown in containers (7×7 cells/container) with a cell size of 128 cm^3 in May 2006 and grown in a plastic greenhouse without heating and additional light. At the beginning of August 2006, the seedlings were removed and grown in open air before planting. The seedlings were planted on a clear-cut area with sandy soil prepared using a plough. A fully randomized single-tree plot design was used. In April 2010,

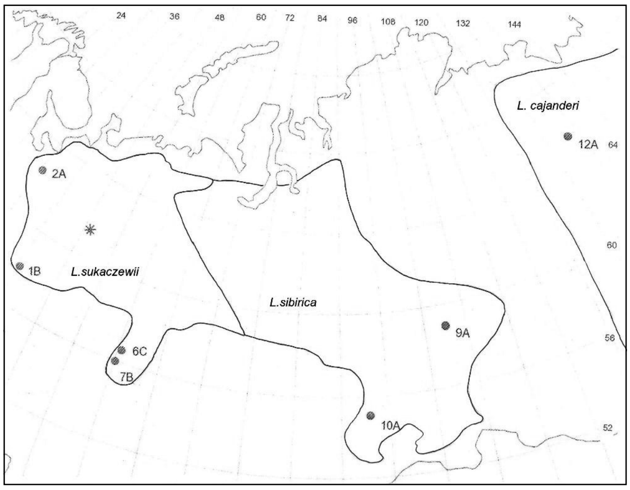

Figure 1. Geographic distribution of studied larch species, provenance origins (•) and location of field trial (*)

when the seedlings were five years old, 20 plants per provenance (1–2 seedlings per half-sib family) were randomly chosen among all living seedlings with undamaged leader shoots

Measurements

Shoot elongation of the terminal shoot was assessed on eight occasions in 2010, from the onset of elongation in June until the growth termination in August. Measurements (in mm) were made from the fixed base point (bud scar from the last year growth) to the tip of the shoot. The final shoot length was measured at the end of the growing season in September. The analysis of growth rhythm was based on a series of relative values, i.e. proportions of shoot elongation achieved on various test occasions relative to the final shoot length. The onset and the cessation of leader shoot elongation were defined as the relative elongation on the test occasions close to 10% and 90%, respectively. The maximum rate of terminal shoot elongation was calculated in mm/day during the week of maximum growth in June (Nilsson 2001). But

Table 1. Identification of provenances studied

Provenance, name of region*	Locality	Geographical location and elevation			Annual mean temperature, ºC**	Continentality index**	Degree days +5º**
		Lat., Nº	Long., Eº	Alt., m			
			Larix sukaczewii Dyl.				
1B Nizhnij Novgorod	Vetluga	57°30’	45°10’	145	3.1	44	1446
2A Plesetsk	Emtsa	63°05’	40°21’	100	1.1	40	1037
6C Perm	Kyshtym	55°43’	60°27’	480	2.2	49	1441
7B Ufa	Miass	54°58’	60°07’	380	1.9	52	1480
			Larix sibirica Ledeb.				
9A Boguchany	Boguchany	58°39’	97°30’	158	-2.6	64	1204
10A Novokuznetsk	Novokuznetsk	53°48’	88°00’	400	1.9	54	1753
			Larix cajanderi Mayr.				
12A Yakutia	Zigansk	66°46’	123°22’	70	-11.5	83	775

Note: *Accordingly to Abaimov et al. (2002), **accordingly to Lukkarinen et al. (2010)

the week of maximum growth was in the middle of June for Yakutia provenance and in the end of June for other provenances. Survival was evaluated as the proportion of living seedlings at the time of assessment.

Statistical analysis

Differences among provenances were tested by one-way analysis of variance of individual values. Differences between the highest mean and lower ones were analyzed using the Scheffe's test. To express the gradually increasing leader shoot elongation during the growing period, the exponential expression was used to fit provenance's means of shoot elongation (y) to the calendar days since March 1 (x) (Eq. 1)

$$y = 1/(1 + be^{(rx+c/x)}) \tag{1}$$

To obtain growth curves the regression coefficients b, r and c were calculated for each provenance by the nonlinear regression model (Nilsson 2001). Using March 1 as a starting point is common in phenological research (Zaitchev 1973). The dependencies between different parameters were tested with the Pearson correlation analysis. The Statistica 6.0 statistical package was used for the statistical analysis (SAS Institute Inc. 2004).

Results

The field survival estimated in September 2008 varied between 92% and 97% among provenances included in the field trial. The provenance origin had a significant (p<0.001) effect on the leader shoot growth characteristics (Table 2). Highly significant differences among provenances were detected for the rate of shoot elongation (p<0.05) and the onset of growth (p<0.001) (Table 3). For cessation of growth the difference was significant (p<0.05) only between Yakutia and Ufa provenances. For annual elongation the difference was significant (p<0.001) only between Plesetsk and Yakutia provenances. The average undamaged leader shoot length was 27 cm and varied considerably over the provenances: 38 cm for Plesetsk and 14 cm for Yakutia. The average rate of growth was 5.2 mm day-1 and the provenance means varied from 8.5 mm day-1 for Plesetsk to 3.4 mm day-1 for Yakutia provenances (Table 3). The earliest time for onset and cessation of leader shoot elongation was for Yakutia provenance and the latest one for Ufa provenance. The range of these provenances was 28 days for start and 46 days for cessation of the growth (Fig. 2).

There was a significant correlation between some of the measured growth rhythm traits and the geographic and climatic variables of the provenance ori-

Table 2. The effect of provenances on shoot elongation characteristics

Trait	df*	MS**	F-value	p-value
Annual elongation	6	65385	6.09	0.000
Growth rate	6	40.20	11.02	0.000
Onset of growth	6	0.2450	16.80	0.000
Cessation of growth	6	0.0142	6.60	0.000

Note: *degrees of freedom; **mean sum of squares

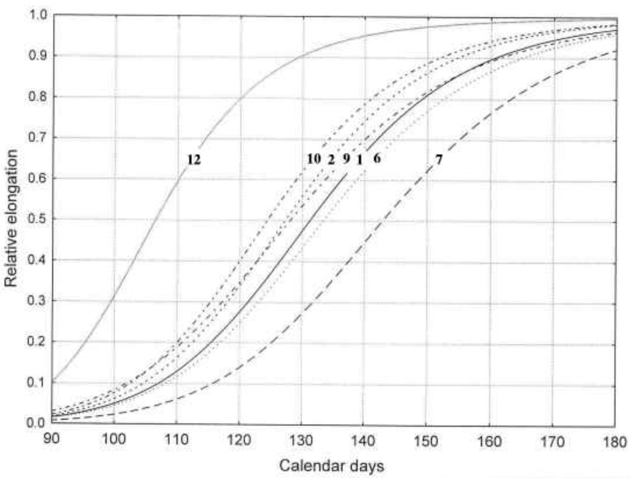

Figure 2. Relationship between sequential day (since March 1) and relative leader shoot elongation of the studied provenances, estimated from the sigmoid function (Eq. 1). (The letters in the provenances ID are omitted)

Table 3. Annual shoot elongation (mm), rate of shoot elongation (mm/day), relative elongation during onset (June 15) and growth cessation (August 9) based on individual measurements

Provenance	Annual elongation			Rate of shoot elongation			Onset of growth			Cessation of growth		
	Mean	SD*	p-value**	Mean	SD*	p-value**	Mean	SD*	p-value**	Mean	SD*	p-value**
Nizhnij	242	52	0.146	4.6	0.7	**0.003**	0.106	0.052	**0.000**	0.962	0.035	0.999
Novgorod	384	146	-	8.5	2.5	-	0.122	0.046	**0.000**	0.975	0.037	1.000
Plesetsk	269	91	0.204	4.4	1.6	**0.000**	0.095	0.039	**0.000**	0.933	0.056	0.698
Perm	324	88	0.961	4.5	1.6	**0.007**	0.073	0.027	**0.000**	0.862	0.066	**0.006**
Ufa	309	102	0.727	5.6	1.4	**0.019**	0.159	0.077	**0.000**	0.977	0.033	1.000
Boguchany	237	92	0.071	5.4	1.5	**0.018**	0.157	0.062	**0.000**	0.991	0.011	0.996
Novokuznetsk	135	25	**0.000**	3.4	0.9	**0.000**	0.568	0.235	-	1.000	0.073	-
Yakutia												

Note: * – standard deviation, ** – p-values obtained by Scheffe's test and statistically significant ones (p<0.05) are highlighted in bold.

gin. The onset of growth correlated positively with the latitude and longitude of the provenance origin, but negatively with annual mean temperature and annual elongation. Positive correlation was observed between the rate of shoot elongation and annual shoot growth (Table 4).

Table 4. Pearson correlation coefficients between the measured variables (n=7). Statistically significant values ($p<0.05$) are highlighted in bold and the significant is shown in parenthesis

Variable	Annual elongation	Rate of elongation	Onset of growth	Cessation of growth
Annual mean temperature, ºC	0.63 (0.132)	0.37 (0.411)	**-0.96** (0.000)	-0.47 (0.293)
Continentality index	-0.72 (0.067)	-0.59 (0.164)	**0.88** (0.009)	0.35 (0.435)
Degree days +5ºC	0.18 (0.700)	-0.06 (0.894)	-0.71 (0.073)	-0.37 (0.420)
Latitude	-0.27 (0.563)	0.10 (0.829)	**0.77** (0.044)	0.51 (0.252)
Longitude	-0.69 (0.085)	-0.51 (0.246)	**0.80** (0.032)	0.46 (0.297)
Annual elongation		**0.79** (0.035)	**-0.77** (0.045)	-0.42 (0.352)
Rate of elongation			-0.43 (0.342)	0.17 (0.711)
Onset of growth				0.54 (0.214)

Discussion and conclusions

The highest leader shoot growth was shown by the northern provenance Plesetsk not by the southern ones as Nizhnij Novgorod, Perm, and Ufa among the provenances of *L. sukazcewii* originating from the European part of Russia. The better seedling growth of Plesetsk provenance compared to the other ones was also observed by Karlman and Martinsson (2005) in a field trial located in Järvträsk (northern Sweden) and by Lukkarinen et al. (2010) in Kivalo (northern Finland). This is in a good agreement with the results obtained by Rehfeldt et al (2003) in a series of larch provenance tests throughout the former Soviet Union where larch growth enhanced when populations are transferred to warmer climates.

In general, shoot growth was better for *L. sukazcewii* compared with *L. sibirica* and *L. cajanderi*. Earlier onset of shoot elongation may be an advantage in *L. cajanderi* over *L. sukazcewii* and *L. sibirica* in utilizing short summers but growth period was shortest for seedlings of this species (Fig.2). Seedlings of Plesetsk provenance also exhibited the rapid rate of shoot elongation. Positive relationship between annual shoot increment and rate of shoot elongation was also observed for jack pine (Magnussen and Yeatman 1989), several larch species (Baltunis and Greenwood 1990, Rehfeldt 1992), and birch (Wang and Tigerstedt 1996).

Geographic variation in Scots pine traits describing growth rhythm in provenance field trials have been reported in numerous studies mainly in Scandinavia, showing clinal relationship between early phenology and latitude of origin (see review in Hannerz 1998, Aitken and Hannerz 2001). The data presented here indicate that there are statistically significant correlations between the onset of growth and latitude as well as climatic variables (annual mean temperature and continentality index) (Table 4). Positive relationship between the latitude of origin and initiation of the growth agree with the general geographical variation of forest trees (Wright 1976).

Also the longitude of origin positively correlated with initiation of the growth. These relationships are mostly caused by *L. cajanderi* (Yakutia) which is clearly northernmost and easternmost and has also the earliest growth rhythm. As it was also revealed by Eysteinsson et al. (2009), provenance geographic longitude was a significant predictor of frost damage score in the spring freezing test (farther east corresponds for more damage). And the earlier start of the growth could be a reason for spring damage of larch seedlings. Accordingly Lukkarinen et al. (2009), the geographical variables of the provenance origin better explained the variation between larch provenances in growth rhythm than the climatic variables, and these geographical variables describe the climate of the provenances though their results were obtained in greenhouse condition.

The climate-transfer models showed long-term evolutionary responses primarily reflected extirpation and immigration for the larch species in Eurasia (Rehfeldt et al. 2003). The results of this study together with the data from comparative trials from other geographic regions can be used in comparison analysis of growth rhythm in different climates over the world and thus will be able to provide new findings about climatic adaptation of larch species and provenances studied.

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СЕЗОННАЯ ИЗМЕНЧИВОСТЬ РОСТА ПОБЕГОВ ЛИСТВЕННИЦЫ В ВЫСОТУ В ГЕОГРАФИЧЕСКИХ КУЛЬТУРАХ НА СЕВЕРО-ЗАПАДЕ РОССИИ

А. Федорков

Резюме

Влияние географического происхождения было статистически значимым на все исследованные признаки: величину годичного прироста в высоту, темп прироста, начало и окончание роста (p<0.001). Средний годичный прирост в высоту составил 27 см и варьировал от 38 см для лиственницы Сукачёва (Плесецк) до 14 см для лиственницы Каяндера (Якутия). Средний темп роста составил 5.2 мм/день и варьировал от 8.5 мм/день для лиственницы Сукачёва (Плесецк) до 3.4 мм/день для лиственницы Каяндера (Якутия). Первыми из исследованных происхождений начали рост растения лиственницы Каяндера из Якутии, они же первыми и закончили рост. Позже всех начали и закончили рост растения лиственницы Сукачёва из Башкирии. Различия между этими двумя происхождениями составили 28 дней для начала и 46 дней для окончания роста. Начало роста положительно коррелировало с географической широтой и долготой происхождения, но отрицательно с годичным приростом. Положительная связь наблюдалась также между темпом роста и длиной побега.

Ключевые слова: лиственница, сезонный рост, фенология, начало роста, окончание роста, длина побега