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Evaluation of survival and growth of *Picea abies* (L.) H. Karst. and *Picea obovata* Ledeb. provenances in the north of Russia

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Abstract

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Adaptation variability and ecological plasticity in the "genotype-environment" system of 22 provenances of *Picea abies* (Linnaeus) H. Karsten, *Picea obovata* (von Ledebour) and their introgressive hybrids growing within the Russian Plain were studied. Provenances grow in provenance trials located in the Arkhangelsk, Vologda Regions, and Komi Republic. For assessment of provenances in the "genotype-environment" system, the ranking method was used. Based on a complex ranking index (survival, diameter, height) two local areas of the most adaptive geographic races of *P. abies*, *P. obovata* and their hybrid forms were distinguished. In the south-western part of the Russian Plain the best provenances are represented by *P. abies* and related hybrids from Karelia, Vologda, Leningrad, and Pskov Regions. In the north-eastern part they are represented by *P. obovata* and its hybrids from the Komi Republic, Arkhangelsk, Sverdlovsk Regions. Provenances of local *P. abies* and related hybrid forms demonstrate high ecological plasticity on their growing in harsh climatic conditions of the north outside of the species distribution area.

Keywords: spruce; provenances test; ranking; adaptation variability

First of all, provenances of the main forest-forming species including Norway spruce have practical importance: provenances are selected to increase plant productivity at reforestation. However, currently scientists recognize their scientific significance for the "genotype-environment" problem (Lindgren, Persson 1995) that is one of the most important problems of provenance selection and gives base for regulations of the transfer of seeds proposed for reforestation (Schultze 1994).

Provenance tests are also used for assessment of species tolerance to climatic variations (Beuker, Koski 1995; Mátyás 1995, 2006; Nakvasina 2003; Andreassen et al. 2006; Suvanto et al. 2016). Research of phenotypic plasticity related to the population origin is considered to be of higher priority (Mátyás 2006). In wide sense, plasticity means the potential of a biological species to adapt to the environment. For an assessment of intrapopulation genetic diversity and phenotypic (ecological) plasticity of a species, provenance tests carried out in different growing conditions are preferable. Such an opportunity was provided by the State provenance network established in the USSR in the late 1970s.

As a rule, provenances are studied with regard to practical regional objectives of reforestation separately for each provenance trial. Unlike the pine (Shutyaev, Giertych 1997), no regular spruce provenance studies using the whole State network were presented. Researches conducted in several spruce test sites (Faizulin et al. 2011; Nikolaeva et al. 2014) were based on conventional approaches.

In our research, we set the following goals:

(*i*) To assess adaptive variability and ecological plasticity in the "genotype-environment" system of *Picea abies* (Linnaeus) H. Karsten, *Picea obovata* (von Ledebour) and their introgressive hybrids growing within the Russian Plain in different climatic conditions for the same provenances;

(*ii*) To recognize provenances (with regard to species and forms) which are the most adaptive and the most tolerant to variations in growing conditions.

MATERIAL AND METHODS

In the European north of Russia, Norway spruce provenances are located at three sites: Cherepovets Forest Division in the Vologda Region ("Vologda"), Plesetsk Forest Division in the Arkhangelsk Region ("Arkhangelsk"), and Kortkeros Forest Division in the Komi Republic ("Komi"). These sites are the northernmost ones in the large-scale test of the State provenance network of the USSR established in the 1970s (Shutyaev 1990; Rodin, Prokazin 1996, 1997).

Provenance trials were established in 1977. For planting 3-year seedlings were used (plant spacing: 0.75 m, row spacing: 2.5 m, average block area: 0.25 ha in 3–6 replications). The Northern Research Institute for Forestry (Arkhangelsk, Russia) is a supervisor of the sites.

In this research, for an assessment of phenotypic plasticity and "genotype-environment" relation 22 spruce provenances growing in all test sites were chosen. In the time of the study, in the Arkhangelsk and Vologda Regions plant age was 34 years, in the Komi Republic plant age was 36 years.

According to the forest zoning, the test plot in the Vologda Region is located in the subzone of southern taiga, the test plots in the Arkhangelsk Region and Komi Republic are located in the subzone of middle taiga. Conditions of provenance growing sites are described in Table 1. In the Vologda and Arkhangelsk Regions the climate is temperate continental, in the Komi Republic the climate is strongly continental.

Original stands grow in the subzones of northern, middle and southern taiga and also in the mixed forest zone distinguished within the Russian Plain by Kurnaev (1973). In the experiment, two spruce species are represented: Norway spruce (*P. abies*) and Siberian spruce (*P. obovata*), and also two introgressive hybrid forms distinguished by seed scale edges of mature spruce cones (Pravdin 1975; Popov 2005; Orlova, Egorov 2010).

Description of spruce provenances used in the research is given in Table 2, their habitats within the Russian Plain are shown in Fig. 1.

The method of examination of geographic variation of the main forest-forming species developed by the All-Union Research Institute of Silviculture and Mechanization of Forestry and approved by the Basic Research Council on Forest Genetics, Selection, and Seed Production was used (Rodin, Prokazin 1997). For each provenance, diameter (DBH) was measured at least in 100 randomly selected plants to the nearest 0.1 cm. The average tree height (m) of a certain provenance was determined by the graph of heights developed based on diameter and height (to the nearest 0.1 m) values for at least 25 trees of different diameter classes for each provenance. The number of survived plants was determined as the percentage of the total number of trees planted in blocks (1,100 plants per block of 0.25 ha area on average).

Provenance response to growing conditions was assessed using three indices: survival, height, and diameter.

The ranking method was used for an assessment of provenances in the "genotype-environment system" growing in three test plots. This method makes it possible to avoid using absolute measures (%, m, cm) describing specific features of provenance survival and growth. We used the approximate multi-criteria ranking of parameters without rank transformation applied in various researches, including the use for coenosis assessment (Bogolyubov 1998; Devjatko 1998; Ustinova et al. 2015). Provenance survival and growth rate indices were

Table 1. Climatic characteristics of test plots in the European north of Russia

Parameter	Plesetsk	Vologda	Komi
Latitude	62°54'	59°15'	61°41'
Longitude	40°24'	37°20'	51°31'
Vegetation period (days)	148	160	141
Sum of temperatures above +5°C	1,810	2,020	1,720
Annual mean temperature (°C)	1.0	2.3	–0.1
Annual rainfall (mm)	530	580	550
Climate continentality (%)	45.0	48.0	50.0

Table 2. Provenance locations and characteristics in the test plots in the European north of Russia

No.	Area, location	Spatial coordinates	Forest vegetation subzone, zone	Plesetsk			Vologda			Komi		
				Sv (%)	DBH (cm)	*h* (m)	Sv (%)	DBH (cm)	*h* (m)	Sv (%)	DBH (cm)	*h* (m)
Picea obovata **(von Ledebour)**												
20	Arkhangelsk, Pinezhskii	64°45', 43°14'	NT	81.3	7.5	8.0	82.4	7.8	8.3	51.9	4.5	4.8
23	Arkhangelsk, Kholmogorskii	64°14', 41°38'	NT	81.3	7.3	7.8	85.5	8.0	8.5	28.5	3.6	3.7
25	Komi, Kortkerosskii	61°41', 51°31'	MT	75.2	8.3	9.5	76.7	8.8	9.7	67.9	8.2	8.5
26	Komi, Sosnogorskii	63°27', 53°55'	MT	68.4	8.3	9.9	81.6	8.6	9.6	46.6	7.3	7.9
40	Sverdlovsk, Karpinskii	59°51', 60°00'	MT	60.5	7.7	7.7	81.8	8.5	9.1	42.4	7.5	7.7
39	Perm, Dobrjanskii	58°16', 56°25'	ST	62.7	7.2	8.4	75.2	9.5	10.3	50.5	4.8	5.1
41	Sverdlovsk, Nizhnetagilskii	57°54', 60°00'	ST	60.5	7.1	7.7	68.8	8.9	10.1	50.5	5.1	5.7
Hybrid forms with properties of *P. obovata*												
2	Karelia, Segezhskii	63°40', 34°23'	MT	68.7	7.1	8.3	78.0	8.9	9.5	54.8	5.3	5.4
22	Arkhangelsk, Kotlasskii	61°15', 46°54'	MT	75.7	8.1	9.9	79.6	8.6	9.5	61.2	5.4	5.8
28	Kirov, Slobodskoi	58°49', 50°06'	ST	71.3	7.0	8.3	77.9	9.8	10.2	51.8	5.6	5.9
35	Udmurtia, Izhevskii	56°50', 53°10'	ST	51.3	6.2	7.7	71.0	8.6	9.7	50.7	3.7	4.1
Hybrid forms with properties of *Picea abies* (Linnaeus) H. Karsten												
3	Karelia, Prjazhinskii	61°40', 33°33'	MT	70.9	8.9	9.8	81.1	8.8	9.6	42.0	4.3	4.7
4	Karelia, Pudozhskii	61°40', 36°40'	MT	78.0	7.6	9.4	79.5	9.1	9.8	47.9	6.0	6.3
24	Vologda, Tserepovetskii	59°07', 37°57'	ST	61.9	9.5	10.1	84.5	10.0	10.7	44.7	4.1	4.4
27	Kostroma, Galitskii	58°24', 42°20'	ST	68.7	7.0	8.6	78.7	9.5	11.4	32.4	3.2	3.4
31	Nizhnii Novgorod, Sharangskii	57°11', 46°39'	MF	48.4	6.1	7.0	77.9	9.2	9.8	32.6	5.9	6.2
P. abies												
5	Leningrad, Tosnenskii	59°30', 30°52'	ST	70.9	8.5	10.7	84.5	10.3	11.5	24.8	4.5	4.6
7	Pskov, Velikolukskii	56°23', 30°30'	MF	54.9	8.7	10.0	84.4	10.2	11.0	15.7	4.9	5.4
30	Tver, Nelidovskii	56°14', 32°48'	MF	62.2	7.3	8.8	63.5	9.5	10.8	36.7	6.2	6.5
8	Estonia, Viljadinskii	58°24', 25°38'	MF	56.1	7.6	9.6	71.6	9.5	10.2	31.2	6.7	7.4
10	Latvia, Daugavpilskii	56°10', 26°30'	MF	53.2	7.7	10.3	69.9	9.5	10.5	28.0	5.9	6.2
29	Moscow, Solnechnogorskii	56°10', 36°58'	MF	66.6	8.7	10.6	61.6	8.8	9.8	31.5	5.5	6.0

NT – northern taiga, MT – middle taiga, ST – southern taiga, MF – mixed forest, Sv – number of survived plants in percent of the total number of trees planted in blocks, DBH – diameter at breast height for 100 randomly selected trees, *h* – average height determined by the graph of heights

ranked based on a principle of maximum towards minimum. In case of equal values for two or more provenances equal points were assigned. For survival the similarity criterion was 0.5%.

For each tested provenance by parameter (survival, height and diameter) the rank was established in each plot (Plesetsk, Vologda, Komi). Average score by parameter was calculated for each provenance (Table 3). A complex rank characterizing the ecological plasticity of a provenance was estimated based on the score of three indices. The position of a provenance in the ranking order was assigned based on the complex rank; the ranking result reflected the ecological plasticity level of a provenance. Provenances in the upper part of the ranking order are considered as the best provenances.

Comparison of individual provenance profiles was carried out based on indices using the Spearman rank correlation method. For assessment of the spruce provenance zone and species/form impact, the single-factor ANOVA (SPSS Version 22, 2013) was used.

RESULTS

Profiles of diameter and height are quite identical (Table 3). Spearman's correlation coefficient (*r*) is 0.955. Profile of survival significantly differs from provenance growth profiles (r = 0.627–0.770). The survival index is the most persistent when the same spruce provenances are grown in different conditions and shows biological tolerance of a genotype to cultivation conditions. Provenance growth is more dependent on growing conditions, which is observed especially in provenance tests carried on

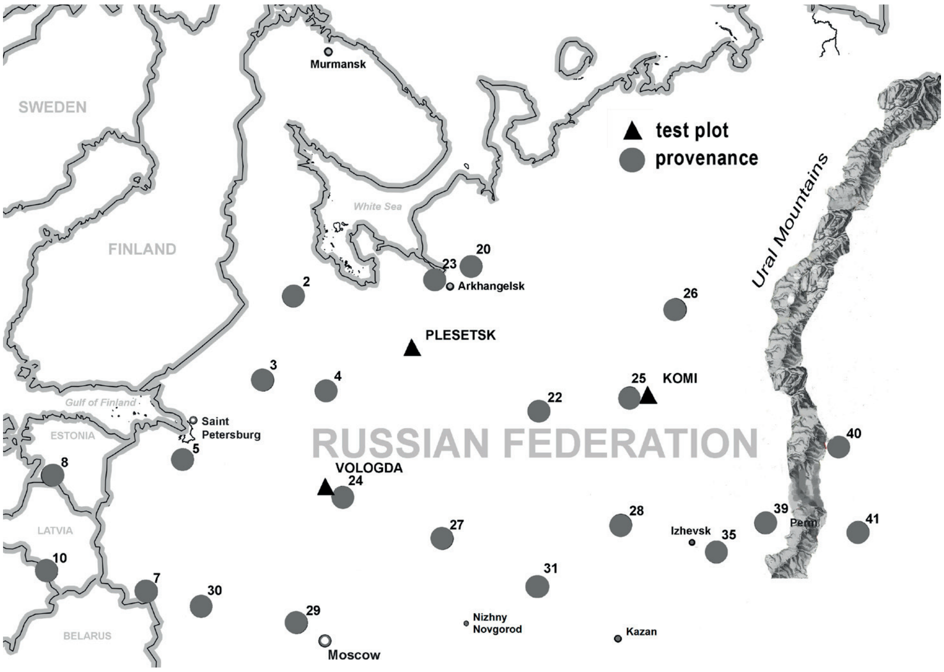

Fig. 1. Location of tested populations and spruce test plots in the European north of Russia

2 – Karelia, Segezhskii, 3 – Karelia, Prjazhinskii, 4 – Karelia, Pudozhskii, 5 – Leningrad, Tosnenskii, 7 – Pskov, Velikolukskii, 8 – Estonia, Viljadinskii, 10 – Latvia, Daugavpilskii, 20 – Arkhangelsk, Pinezhskii, 22 – Arkhangelsk, Kotlasskii, 23 – Arkhangelsk, Kholmogorskii, 24 – Vologda, Tserepovetskii, 25 – Komi, Kortkerosskii, 26 – Komi, Sosnogorskii, 27 – Kostroma, Galitskii, 28 – Kirov, Slobodskoi, 29 – Moscow, Solnechnogorskii, 30 – Tver, Nelidovskii, 31 – Nizhnii Novgorod, Sharangskii, 35 – Udmurtia, Izhevskii, 39 – Perm, Dobrjanskii, 40 – Sverdlovsk, Karpinskii, 41 – Sverdlovsk, Nizhnetagilskii

Table 3. Ranking order of spruce provenances by the survival and growth parameters in the test plots in the European north of Russia

No.	Area	Rank by parameter (score)			Complex rank	
		Sv	DBH	*h*	average score	position
20	Arkhangelsk	2.7	12.3	15.0	10.0	15
23	Arkhangelsk	5.0	13.7	16.7	11.8	18
25	Komi	4.7	4.7	7.0	5.5	1
26	Komi	5.7	6.0	6.7	6.1	2
40	Sverdlovsk	5.7	6.7	11.0	7.8	8
39	Perm	8.9	10.0	11.0	10.0	15
41	Sverdlovsk	9.3	10.7	12.0	10.7	16
2	Karelia	5.7	10.3	13.0	9.7	14
22	Arkhangelsk	3.7	8.7	9.7	7.4	6
28	Kirov	5.7	8.3	10.3	8.1	10
35	Udmurtia	10.3	14.0	15.3	13.2	19
3	Karelia	6.3	9.0	11.3	8.9	13
4	Karelia	4.7	7.0	8.7	6.8	4
24	Vologda	6.3	7.0	8.7	7.3	5
27	Kostroma	8.0	12.7	11.3	10.7	16
31	Nizhnii Novgorod	11.3	9.3	11.7	10.8	17
5	Leningrad	7.3	6.7	6.0	6.7	3
7	Pskov	10.0	6.0	6.7	7.6	7
30	Tver	11.0	6.7	6.7	8.1	10
8	Estonia	11.3	5.7	6.7	8.0	9
10	Latvia	13.0	6.3	5.3	8.2	11
29	Moscow	11.3	7.0	6.7	8.3	12

Sv – number of survived plants in percent of the total number of trees planted in blocks, DBH – diameter at breast height for 100 randomly selected trees, *h* – average height determined by the graph of heights

Table 4. Spearman's rank order correlations between test plots and survival and growth parameters

Parameter	Plesetsk-Vologda	Plesetsk-Komi	Vologda-Komi
Sv	0.762*	0.686*	0.500*
DBH	0.698*	0.381	0.316
h	0.679*	0.355	0.282

Sv – number of survived plants in percent of the total number of trees planted in blocks, DBH – diameter at breast height for 100 randomly selected trees, *h* – average height determined by the graph of heights, *significant at 0.05 level

in strongly continental climate of the Komi Republic (Table 4).

Tested provenances were assessed by spruce species-forms and zones-subzones of original stands (Tables 5 and 6).

Cluster analysis of data was carried out on the complex ranks for each provenance (Fig. 2).

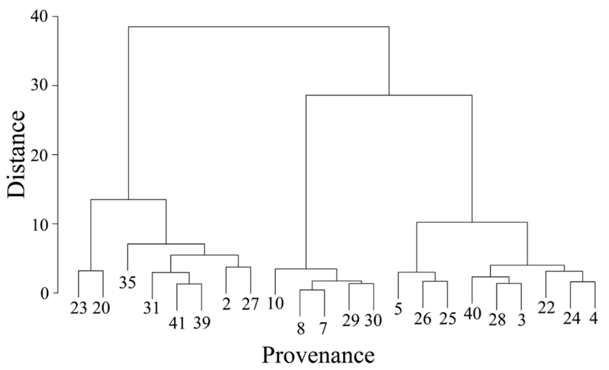

Fig 2. Dendrogram of similarities and differences between provenances in provenance trials (Ward method, Euclidian distance)

Table 6. Fisher values (*F*) and statistical significances (*P*-values) of main effects of forest vegetation subzone-zone and spruce species on survival and growth parameters of spruce provenances (one-way ANOVA), *df* = 3, F_{crit} = 3.160 at 0.05 level

Trait	Spruce species and forms		Subzone-zone	
	F	*P*	*F*	*P*
Sv	4.825	0.012	31.983	0.001
DBH	2.338	0.108	5.987	0.005
h	5.794	0.006	6.428	0.004

Sv – number of survived plants in percent of the total number of trees planted in blocks, DBH – diameter at breast height for 100 randomly selected trees, *h* – average height determined by the graph of heights

DISCUSSION

The fact that within the Russian Plain *P. abies* comes in contact with *P. obovata* resulting in natural (introgressive) hybrids is of specific interest. For the purposes of reforestation, spruce growing within the Russian Plain can be considered (Popov 2005) as a single combined species *P. abies* × *P. obovata*. However, the study of ecological plasticity in the "genotype-environment" system demonstrates that species and dispersal history of species have resulted in unexpected population changes in growth and stability of provenances (Kapeller et al. 2012, 2013). Provenance tests in the European north of Russia made it possible to study specific features of spruce species growth in areas with extreme temperature conditions and for *P. abies* – also outside of its distribution area.

Table 5. The average ranks of the survival and growth parameters by the spruce species (form) and subzone-zone of original locations

Spruce species (form)	Parameter			Mean ± SD
	Sv	DBH	*h*	
Picea obovata (von Ledebour) (7)[1]	6.00 ± 0.87	9.16 ± 1.28	11.34 ± 1.40	8.83 ± 1.18
Hybrid forms with properties of *P. obovata* (4)	6.35 ± 1.40	10.33 ± 1.30	12.08 ± 1.30	9.59 ± 1.33
Hybrid forms with properties of *Picea abies* (Linnaeus) H. Karsten (5)	7.30 ± 1.12	9.00 ± 1.04	10.3 ± 0.67	8.87 ± 0.94
P. abies (6)	10.65 ± 0.78	6.40 ± 0.20	6.56 ± 0.24	7.87 ± 0.41
Subzone-zone				
Northern taiga (2)	3.85	13.00	15.85	10.9
Middle taiga (7)	5.21 ± 0.33	7.49 ± 0.73	9.63 ± 0.88	7.45 ± 0.65
Southern taiga (7)	7.97 ± 0.63	9.91 ± 1.05	10.66 ± 1.08	9.51 ± 0.92
Mixed forests (6)	11.32 ± 0.39	6.80 ± 0.53	7.30 ± 0.91	8.47 ± 0.61

[1]number of provenances, Sv – number of survived plants in percent of the total number of trees planted in blocks, DBH – diameter at breast height for 100 randomly selected trees, *h* – average height determined by the graph of heights, SD – standard deviation

Species differentiation of spruce impacts, first of all, on spruce survival and height. As for survival, *P. obovata* provenances are ranked to the top of the ranking order, and *P. abies* provenances are at the top of the ranking order by growth rate. Hybrids are in the intermediate positions. The highest growth rates of *P. abies* outside of its distribution area were observed earlier for provenances in Siberia, European North and Bashkortostan (Terentyev, Milutin 2008; Faizulin et al. 2011; Nikolaeva et al. 2014).

The impact of plant origins (zone-subzone) is significant for all considered parameters (P = 0.001–0.005). However, provenance distribution by zones and subzones depends on species differentiation of provenances, which determines the provenance position in the ranking order. The most obvious difference is observed in provenance survival. Northern and middle taiga provenances are at the top of the survival ranking order, and spruce provenances from the mixed forest zone represented by *P. abies* are in the lowest positions of the ranking order. Provenances from the mixed forest zone are also the best in height and diameter rank, especially in comparison with spruce provenances from the northern taiga represented by *P. obovata*.

On calculation of the complex index based on three indices, the levelling of provenance profiles and ranks takes place; it reflects the complex impact of provenance zone/subzone, species and forms. As a result, the distribution of complex ranks of provenances is not clearly differentiated either by species-forms or by subzones-zones. The top positions in the ranking order are assigned to provenances both of *P. obovata* and *P. abies* and of their hybrids from different forest zones and subzones.

The diagram (Fig. 2) shows that provenances of *P. obovata* and *P. abies* are in the same groups. First of all, it is obvious in a group of provenances assigned to the top of the ranking order. There is no distinct cluster grouping of provenances tested in the course of the experiment (22 provenances) by certain spruce species and forms or by zones and subzones.

In the south-western part of the Russian Plain the best provenances are represented by *P. abies* and similar hybrid forms from Karelia (Pudozh, provenance No. 4), Vologda (Cherepovets, provenance No. 24), Leningrad (Tosno, provenance No. 5), Pskov (Velikie Luki, provenance No. 7) regions. In the north-eastern part of the Russian Plain the best provenances are represented by *P. obovata* and its hybrids from the Komi Republic (Kortkeros – provenance No. 25, Sosnogorsk – provenance No. 26), Arkhangelsk (Kotlas, provenance No. 22) and Sverdlovsk (Karpinsk, provenance No. 40) regions. Between them an assimilation zone (introgressive hybridization) is located. Stands growing here are distinctive by mean ecological plasticity in conditions of the European north.

Such spruce species distribution is related with the history of spruce species dispersal within the Russian Plain in Holocene: *P. abies* propagated from the south-west, *P. obovata* – from Siberia via the Urals (Popov 2005; Dering, Lewandowski 2007). Provenances of local *P. abies* and related hybrids have better ecological plasticity when grown in harsh climatic conditions of the north outside of the species distribution area in spite of the long distance of dispersal up to 3–6°N and 20°E. With such plasticity of *P. abies*, its active propagation as a response to weather changes (climate warming) and increased introgression of two spruce species in the contact zone can be expected.

CONCLUSIONS

The study of 22 spruce provenances growing in the conditions of the Russian taiga zone proved that the postglacial dispersal of two spruce species *P. abies* and *P. obovata* and their hybrids growing in the introgressive hybridization zone over the Russian Plain impact on production properties and adaptive plasticity of provenances.

Areas of the most adaptive spruce provenances recognized within the Russian Plain could be used as centres of plant breeding monitoring, genetic reserves, seed plantations. Two areas of the best provenances of *P. abies* and *P. obovata* within the Russian Plain should be taken into consideration in the course of tree seed zoning and transfer of seeds intended for reforestation.

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