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Short Communication

Shoot structure variation in latitudinal and longitudinal ecotypes of *Pinus sibirica* in a common garden experiment

Bir bahçe deneyiminde *Pinus sibirica*'nın enlem ve boylam ekotiplerinde aşı kalemi yapısı değişimleri

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ABSTRACT

Pinus sibirica Du Tour is one of the primary forest species in Russia. This work aimed to determine the variation in growth and elementary structure of shoots in latitudinal and longitudinal ecotypes using a common garden experiment, with emphasis on the ratio between shoot metamere types. The study was conducted in the southern taiga ecoregion in the south-east of the West Siberian Plain in Russia. We investigated 23-year-old grafts from eight *Pinus sibirica* ecotypes grown under uniform conditions. Ten-year-old branches were selected from the crowns of the grafted trees, and a retrospective analysis of shoot structure was conducted. The length and metameric composition of the branches varied significantly between different latitudinal and longitudinal ecotypes. Growth rates in the southern and eastern ecotypes were higher than those in the northern and western ecotypes. However, the proportions of auxiblasts did not differ between ecotypes. The southern ecotype showed the largest shoot sterile zone and the longest internodes and needles. The eastern ecotype showed the largest number of brachyblasts and relatively long internodes. Thus, the proportions of metameres involved in shoot elongation and internode length depend on the geographic origin of ecotypes when growing their vegetative progeny *ex situ*

Keywords: Adaptive traits, boreal conifers, grafts, intraspecies variation, shoot metameres

ÖZ

Pinus sibirica Du Tour, Rusya'daki başlıca orman ağacı türlerinden bir tanesidir. Bu çalışma, ortak bir bahçe deneyi kullanarak enlem ve boylam ekotiplerinde sürgünlerin büyüme ve temel yapısındaki değişimlerin, sürgün metamere türleri oranına vurgu yaparak belirlenmesi amaçlanmıştır. Çalışma, Rusya'daki Batı Sibirya Ovası'nın güney doğusundaki güney tayga ekolojik bölgesinde gerçekleştirilmiştir. Eşit şartlar altında yetiştirilen sekiz *Pinus sibirica* ekotipinden 23 yaşındaki aşı kalemleri araştırılmıştır. Aşılanmış ağaçların taçlarından on yaşındaki dallar seçilerek ve sürgün yapısında geriye dönük analizler yapılmıştır. Dalların uzunluğu ve metamerik bileşimleri, farklı enlem ve boylam ekotipleri arasında önemli farklılıklar gösterdiği saptanmıştır. Güney ve doğu ekotiplerindeki büyüme oranlarının, kuzey ve batı ekotiplerindeki büyüme oranlarından daha yüksek olduğu tespit edilmiştir. Bununla birlikte, oksiblast oranlarında ekotipler arasında farklılık bulunmamıştır. Güney bölgesi ekotipi en büyük sürgün steril bölgesini ve en uzun internod ve iğne yapraklarına sahip olduğunu göstermiştir. Doğu bölgesi ekotipi ise, en fazla sayıda brakilast ve nispeten daha uzun internodlara sahip olduğu görülmüştür. Bu nedenle, sürgün uzaması ve internod uzunluğuna dahil olan metamerlerin oranları vejetatif sürgünleri doğal gelişmenin üzerinde büyüdüğü görülürken, bu durumun ekotiplerin coğrafi kökenine bağlı bulunduğu sonucuna varılmıştır.

Anahtar Kelimeler: Uyarlanabilir özellikler, kuzey bölgesi iğne yapraklı ağaçları, aşı kalemi, tür içi değişim, sürgün metamerleri

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INTRODUCTION

Widely distributed tree species show intraspecific variation associated with their adaptation to specific environments in different parts of their range. Intraspecific variation in forest trees most often manifests itself in significant variation, between populations, in growth rate and duration, flowering time, and crown size and structure.

Table 1. Location and geographic characteristics of the eight Pinus sibirica ecotypes and study area in Russia

Region of ecotype origin	Latitude, N	Longitude, E	Elevation(m, asl)	Vegetation zone (according to Kurnaev, 1973)	Parental tree age (years)
Latitudinal ecotypes					
1. Abaza	52°30′	90°05′	350	Southern taiga	100
2. Strezhevoy	60°45′	77°30′	40	Northern part of middle taiga	140
3. Noyabrsk	63°10′	75°20′	110	Southern part of northern taiga	160–210
4. Urengoy	65°50′	78°10′	40	Forest and tundra	100–170
Longitudinal ecotypes					
5. Nevyansk	57°15′	60°10′	300	Subtaiga	120
6. Tayshet	55°50′	98°00′	350	Southern taiga	160
7. Sludyanka	51°30′	103°40′	900	Low part of forest belt	200
8. Severobaikalsk	55°40′	109°25′	700	Low part of forest belt	180
Study area					
Tomsk region	56°13'	84°51'	80	Southern taiga	–

Common garden studies have confirmed the inheritance of geographical variation in conifers (Sáenz-Romero et al., 2019). These studies distinguish genetic variation and modification in trees from different provenances, thereby revealing general patterns in growth variation for different coniferous species. Common garden experiments on individuals from environments with harsh climatic conditions have shown that they have a shorter period of seasonal growth (Andersson Gull et al., 2018), fewer frost injuries (Malmqvist et al., 2017), a slower growth rate (Vitasse et al., 2009), and a lower trunk height (Nagamitsu et al., 2018) than trees from a relatively mild climate. The level of species variation depends on the distance between the origin of the species and the location of the experiment, the climatic heterogeneity of the species range (Ye and Jayawickrama, 2014), and genetic variation in the species (Martínez-Berdeja et al., 2019). Notably, adaptation to climatic conditions requires more than adaptation to seasonal temperatures. Therefore, the effect of heat on transferred trees during the growing season can be influenced by other environmental factors (Liepe et al., 2016).

The Siberian stone pine, *Pinus sibirica* Du Tour, is one of the primary forest species in Russia. Patterns of intraspecific variation in Siberian stone pine largely correspond to those of other boreal conifers (Khutornoy et al., 2018; Zhuk and Goroshkevich, 2018). Most investigations on Siberian stone pine and other conifers deal with geographical variation in traits characterizing growth rate and resistance to external factors. However, limited research has been conducted on elementary shoot structure and ratios of metamere types. Shoot structure in natural populations of Siberian stone pine varies significantly, with different ratios of metamere types involved in shoot growth and branching (Goroshkevich and Popov, 2004). However, it is unclear whether this ratio is retained when trees are grown *ex situ*.

This study aimed to assess variation in growth and elementary structure of shoots in 10-year-old branches in different latitudinal and longitudinal ecotypes of Siberian stone pine, with emphasis on the ratio between shoot metamere types, using a common garden experiment.

MATERIALS AND METHODS

Study Area

The study was conducted in the southern taiga ecoregion on the West Siberian plain, Russia (56°13′ N 84°51′ E). The investigation was conducted using eight ecotypes of Siberian stone pine (Table 1) from different parts of the species range (Figure 1), which were grown in a common garden. Each latitudinal ecotype represented one of the vegetation zones on the West Siberian plain, which has a transect length of ~1600 km. The longitudinal ecotypes represented two vegetation zones and the same part of different mountain forest belts. The longitudinal transect length was ~3000 km, but it had a gap due to the lack of *Pinus sibirica* in some southern vegetation zones of Russia. Only natural stands that were typical for each region were included in the investigation.

Sample Collection and Measurement

Scions were cut from 9 to 19 randomly selected trees in a natural stand and grafted onto local 4-year-old Siberian stone pine seedlings in the spring of 1996. The grafts were grown with a spacing of 3 × 6 m in a common garden experiment at the "Kedr" Scientific Station, which is managed by the Institute of Monitoring of Climatic and Ecological Systems, Russian Academy of Sciences, Tomsk, Russia.

In 2018, 10-year-old branches were chosen on the southern side of the crown in the 23-year-old grafts, and retrospective analysis of the shoot structure along the branches was performed (Vo-

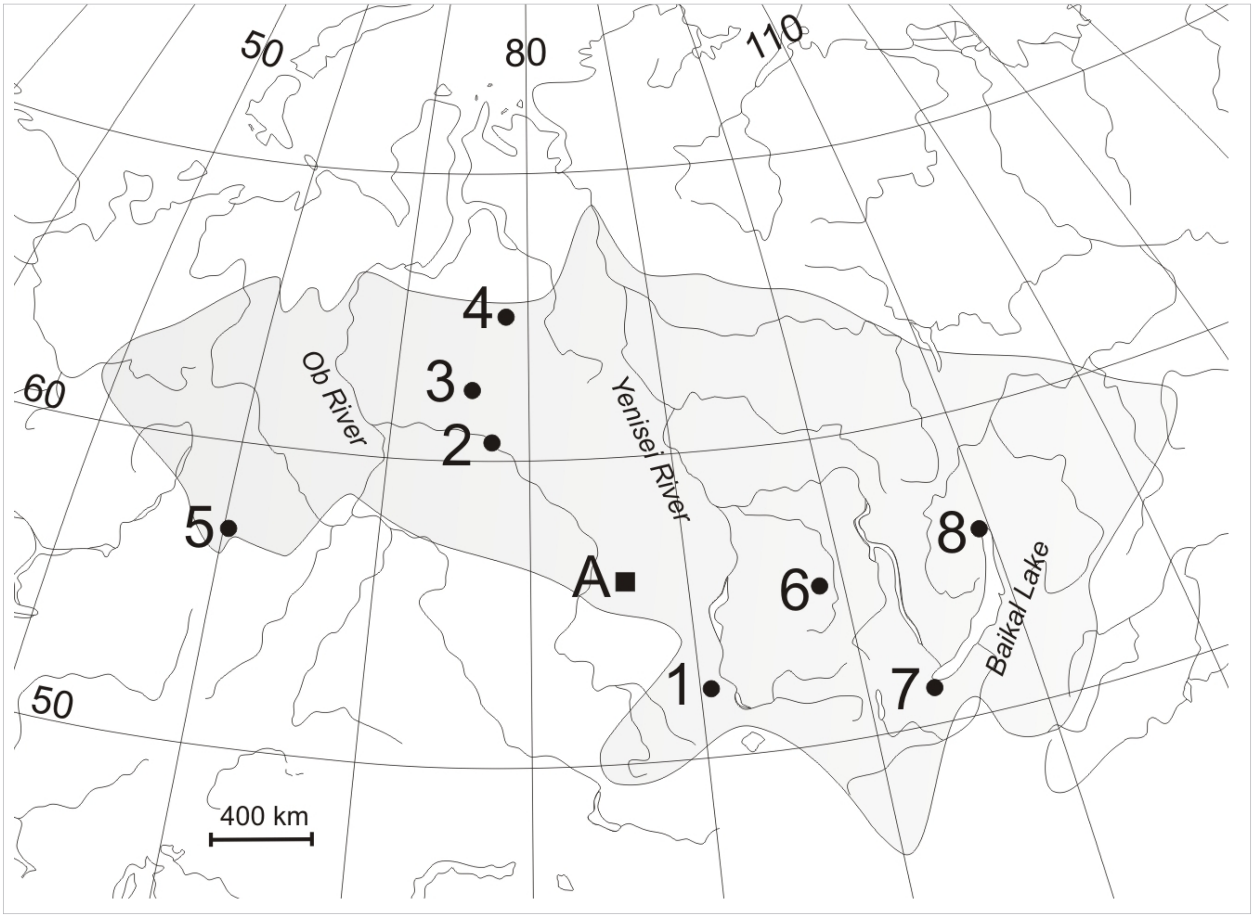

Figure 1. Geographical distribution of *Pinus sibirica*. Each point represents an ecotype or common garden plantation. Latitudinal ecotypes: 1, Abaza, 2, Strezhevoy, 3, Noyabrsk, and 4, Urengoy. Longitudinal ecotypes: 5, Nevyansk, 6, Tayshet, 7, Sludyanka, 8, Severobaikalsk. A, common garden plantation. All the points are located in Russia

robjev et al., 1992). The length of all 10 shoots and needles on the three youngest shoots was measured to the nearest 1 mm using a measuring tape, and the number of sterile cataphylls, brachyblasts, lateral auxiblasts, and sleeping buds was counted on each shoot. The number of fallen axillary structures was estimated using traces on the shoot bark.

Statistical Analysis

Raw data consisted of trait means for each clone, and the value for needle length was averaged over three years. The variances of these values for the different ecotypes were homogeneous. According to the Kolmogorov–Smirnov test, all trait means were normally distributed. Differences between the ecotypes were determined using analysis of variance (ANOVA). When significant differences ($p<0.05$) were detected, comparisons between ecotypes were conducted using Duncan's test.

RESULTS AND DISCUSSION

After the first year of branch appearance, differences between ecotypes were small, but they gradually increased with age. By the tenth year of branch life, differences between the latitudinal ecotypes reached 1.4 times, while that between the longitudinal ecotypes was 1.2 times. Based on ANOVA and Duncan's test, significant differences were found in branch length. Among the latitudinal ecotypes, the southern ecotype Abaza showed the highest growth rate, and the northern ecotypes Urengoy and Noyabrsk showed the weakest growth (Figure 2a). The intermediate ecotype Strezhevoy had a moderate growth rate.

Among the longitudinal ecotypes, the south-eastern ecotype Sludyanka had the highest growth rate. All other ecotypes, the western ecotype Nevyansk, the intermediate ecotype Tayshet and the north-eastern ecotype Severobaikalsk, showed relatively low growth (Figure 2b).

Shoot structure also varied significantly between different latitudinal and longitudinal ecotypes. Among the latitudinal ecotypes, the results of the ANOVA and Duncan's test showed that there were differences in the number of sterile cataphylls and brachyblasts, which are elongation structures, but no differences in the number of auxiblasts, which are branching structures (Table 2). From the southern to northern ecotypes, the number of sterile cataphylls and brachyblasts decreased by 1.6

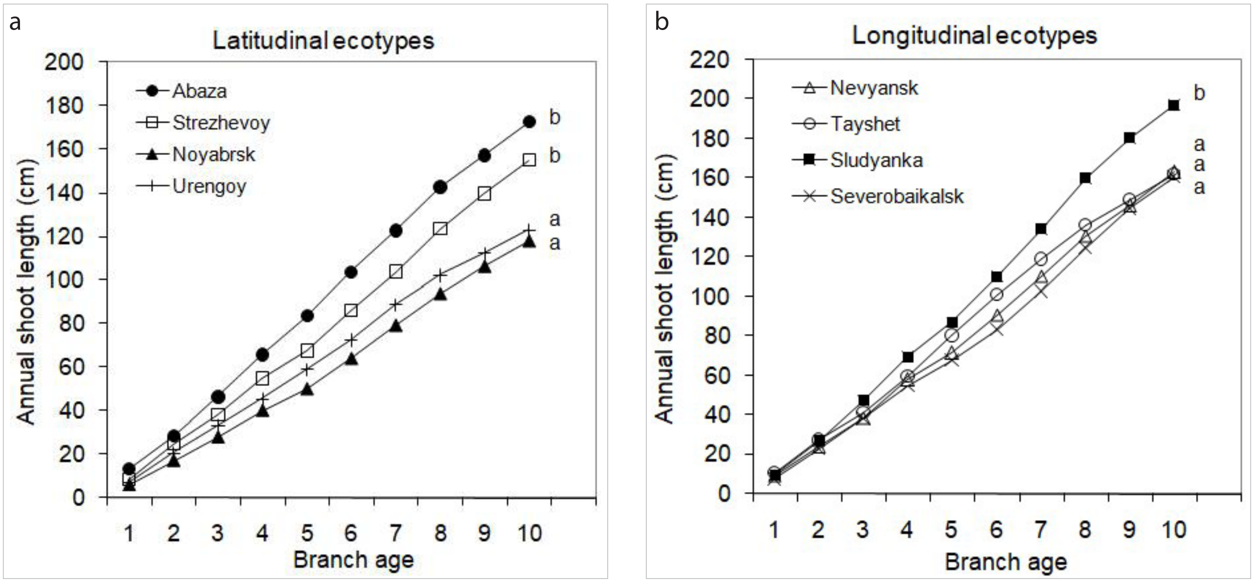

Figure 2. a, b. Growth rate of 10-year-old branches in *Pinus sibirica* ecotypes: (a), latitudinal ecotypes and (b), longitudinal ecotypes. Means associated with a different letter are statistically different ($p<0.05$), according to Duncan's test

Table 2. Total number of different axillary structures, and internode and needle length on the 10-year old branches of *Pinus sibirica*

Ecotype	Number of sterile cataphylls on the branch	Number of brachyblasts on the branch	Number of auxiblasts on the branch	Internode length in the annual shoot, mm	Needle length, cm
Latitudinal ecotypes					
1. Abaza	106.3±13.9[b]	694.8±81.5[b]	28.6±8.5[a]	2.1±0.3[b]	11.2±0.8[b]
2. Strezhevoy	79.0±18.9[a]	667.3±97.8[b]	34.1±4.7[a]	2.0±0.2[ab]	10.6±0.6[b]
3. Noyabrsk	77.4±20.4[a]	582.6±109.3[a]	29.7±6.8[a]	1.7±0.2[a]	9.0±1.0[a]
4. Urengoy	66.7±16.2[a]	577.8±109.3[a]	27.8±5.2[a]	1.8±0.2[ab]	8.5±0.6[a]
Longitudinal ecotypes					
5. Nevyansk	84.3±17.4[a]	718.1±116.1[a]	31.3±5.2[a]	1.9±0.2[a]	9.9±0.9[a]
6. Tayshet	79.2±14.4[a]	668.8±76.8[a]	29.5±2.4[a]	2.1±0.1[b]	10.9±0.9[b]
7. Sludyanka	90.6±26.2[a]	903.3±200.5[b]	34.1±7.5[a]	1.9±0.2[a]	10.4±0.9[ab]
8. Severobaikalsk	80.1±18.7[a]	725.1±126.9[a]	33.1±4.9[a]	1.9±0.2[a]	10.3±0.5[ab]

Comparisons were made between latitudinal and longitudinal ecotypes separately. Means associated with a different letter are statistically different ($p<0.05$), according to Duncan's test.
Means±standard deviations are indicated

and 1.2 times, respectively. In addition, the southern ecotype had the longest internodes, which made shoot elongation even more effective. This ecotype, together with the intermediate one, also had the longest needles, probably to support the intensive growth.

The tendency in the variation among the longitudinal ecotypes was unambiguous. There were differences in the number of brachyblasts, but no differences in the number of sterile cataphylls and auxiblasts. The south-eastern ecotype had the highest number of brachyblasts. Despite their origins, the other ecotypes did not show any differences. However, an intermediate ecotype had the longest internodes and needles.

Thus, significant variation among latitudinal and longitudinal ecotypes *ex situ* was observed both in branch growth and shoot structure, but the ecotypes from the profiles showed different patterns of variation. There was no variation among all ecotypes in the number of branching structures. The number of elongation structures and the length of internodes were maximal in the southernmost ecotypes in both profiles. From southern to northern ecotypes, the tendency to decrease structures was pronounced, but there was no pronounced tendency from western to eastern ecotypes.

Variation in the growth rates of Siberian stone pine ecotypes was comparable with the variation in other boreal conifers both in direction and magnitude. The variation in growth between different species, when growing under uniform conditions, depends on the experimental region and the observation period (Nord-Larsen and Pretzsch, 2017). However, in most cases, ecotypes from regions with relatively high growing-season temperatures showed high growth rates *ex situ*. In previous experiments, this pattern was found for *Pinus sylvestris* L. (Govindarajulu, 2014), *P. pinea* L. (Loewe Muñoz et al., 2017) and *Larix gmelinii* Rupr. (Lukkarinen et al., 2010). Therefore, there seems to be an adaptive convergence of latitudinal ecotypes of most coniferous species, although the degree of intraspecific variation may vary between species and depend on the origin of ecotypes.

Branch length varied significantly between the ecotypes of Siberian stone pine. Further, ecotypes originating from the most favorable conditions had the longest branches. Over the 10 years of branch growth, the annual growth rate, with the exception of several years, showed similar differences between ecotypes. The age-related growth curves of tree species usually demonstrate that annual growth is relatively fast at first and decreases throughout life. This is associated with tree aging and the accompanying changes in root-leaf relationships (Bond et al., 2007). The growth curves of branches in the Siberian stone pine ecotypes showed that there was no apparent age-related growth decrease in any ecotype over the 10-year period. The only intermediate ecotype, Tayshet, showed a remotely similar trend over the last four years. This differentiated the lateral branches from the tree trunk. This finding is explained by a previous study, which showed that stem growth in 23-year-old ecotypes did not decrease with age in the southern ecotype, while the northern ecotype showed an annual growth that halved over the last five years (Zhuk and Goroshkevich, 2018).

Needle length varied significantly among the Siberian stone pine ecotypes. Again, ecotypes from favorable conditions had the longest needles. Together with physiological characteristics, needle length is an important indicator of the growth energy of a tree and its sensitivity to external impacts (Grulke, 2010). Thus, ecotypes with long needles have the highest growth rates of branches.

The number and proportion of metameres responsible for elongation of the shoot, as well as internode length, varied significantly among the ecotypes. Two ecotypes contributed most to the variation: the eastern ecotype had the largest number of brachyblasts, and the southern ecotype had the largest shoot sterile zone and the longest internodes. A large number of metameres and long internodes are adaptive traits that allow trees to compete sufficiently for the first layer of the forest stand. This is especially relevant in relatively mild environments where intraspecific and interspecific competition is most pronounced. Both the number of metameres responsible for branching and their proportion of the total number of metameres were similar for all ecotypes. In contrast, among altitudinal Siberian stone pine ecotypes *ex situ*, significant differentiation was found, and high-altitudinal ecotypes had a larger number of latent buds, which are part of the branching metameres (Zhuk, 2010). Having a large number of latent buds allows adaptiveness, as apical growth can resume after frost injuries of shoots. Perhaps, unlike for mountain ecotypes, latitudinal and longitudinal ecotypes form metameres in mild conditions. Therefore, in the geographical ecotypes of Siberian stone pine, the number of metameres responsible for shoot elongation as well as internode and needle length are the primary adaptive traits.

CONCLUSION

The length and metameric composition of branches varied significantly among both latitudinal and longitudinal ecotypes of *Pinus sibirica* in a common garden experiment. The growth rates in the southern and eastern ecotypes were higher than those in the northern and western ecotypes. However, the proportions of auxiblasts involved in branching did not differ among ecotypes. The proportions of metameres involved in shoot elongation and internode length depended on the geographic origin of ecotypes when growing their vegetative progeny *ex situ*. Both latitudinal and longitudinal ecotypes were less morphologically differentiated than the altitudinal ecotypes of *Pinus sibirica*, despite their much longer transect lengths.

Ethics Committee Approval: Ethics committee approval is not applicable for this type of research in Russia because this article does not contain any studies with human or animal subjects.

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Conflict of Interest: The author have no conflicts of interest to declare.

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REFERENCES

- Andersson Gull, B., Persson, T., Fedorkov, A., Mullin, T.J., 2018. Longitudinal differences in Scots pine shoot elongation. *Silva Fennica* 52 (5): id 10040. [Crossref]
- Bond, B.J., Czarnomski, N.M., Cooper, C., Day, M.E., Greenwood, M.S., 2007. Developmental decline in height growth in Douglas-fir. *Tree Physiology* 27 (3): 441-453. [Crossref]
- Goroshkevich, S.N., Popov, A.G., 2004. Shoot morphological structure of the Russian *Pinus* species from the group *Cembrae* (*Pinaceae*). *Botanicheskii Zhurnal* 89 (7): 1077-1092.
- Govindarajulu, A., 2014. Adaptive variation in extent and timing of growth of Scottish Scots pine (*Pinus sylvestris* Linn). *Journal of Biodiversity & Endangered Species* 2 (3): 1000125. [Crossref]
- Grulke, N.E., 2010. Plasticity in physiological traits in conifers: implications for response to climate change in the western U.S. *Environmental Pollution* 158 (6): 2032-2042. [Crossref]
- Khutornoy, O.V., Zhuk, E.A., Bocharov, A.Ju., 2018. Radial Growth of Eurasian species of five-needle pines in the clone archive in the

south of the Tomsk oblast. *Journal of Siberian Federal University Biology* 11 (3): 260-274. [Crossref]
- Liepe, K.J., Hamann, A., Smets, P., Fitzpatrick, C.R., Aitken, S.N., 2016. Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications* 9 (2): 409-419. [Crossref]
- Loewe Muñoz, V., Balzarini, M., Delard Rodriguez, C., Álvarez Contreras, A., Navarro-Cerrillo, R.M., 2017. Growth of Stone pine (*Pinus pinea* L.) European provenances in central Chile. *iForest* 10 (1): 64-69. [Crossref]
- Lukkarinen, A.J., Ruotsalainen, S., Nikkanen, T., Peltola, H., 2010. Survival, height growth and damages of Siberian (*Larix sibirica* Ledeb.) and Dahurian (*Larix gmelinii* Rupr.) larch provenances in field trials located in southern and northern Finland. *Silva Fennica* 44 (5): 727-747. [Crossref]
- Malmqvist, C., Wallin, E., Lindström, A., Säll, H., 2017. Differences in bud burst timing and bud freezing tolerance among interior and coastal seed sources of Douglas fir. *Trees Structure and Function* 31 (6): 1987-1998. [Crossref]
- Martínez-Berdeja, A., Hamilton, J.A., Bontemps, A., Schmitt, J., Wright, J.W., 2019. Evidence for population differentiation among jeffrey and ponderosa pines in survival, growth and phenology. *Forest Ecology and Management* 434: 40-48. [Crossref]
- Nagamitsu, T., Matsuzaki, T., Nagasaka, K., 2018. Provenance variations in stem productivity of 30-year-old Japanese larch trees planted in northern and central Japan are associated with climatic conditions in the provenances. *Journal of Forest Research* 23 (5): 270-278. [Crossref]
- Nord-Larsen, T., Pretzsch, H., 2017. Biomass production dynamics for common forest tree species in Denmark – Evaluation of a common garden experiment after 50 yrs of measurements. *Forest Ecology and Management* 400 (15): 645-654. [Crossref]
- Sáenz-Romero, C., Kremer, A., Nagy, L., Újvári-Jármay, É., Ducousso, A., Kóczán-Horváth, A., Hansen, J.K., Mátyás, C., 2019. Common garden comparisons confirm inherited differences in sensitivity to climate change between forest tree species. *PeerJ* 15 (7): e6213. [Crossref]
- Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R., Kremer, A., 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal of Forest Research* 39 (7): 1259-1269. [Crossref]
- Vorobjev, V.N., Goroshkevich, S.N., Savchuk, D.A., 1992. Method of retrospective study of seminiference dynamics in *Pinaceae*. In: Proceedings of International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge. September 5-11, St. Moritz, Switzerland.
- Ye, T.Z., Jayawickrama K.J.S., 2014. Geographic variation and local growth superiority for coastal Douglas-fir – rotation-age growth performance in a Douglas-fir provenance test. *Silvae Genetica* 63 (3): 116-125. [Crossref]
- Zhuk, E.A., Goroshkevich, S.N., 2018. Growth and reproduction in *Pinus sibirica* ecotypes from Western Siberia in a common garden experiment. *New Forests* 49 (2): 159-172. [Crossref]
- Zhuk, E.A., 2010. Shoot morphogenesis and crown structure of Siberian stone pine mountain ecotypes: *ex situ* experiment. *Tomsk State University Journal of Biology* 2 (10): 89-96.