SILVA FENNICA

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Performance variation of lodgepole pine provenances in Latvia

Highlights

- Performance of 36 provenances of lodgepole pine in 14 trials was studied.
- The 29 year survival was ca. 40%.
- Provenance and provenance × trial interaction affected dimensions of lodgepole pine.
- Provenances from lower latitudes were the most productive.

Abstract

Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) has been extensively introduced in Scandinavia on less productive sites. Under a changing climate, it also has a high potential in the eastern Baltic region; still, its performance there has scarcely been reported. This study investigated the performance of 36 Canadian provenances in 14 trials in western Latvia. Tree dimensions showed notable provenance and provenance-by-environment variation, implying that local selection by provenance can be applied for improved yield. Southern provenances showed the best height growth, while southwestern (more oceanic) provenances excelled in diameter growth. Most of the quality traits were affected by provenance or provenance-by-environment interaction, yet the variation was lower than for the growth traits.

1 Introduction

Introductions of exotic tree species have been made to maximise yields and the sustainability of stands (Savill 1997). The resistance of species to weather extremes, which are projected to intensify (IPCC 2013), has been identified as a major issue (Schlyter et al. 2006). In Northern Europe, particularly Fennoscandia, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) is among the few systematically introduced species aiming for improvement of yields, especially in less productive sites, thus meeting the increasing demand for timber (Lindgren 1993; Elfving et al. 2001). The species has been productive, especially at a young age, mostly exceeding local Scots pine (*Pinus sylvestris* L.) (Larsen and Nielsen 1982; Stephan 1982; Elfving et al. 2001; Kuznetsova et al. 2009), thus aiding for the reduction of rotation period (Elfving et al. 2001), while maintaining comparable wood properties (Sable et al. 2012). At present in Scandinavia, application of lodgepole pine in commercial forestry has been paused due to concerns about potential biotic risks (Despain 2001); still, considering the growing demand for timber, wider use of the species might be resumed (Nilsson et al. 2011).

Tree species with a wide distribution range, including lodgepole pine (Little 1979), have evolutionarily adapted to diverse environments (Fazekas and Yeh 2001). Accordingly, the selection optimally adapted provenances can maximise the performance and sustainability of stands (Ying 1991; Bolte et al. 2009). In Fennoscandia, provenances of lodgepole pine from British Columbia have shown the best performance (Elfving et al. 2001), while provenances from Oregon, Washington and southern parts of British Columbia shown better performance in Germany and Poland (Larsen and Nielsen 1982; Stephan 1982).

In the Baltic States, growth trials of lodgepole pine provenances were established during 1970–1990, yet few results of these trials have been published (Kuznetsova et al. 2009; Jansons et al. 2013b). Considering long-term decisions in forestry, such results are necessary for wider commercial application of the species. The regional specifics in tree growth (Lindner et al. 2010) also imply that local data are essential. The aim of this study was to quantify the variance in the growth and quality traits of lodgepole pine in Latvia for assessment of their potential improvement by selection among provenances.

2 Materials and methods

2.1 Trials and measurements

The study was based on 14 field trials of lodgepole pine established in Latvia (56°34′–57°16′N, 22°12′–24°09′E) during 1979–1994 with one- and two-year-old seedlings to test 36 Canadian provenances (Table 1). The trials had a randomised complete-block design with 4–8 replications and 12–48 tree plots of 3–13 provenances. Most of the provenances were represented in less than four trials (Table 1). The initial spacing of the trees was 2×1 m, yet in the older trials thinning (leaving ca. 40 of trees) was performed at the age 20–22 years. The trials were growing in lowland conditions (elevation < 60 m a.s.l.) on sandy oligotrophic soils and flat topography. The mean annual temperature (±confidence interval) was 6.2±0.3 °C, and the mean monthly temperature ranged from –3.7±1.6 to 17.1±0.7 °C in February and July, respectively. The mean annual precipitation was 653±37 mm.

The trials were measured at the age of 10–29 years; many of them multiple times. Height (H), stem diameter at breast height (DBH), and diameter of the thickest branch up to 2 m height were measured on each on each tree. The presence of spike knots and animal damage were recorded

Table 1. The origin of the studied Canadian provenances of lodgepole pine (WGS84). NA – not available.

Provenance	Latitude (N)	Longitude (W)	Altitude, m	N of trials	Measurement age
Babine Lake	54°24′	125°30′	1000	2	10, 11, 12, 13, 24, 29
Beaton River	56°50′	121°22′	800	1	17
Buick Creek	56°52′	121°30′	850	2	16, 17
Cassior	58°50′	129°25′	900	2	16, 17
Cecil Lake	56°25′	120°00′	700	3	16, 22
Dease Lake	58°15′	130°10′	850	2	16, 17
Ethel Lake	63°20′	NA	900	1	16
Falkland	50°32′	119°40′	1300	4	12, 16, 22
Fly Hilla	50°40′	119°29′	1100	2	10, 11, 12, 13, 24, 29
Fort Nelson	58°38′	122°41′	500	2	7, 9, 24, 25
Fort St. James	54°30′	124°10′	900	5	12, 16, 18, 22
Francis Lake	61°10′	129°27′	950	1	16
Halfway River	56°32′	122°15′	900	1	17
Hazelton	55°30′	NA	600	1	16
Hudson Hope	56°03′	121°47′	650	1	22
Jackfish Lake	63°00′	NA	650	1	16
Lac La Hache	51°54′	121°27′	1050	2	10, 11, 12, 13, 24, 29
Lac le Jeune	50°29′	120°29′	1250	5	12, 16, 18, 22
Lacobie Creek	52°30′	122°00′	1000	2	10, 11, 12, 13, 24, 29
Little Salmon	62°10′	NA	700	1	16
Mackensia	58°50′	129°25′	900	1	17
Moberly Lake	55°40′	121°25′	750	5	12, 16, 22
Monashee	50°08′	118°30′	950	4	12, 16, 22
Muskey Lake	55°30′	NA	900	3	16, 22
Nation River	55°15′	124°10′	550	3	10, 11, 12, 13, 18, 24, 29
Nordegg	52°20′	116°25′	1400	4	12, 16, 22
Pink Mountain	57°00′	122°30′	850	8	7, 9, 12, 16, 17, 22, 24, 25
Rocky Mountain House	52°37′	115°20′	1000	3	12, 22
Smithers	54°15′	127°00′	650	5	12, 16, 18, 22
Summit Lake	54°24′	122°37′	800	2	7, 9, 24, 25
Teslin, Yukon	60°15′	132°50′	750	4	12, 16, 22
Tungsten	61°00′	128°50′	1050	1	16
Upper Liard Rivers	60°10′	128°50′	700	2	10, 11, 12, 13, 24, 29
Valemount	53°00′	119°00′	850	5	16, 22, 23
Watson Lake	60°05′	128°37′	700	2	10, 11, 12, 13, 24, 29
Wonowon	56°36′	121°36′	850	3	10, 11, 12, 13, 17, 24, 29

as binary variables. Stem straightness was evaluated according to three grades (straight, slightly curved, and curved).

2.2 Data analysis

The measurements of DBH and H were scaled (z-scores) by trial to account for the heterogeneity of variance across the trials due to different measurement age (Table 1). Trees with broken tops and leaning stems were excluded from the analysis (2.8% of observations). Random effects models were used to estimate variance components of provenance and provenance × trial interaction of the studied traits. The restricted maximum likelihood approach was used. Analyses were done on tree-level observations. The statistical model in general form was:

$$y_{ijlm} = \mu + p_i + pt_{ij} + t_j + b(t)_{lj} + \varepsilon_{ijlm} , \qquad (1)$$

where y_{ijlm} – observation (tree), μ – grand mean, p_i –effect of provenance i, pt_{ij} – effect of interaction between provenance i and trial j, t_j – effect of trial j, and $b(t)_{lj}$– effect of replication l nested within trial j. The influence of individual provenance on the pt_{ij} interaction was checked using the leave-one-out approach.

The relationships between latitude, longitude, and altitude of origin (of provenance) and the traits showing a significant provenance variance component were assessed using quadratic two-factor linear regression analysis. The statistical model was:

$$Y_{ij} = \beta_0 + \beta_1 X1_i + \beta_2 X2_j + \beta_3 X1_i{}^2 + \beta_4 X1_i X2_j + \beta_5 X2_j{}^2 + \varepsilon_{ij}, \tag{2}$$

where Y_{ij} – provenance mean at each trial and age, $\beta_{0..6}$ – parameter estimates, $X1_i$, $X2_j$ – predictors. The best models (pairs of the best predictors) were selected by the fit statistics (e.g. R^2, root mean square error, etc.). Data were analysed in R v. 3.5.1 (R Core Team 2018), using the package lme4 (Bates et al. 2015).

3 Results

The overall 29-year survival of the lodgepole pine was ca. 40%. The overall mean (±confidence interval) H and DBH ranged from 1.36±0.01 to 11.43±0.14 m and from 1.36±0.02 to 12.31±0.25 cm at the age 7 and 29 years, respectively. The provenance and provenance-by-trial variance components of H and DBH were significant (p-value < 0.05) and had a similar magnitude (Table 2), indicating local specifics in the responses of provenances to environment. The probability of wildlife damage showed significant variance by provenance, while the probability of spike knots and survival showed significant interaction variance; yet, the magnitude of the variances were lower than for H and DBH. The provenances had generally similar influence on the interaction, although

Table 2. Variance of random effects of provenance, provenance-by-trial, trial, and replication for the studied traits.

	Provenance			Provenance × trial			Trial			Replication			Residual variance
	Variance	St. error	p-values	Variance	St. error	p-values	Variance	St. error	p-values	Variance	St. error	p-values	
Continuous (z-scores)													
Tree height	6.85	2.62	<0.01	6.14	2.48	<0.01	-	-	-	8.98	2.99	<0.01	52.66
Stem diameter	3.67	1.92	<0.01	2.42	1.56	<0.01	-	-	-	4.05	2.01	<0.01	62.17
Diameter of the thickest branch	<0.01	<0.01	0.99	0.31	0.55	0.26	-	-	-	1.21	1.10	<0.01	53.52
Binomial													
Probability of spike knots	0.01	0.10	0.54	0.04	0.18	<0.01	4.28	2.07	<0.01	0.06	0.24	<0.01	-
Probability of wildlife damages	0.12	0.35	0.01	0.02	0.13	0.54	7.20	2.68	<0.01	0.55	0.74	<0.01	-
Survival (29 year)	<0.01	0.06	0.88	0.10	0.24	0.04	1.85	1.36	<0.01	<0.01	0.03	0.94	-
Multinomial													
Stem straightness	<0.01	0.02	0.54	<0.01	<0.01	0.99	<0.01	0.08	0.02	0.01	0.07	<0.01	-

contribution of Summit Lake was slightly (ca. 5%) higher compared to others, in the case of DBH and H. The among-trial variation was strong for all binomial traits. Stem straightness and branch diameter showed only replication-related variance.

The latitude and altitude of the origin of provenance were the best predictors of H ($R^2 = 0.53$), while DBH was best described by latitude and longitude ($R^2 = 0.46$; Fig. 1). The probability of spike knots and wildlife damage were less related to the coordinates of origin ($R^2 < 0.15$). The response surface estimated the best H for provenances from the lower latitudes and intermediate altitudes (50°53´N and 800–1200 m a.s.l., e.g. Fly Hilla, Lac La Hache, and Lacobie Creek), with a distinct decrease under an increasing latitude and altitude (e.g. Dease Lake and Cassior).
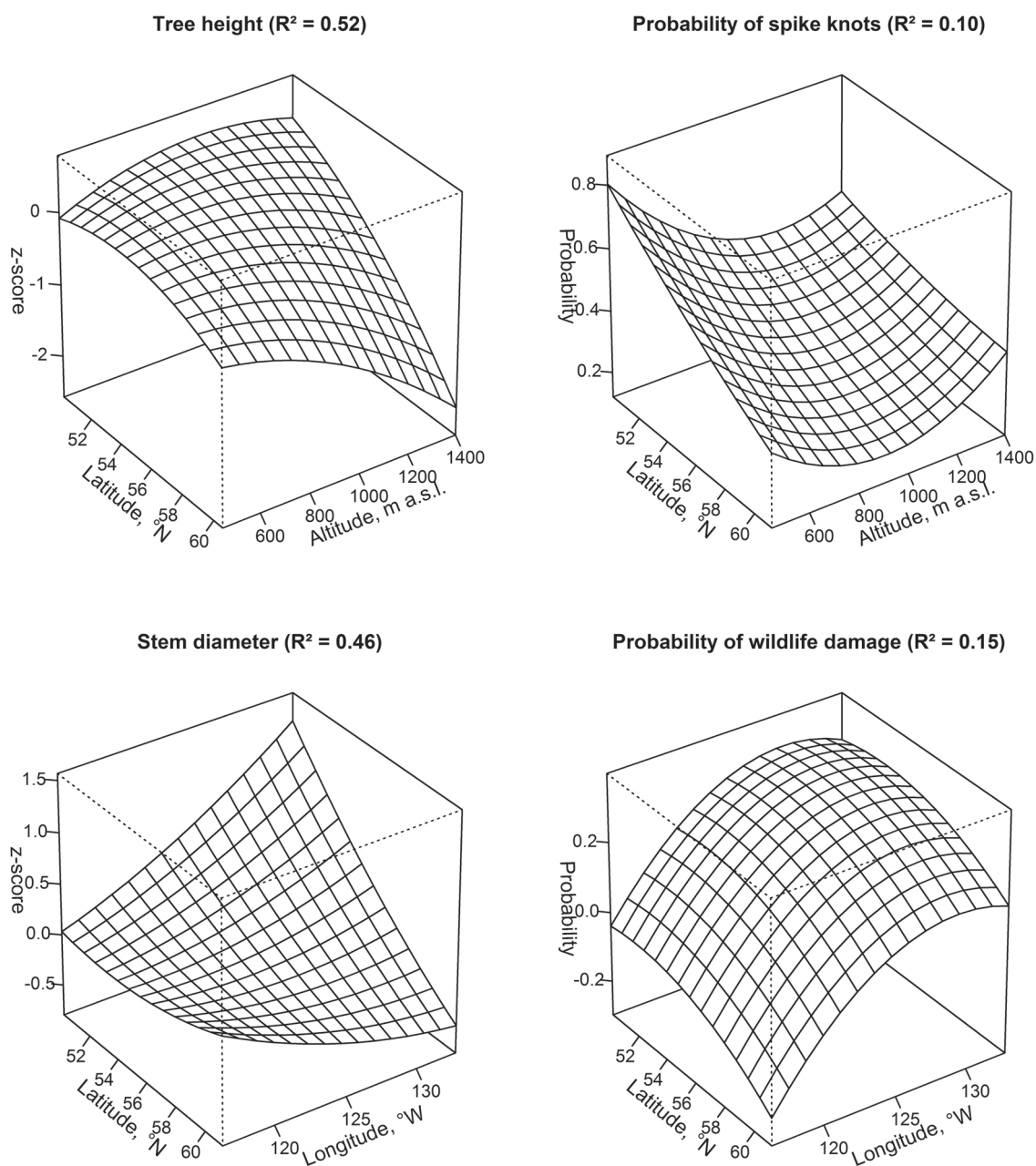

Fig. 1. Predicted tree height, stem diameter at breast height, probability of spike knots, and ungulate damage of the studied lodgepole pine provenances in Latvia according to their origin (longitude, latitude, and altitude). Note that the Y axis differs among the panels.

The largest DBH was associated (Fig. 1) with provenances from low latitudes and high longitudes (50°54′N and >125°W, e.g. Smithers and Babine Lake). Still, the best growing (DBH) provenances were Lacobie Creek, Halfway River, and Fly Hilla (their mean z-score ranging 0.31–0.45, respectively). The probability of spike knots showed the tendency to increase with decreasing latitude, particularly for the lower and higher altitudes. The probability of wildlife damage showed stationary maxima for provenances from mid-latitudes and longitudes, such as Beaton River and Dease Lake, while the Nordegg and Fort Nelson provenances were the less damaged. The most productive Fly Hilla provenance had an intermediate probability of wildlife damage and spike knots (0.15 and 0.37, respectively).

4 Discussion

The overall survival of lodgepole pine, considering self-thinning, was high, suggesting that it might be grown in Latvia. Nevertheless, the significant provenance-by-trial interaction indicated local differences, which were likely due to differing ungulate (e.g. *Cervus elaphus* L.) population density, hence the intensity of browsing damage (Table 2), which is becoming a more important issue in Eastern Europe (Borkowski et al. 2017). The provenance-by-trial interactions of tree dimensions (Table 2) also suggested effect of site factors, which are significant for trees growing in optimal conditions (Elfving et al. 2001; Düthorn et al. 2013), e.g. under milder climate. Nevertheless, the variation of tree dimensions were affected by provenance (Table 2), indicating the possibility to improve yield by selection among the provenances (Wu and Ying 2004; Bolte et al. 2009). The provenance, hence population related variation of tree dimensions (Table 2) also suggested the potential for breeding (Lindgren 1993; Elfving et al. 2001).

The dimensions of lodgepole pine were related to the geographic location of origin of provenances (Fig. 1), as observed in other studies (Rehfeldt 1987; Lindgren 1993; Elfving et al. 2001; Wu and Ying 2004). Tree height, which is a proxy for productivity (Savill 1997), was superior for the southern provenances from mid-altitudes (Fig. 1), as observed in Germany and Denmark (Larsen and Nielsen 1982; Stephan 1982). Such a response might be explained by an optimum climatic transfer distance comparable to ca. 1–2° degrees of latitude (Rehfeldt 1987), allowing trees to benefit from an altered temperature regime (Jansons et al. 2013a).

The provenance variation in DBH was mainly related to longitude (Fig. 1). This could be explained by the continentality of the origin of provenance. Accordingly, the best performance is expected for trees from the southwestern parts of the distribution, where the climate was milder. This exceeded the considered optimum transfer distance (Rehfeldt 1987), probably due to differences in elevation, indicating the plasticity of secondary growth. However, the predictions of the model (Fig. 1) did not meet any actual provenance (Table 1), suggesting that the effect of latitude and longitude were independent. This might be due to specifics of climate in Northern America as determined by relief and air circulation (Little 1979). The relationship between coordinates of origin and the probability of spike knots and wildlife damage were weaker (Fig. 1), likely due to specialization to local rather than regional conditions (Wu and Ying 2004). Still, the probability of spike knots and wildlife damage was higher for the provenances from lower latitudes, suggesting correlation with productivity (Fig. 1). Alternatively, spike knots might indicate maladaptation to climate (Wu and Ying 2004). Considering that the studied provenances only partially covered the native range of lodgepole pine (Little 1997), the predictions might be slightly biased, and the effect of altitude less pronounced compared to the studies of Rehfeldt (1987) and Ying (1991). Considering optimum transfer distances (Rehfeldt 1987), the results might be extrapolated to the neighbouring Estonia and Lithuania.

Acknowledgements

References

Bates D., Maechler M., Bolker B., Walker S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01.

Bolte A., Ammer C., Löf M., Madsen P., Nabuurs G.-J., Schall P., Spathelf P., Rock J. (2009). Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. Scandinavian Journal of Forest Research 24(6): 473–482. https://doi.org/10.1080/02827580903418224.

Borkowski J., Dobrowolska D., Dąbrowski W., Banul R., Załuski D. (2017). Young conifer stands form a deer browsing refuge for an oak admixture: silvicultural implications for forest regeneration under herbivore pressure. European Journal of Forest Research 136(5–6): 787–800. https://doi.org/10.1007/s10342-017-1070-3.

Despain D.G. (2001). Dispersal ecology of lodgepole pine (*Pinus contorta* Dougl.) in its native environment as related to Swedish forestry. Forest Ecology and Management 141(1–2): 59–68. https://doi.org/10.1016/S0378-1127(00)00489-8.

Düthorn E., Holzkämper S., Timonen M., Esper J. (2013). Influence of micro-site conditions on tree-ring climate signals and trends in central and northern Sweden. Trees 27(5): 1395–1404. https://doi.org/10.1007/s00468-013-0887-8.

Elfving B., Ericsson T., Rosvall O. (2001). The introduction of lodgepole pine for wood production in Sweden. Forest Ecology and Management 141 (1–2): 15–29. https://doi.org/10.1016/S0378-1127(00)00485-0.

Fazekas A.J., Yeh F.C. (2001). Random amplified polymorphic DNA diversity of marginal and central populations in *Pinus contorta* ssp. *latifolia*. Genome 44(1): 13–22. https://doi.org/10.1139/g00-082.

IPCC (2013). Climate change 2013: the physical science basis. Cambridge University Press, Cambridge. 1535 p.

Jansons A., Matisons R., Libiete-Zālīte Z., Baders E., Rieksts-Riekstiņš J. (2013a). Relationships of height growth of lodgepole pine (*Pinus contorta* var. *latifolia*) and Scots pine (*Pinus sylvestris*) with climatic factors in Zvirgzde, Latvia. Baltic Forestry 19: 236–244.

Jansons A., Sisenis L., Neimane U., Rieksts-Riekstins J. (2013). Biomass production of young lodgepole pine (*Pinus contorta* var. *latifolia*) stands in Latvia. iForest 6: 10–14. https://doi.org/10.3832/ifor0637-006.

Kuznetsova T., Tilk M., Ots K., Lukjanova A., Pärn H. (2009). The growth of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) in a reclaimed oil shale mining area, abandoned agricultural land and forestland. Baltic Forestry 15: 186–194.

Larsen J.B., Nielsen C.N. (1982). Proveniensforsog med contortafyr (*Pinus contorta* Dougl.) i Danmark. [Provenance trials with *Pinus contorta* in Denmark]. Forstlige Forsoegsvaesen i Danmark 38(3): 239–272. [In Danish].

Lindgren D. (1993). Breeding *Pinus contorta* in different countries. In: Lindgren D. (ed.). Proceedings of *Pinus contorta* – from untamed forest to domesticated crop. Frans Kempe Symposium, Umeå, August 24–28, 1992.

Lindner M., Maroschek M., Netherer S., Kremer A., Barbati A., Garcia-Gonzalo J., Seidl R., Delzon S., Corona P., Kolström M., Lexer M.J., Marchettie M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259(4): 698–709. https://doi.org/10.1016/j.foreco.2009.09.023.

Little E.L. (1979). Checklist of United States trees (native and naturalized). USDA Agriculture Handbook No. 541, Washington, D.C. 375 p.

Nilsson U., Fahlvik N., Johansson U., Lundström A., Rosvall O. (2011). Simulation of the effect of intensive forest management on forest production in Sweden. Forests 2(1): 373–393. https://doi.org/10.3390/f2010373.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rehfeldt G.E. (1987). Components of adaptive variation in *Pinus contorta* from the Inland Northwest. USDA Forest Service Intermountain Research Station Research Paper INT-375. Moscow, Idaho. 11 p. https://doi.org/10.5962/bhl.title.68869.

Sable I., Grinfelds U., Jansons A., Vikele L., Irbe I., Verovkins A., Treimanis A. (2012). Comparison of the properties of wood and pulp fibers from lodgepole pine (*Pinus contorta*) and Scots pine (*Pinus sylvestris*). BioResources 7(2): 1771–1783. https://doi.org/10.15376/biores.7.2.1771-1783.

Savill P., Evans J., Auclair D., Falck J. (1997). Plantation silviculture in Europe. Oxford University Press, Oxford. 308 p.

Schlyter P., Stjernquist I., Bärring L., Jönsson A.M., Nilsson C. (2006). Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. Climate Research 31(1): 75–84. https://doi.org/10.3354/cr031075.

Stephan B.R. (1982). Herkunftsversuche mit *Pinus contorta* in der Bundesrepublik Deutschland. [Provenance trials of *Pinus contorta* in the Federal Republic of Germany]. Forstwissenschaftliches Centralblatt 101(1): 245–259. [In German]. https://doi.org/10.1007/BF02741182.

Wu H.X., Ying C.C. (2004). Geographic pattern of local optimality in natural populations of lodgepole pine. Forest Ecology and Management 194(1–3): 177–198. https://doi.org/10.1016/j.foreco.2004.02.017.

Ying C.C. (1991). Performance of lodgepole pine provenances at sites in southwestern British Columbia. Silvae Genetica 40: 215–223.

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