Cent. Eur. For. J. 65 (2019) 121–128 sciendo DOI: 10.2478/forj-2019-0012

CENTRAL EUROPEAN Forestry Journal

http://www.nlcsk.sk/fj/

ORIGINAL PAPER

Assessment of phenotypic plasticity of spruce species *Picea abies* (L.) Karst. and *P. obovata* (Ledeb.) on provenances tests in European North of Russia

Elena Nakvasina[1, *], Nadezhda Demina[2], Nadezhda Prozherina[3], Natalia Demidova[2]

[1] *Northern (Arctic) Federal University of M. V. Lomonosov, Department of Forestry and Forest Management Severnaya Dvina emb. 17, 163002, Arkhangelsk, Russia*
[2] *Northern Research Institute of Forestry, Nikitova 13, 163062, Arkhangelsk, Russia*
[3] *N. Laverov Federal Center for Integrated Arctic Research, Laboratory of Population Ecology, Severnaya Dvina emb. 23, 163000, Arkhangelsk, Russia*

Abstract

Phenotypic plasticity of 22 spruce provenances in three test plots located in the European North of Russia was studied. Parent spruce stands are located within the Russian Plain and are represented by *Picea abies* (L.) Karst.*, P. obovata* (Ledeb.) and two introgressive hybrids. In the test plots located in the middle and southern taiga subzones *P. abies* provenances are tested northward of its distribution area and *P. obovata* provenances are tested within the distribution area and nearby its boundaries. phenotypic plasticity of the spruce provenances was assessed. Straight-line regression coefficient based on survival, diameter, and height was calculated. All provenances are divided into two groups: plastic and non-plastic provenances. High plasticity is observed more often for *P. abies* and hybrids forms with properties of *P. abies*. Plastic provenances based on three parameters grow in the Leningrad, Pskov, Vologda, Kostroma and Karelia. Area of parent stands growing is quite small-size and lies between 56°30´ – 61°40´ N and 30°30´ – 42°30´ E. Adaptive provenances of *P. obovata* and its related hybrids forms grow in the North-Eastern part of the Russian Plain that could be consequence of its distribution in Holocene. *Picea abies* being the more adaptive species would be more responsive to climate changes in terms of survival and growth rate than *P. obovata*. Therefore, in case of sustainable climate warming in the Northern areas of the Russian Plain, the further propagation and major distribution of *P. abies* with further competitive replacement of *P. obovata* can be expected.

Key words: *Picea*; provenance test; survival; growth; phenotypic plasticity

Editor: Dušan Gömöry

1. Introduction

Provenance tests have more value in gen-ecological studies. Provenance trials contain large-scale genetic resources *ex situ* concentrated within small-size areas. They are objects of genetic monitoring (Iroshnikov 2002) providing multivariate stationary studies and assessment of provenances adaptive capacity based on their age and ecological stability (Rone 1979).

At present, it is considered that provenance trials can be used not only for provenances selection for the purpose of reforestation in certain regions as well as for seeds transfer. These experiments can be used for study of species history and their distribution within a certain territory (Lindgren & Persson 1995), for study genetic variations and migration (Potokina et al. 2015). A provenance trial can be used as a model for prediction of climate changes impact on species productivity and survival is of a special interest (O'Neill et al. 2008; Gömöry et al. 2012; Kapeller & Schüler 2012). Natural climate warming (shift towards south) or cooling (shift towards north) is simulated in provenance test when we use seeds from the parent stands from the north or to the south of a test plot. In new conditions, wide range of genetic variations of a species demonstrating its genetic differentiation and environmental sustainability can be observed (Petrov 1987). In the opinion of I. I. Kamalova (Nakvasina et al. 2008), it can take place because of genotype frequency shift from homeostasis in the areas of parent stands growing.

To study different adaptation of tree provenances to climate changes various parameters are used. For spruce provenances, height of trees of different ages (Beaulieu

**Corresponding author. Elena Nakvasina, e-mail: nakvasina@yandex.ru, phone: +7818 2216174*

& Rainville 2005; Gömöry et al. 2012; Kapeller et al. 2012) or diamter growth (Suvanto et al., 2016) were used. We carried out the similar studies on Scots pine and spruce provenances response to climate change in terms of growth rate and seeds production (Nakvasina 2003, 2014; Nakvasina et al. 2008, 2016).

Study of intraspecific variability and phenotypic plasticity related to population origin and growing conditions is considered of higher priority (Mátyás 2006; Garzón et al. 2011; Kapeller et al. 2012; Suvanto 2016).

In wide sense, plasticity means biological ability of species to adapt to environmental conditions. Phenotypic plasticity means ability of an organism to change its phenotype in response to changes in the environment without genetic change (Gienapp et al. 2008; Price et al. 2003). Plasticity is based on homeostatic responses. Phenotypic plasticity provides stability of large populations, such as spruce populations (Gomez-Mestre & Jovani 2013).

However, species tests beyond its natural distribution area is of specific interest (Kapeller & Schüler 2012), as species response to climate changes can be explained by species distribution history, its migration from the distribution area center (Kapeller et al. 2012). For *P. abies* such opportunity is provided by provenance tests established in Russia. The eastern boundary of this species distribution area goes just within the Russian Plain area. Here, the species comes in contact with *P. obovata* and forms an introgressive hybridization zone.

We studied provenances of *Picea abies* (L.) Karst. and *P. obovata* (Ledeb.) in provenance trials located in the European North of Russia within the natural distribution area of *P. obovata*. *Picea abies* provenances grow in provenance trials beyond the distribution area of this species. Environmental conditions of the taiga zone considerably differ from optimal growing conditions for this species in the distribution area and therefore, it would make it possible to assess its phenotypic plasticity in extreme growth conditions. We can also compare phenotypic plasticity of *P. abies* and *P. obovata*. Provenances of *P. obovata* are tested in optimal growing conditions for this species or in simulated climate warming conditions.

2. Materials and methods

In the European North of Russia spruce provenances were tested in three test plots (Fig. 1) located in the southern taiga subzone (the Vologda Region, "Vologda" test plot, and in the middle taiga subzone (the Arkhangelsk Region, "Plesetsk" test plot, Komi Republic, "Komi" test plot). These plots make a part of the State Provenance Trial Network of the USSR established in 1970s (Rodin & Prokazin 1996, 1997; Shutyaev 1990). Geographical and environmental characteristics of the test plots are given in Table 1. Latitude difference of the test plots is 2.5–3.5° N, longitude difference is up to 14° E. In the Arkhangelsk and Vologda Regions climate is continental, in Komi Republic climate is strong continental result from proximity of the Urals. Provenances are grown on podsolic soils in spruce-blueberry shrub forest type.

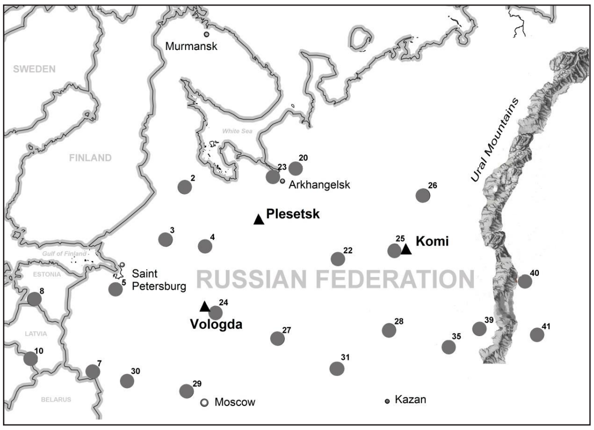

Fig. 1. Location of tested populations and spruce test plots in the European North of Russia (triangle – test plots location, dark circles – provenance location).

Table 1. Characteristics of geographic coordinates and climatic parameters of the experimental plots.

Parameters	Plesetsk	Vologda	Komi
Age [years]*	31/34	31/34	33/36
Latitude, [°N]	62°54'	59°15'	61°41'
Longitude, [°E]	40°24'	37°20'	51°31'
Vegetation period [days]	148	160	141
Sum of temperatures above +5 °C	1810	2020	1720
Annual mean temperature, [°C]	1	2.3	−0.1
Mean temperature in January, [°C]	−12	−12	−15
Mean temperature in July, [°C]	10.0	17.5	16.0
Annual rainfall [mm]	530	580	550
Climate continentality, [%]	45.0	48.0	50.0

* – The age of plantation / the biological age of trees at the time of study.

Provenance trials were established in 1977. For tree planting 3-year seedlings were used for planting. Plant spacing: 0.75 m, row spacing: 2.5 m. Average block area – 0.25 ha, number of planted trees is about 400 in 3–6 replications. Supervisor of the test plots (Northern Research Institute of Forestry, Arkhangelsk, Russia) carries on regular observations.

For study of spruce provenances, the generally accepted Russian method of provenance tests of the main forest-forming species (Prokazin 1972) approved by the Basic Research Council on Forest Genetics, Selection, and Seed Production was used. For each provenance diameter (DBH) was measured at least for 100 randomly selected plants with accuracy of 0.1 cm. Average tree height for the provenance was determined using a height profile developed based on diameter and height values measured for at least 25 plants of different diameter classes in each variant. Survival was determined (in per cent) by number of survived trees against total number of trees initially planted out in blocks.

In our research 22 spruce provenances growing in each test plot were chosen. Geographical coordinates and forest types of their parent stands and taxation parameters of tested provenances are given in Table 2. List of tested provenances includes provenances from the northern, middle, and southern taiga subzones and mixed forest zone located within the Russian Plain (Fig. 1). Seven from 22 provenances are represented by *P. obovata* (L.) Karst., and six are represented by *P. abies* (Ledeb.). The rest provenances are represented by their introgressive hybrid forms distinguished by scale edges of mature macrostrobiles (Pravdin 1975; Orlova & Egorov 2010). Provenances represented by hybrid forms are of two types: hybrids with *P. obovata* characters (4 provenances) and hybrids with *P. abies* characters (6 provenances).

For ecological plasticity calculation the method developed by S. Eberhart and W. Russel (1966) in S. A. Petrov (1984) interpretation was used. The method is used in system experiments when the same provenances (at least three) are cultivated in different environmental conditions. The method by S. Eberhart and W. Russell (1966) is widely use in Russia and other countries for assessment of agricultural field and fruit sorts and species crop capacity (Scapim et al. 2000; Besedina et al. 2014; Gulnyashkin et al. 2014; Krasnova et al. 2014). This method was used in provenance trials for forest species plasticity assessment (Shutyaev & Giertych 1997, 2000; Nakvasina et al. 2008).

According to the method (Eberhart & Russell 1966), total variability (plasticity) of a provenance under test conditions is characterized by linear regression coefficient (b_i). Provenances with $b_i > 1$ are characterized by high plasticity and easily adapt to cultivation conditions; in case of cultivation conditions improvement better results can be expected. Provenances with $b_i < 1$ have low

Table 2. Location, survival (%) and mean diameters and tree heights of spruce provenances.

No	Provenance area and location	Spatial coordinates	Forest vegetation subzone, zone	Plesetsk			Vologda			Komi		
				Sv	DBH	H	Sv	DBH	H	Sv	DBH	H
							Picea obovata (Ledeb.)					
20	Arkhangelsk Pinega	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 Kholmogy	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 Karpinsk	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 Dobrjanka	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 Nizhnij Tagil	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 *Picea obovata* (Ledeb.)					
2	Karelia Segezha	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 Kotlass	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 Slobodskoj	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 Izhevsk	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* (L.) Karst.					
3	Karelia Prjazha	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 Pudozh	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 Cherepovets	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 Galich	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 Sharanga	57°11' 46°39'	MF	48.4	6.1	7.0	77.9	9.2	9.8	32.6	5.9	6.2
							Picea abies (L.) Karst.					
5	Leningrad Tosno	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 Velikie Luki	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 Nelidovo	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 Viljandi	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 Daugavpils	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 Solnechnogorsk	56°10' 36°58'	MF	66.6	8.7	10.6	61.6	8.8	9.8	31.5	5.5	6.0

No – provenance identification number; area and location as in the State Register; NT – northern taiga, MT – middle taiga, ST – southern taiga, MF – mixed forest; Sv – survival [%], DBH – diameter at breast height [cm], H – height [m].

phenotypic plasticity and weak response to environmental conditions change; on cultivation conditions improvement better results are not expected. At the same time, in case of condition decline, results would not downgrade considerably. Provenances with $b_i = 0$ are in intermediate position (with average plasticity). This makes it possible to assess spruce provenances both in terms of their use for forest cultivation and in terms of their adaptation to climate changes.

The method makes it possible to calculate environmental condition index intended for assessment of differentiation of provenance cultivation conditions (Eberhart & Russell 1966; Petrov 1984).

The present study is based mainly on Eberhart and Russell (1966) model. Wricke's ecovalence (1962) evaluate genotype stability and complements the Eberhart and Russell (1966) regression analysis. According to Kang et al. (1987) Wricke's ecovalence is equivalent to Shukla (1972) and gives similar results for genotype ranking. A high value of Wricke's ecovalence (W_i^2) is considered as an indicator of low stability, while $W_i^2 = 0$ gives the most stability. The regression coefficient of Eberhart and Russell (b_i) and the Wricke's ecovalence (W_i^2) were calculated for each genotype and compared by correlation analysis.

Phenotypic plasticity was estimated based on three parameters: survival, diameter, height. For estimation of growth parameters of phenotypic plasticity we used average increment calculated as height and diameter divided by biological age of a spruce because the differences in years of observations and stands ages.

ANOVA (SPSS v 22.0, GLM procedure) with groups of plasticity and spruce species on survival and growth parameters of spruce provenances as fixed factors was used to test differences in survival and growth parameters, and interactions between them. For the statistical data analysis, correlation analysis was used. Significant value was accepted at the $P < 0.05$ level.

3. Results

Differences in growth conditions in the spruce test plots in the taiga zone of the Russian Plain are proved by environmental condition indices determined using the S. Eberhart & W. Russell (1966) method (Table 3). The best conditions when the index has positive value, the worst conditions when the index has negative value (Korzun & Bruilo 2011). In the test plots Plesetsk and Vologda environmental conditions of spruce growth are quite favorable; in the test plot Komi growth conditions are worse. Environmental conditions impact spruce provenance survival rather than diameter and height of survived trees.

Survival and growth rate of 22 spruce provenances in different test plots differ but have common behavior related to spruce age. Spruce provenances from low-latitudes *(P. abies)* have worse survival during first years after planting out. In this period northern provenances represented by *P. obovata* have better resistance to environmental conditions (Nakvasina et al. 1990; Tarkhanov 1998). They maintain better survival also later. In most cases, survived *P. abies* trees have higher growth rate than *P. obovata* (Nakvasina & Gvozdukhina 2005; Faizulin et al. 2011; Demina et al. 2013).

Table 3. Environmental indices in spruce test plots.

Parameters	Plesetsk	Vologda	Komi
Survival	+4.203	+15.430	–19.633
Height	+2.726	+5.212	–7.938
DBH	+0.119	+0.534	–0.653

Table 4 shows the parameters of the phenotypic plasticity of the origin of spruce: Eberhart and Russell's b_i and Wricke's W_i^2. Provenances of plastic and non-plastic groups ($b_i > 1$ and $b_i < 1$) by growth and survival occur among *P. obovata*, *P. abies* and their hybrid forms. Grouping of provenances by plasticity does not agree in some parameters. Plasticity grouping by survival and growth is the most similar in two biometrical indices (DHB and height), correlation ratio *r* is 0.7258 (significant at $P = 0.05$). Wricke's ecovalence (W_i^2) is an indicator of genotype stability. A high value shows the low genotype stability, while $W_i^2 = 0$ gives the greatest stability. In our experiment, W_i^2 had the more variations in survival (from 2.68 to 456.49) and lower in DBH and height (0.09 – 4.98 and 0.32 and 6.96). This is close to variability of Eberhart and Russell's liner regression parameter b_i.

Correlation coefficients (Table 5) were important for estimating mean values of and Eberhart and Russell's coefficient (b_i) and Wrick's ecovalence (W_i^2), as well as pair combinations between them. The correlation between the coefficients was significant for survival (0.417). The same indicator has a significant correlation between mean values and Eberhart and Russell's coefficient (b_i). Correlations between the other pairs of combinations were not significant. It can be assumed that with a larger number of tested genotypes this effect can be stronger (Becker 1981).

4. Discussion

For practical purposes it is important to select genotypes that will respond to a changed environment and give the best results. Such a possibility is provided by the approach of Eberhart and Russell (1966), which proposes to evaluate the plasticity by the coefficient b_i. Therefore, according to the linear regression indicator, the tested genotypes were divided into two groups: Group 1 – ($b_i > 1$) – plastic populations; Group 2 – ($b_i < 1$) – non-plastic.

Among *P. obovata* and its hybrid forms, the most provenances are assigned by survival and growth to Group 2 ($b_i < 1$), i.e. non-plastic. It is especially typical

Table 4. Phenotypic plasticity of spruce parameters by survival (Sv), height (H) and diameter (DBH).

No	Provenance area	Means			Eberhart and Russell's b_i			Wricke's W_i^2		
		Sv	DBH	H	Sv	DBH	H	Sv	DBH	H
20	Arkhangelsk	71.9	6.6	7.0	0.93	0.93	0.86	51.45	0.62	0.35
23	Arkhangelsk	65.1	6.3	6.7	1.72	1.18	1.06	456.49	0.94	0.34
25	Komi	73.3	8.4	9.2	0.26	0.26	0.51	352.62	5.21	5.09
26	Komi	65.5	8.1	9.1	0.99	0.44	0.63	2.68	2.98	3.30
40	Sverdlovsk	61.6	7.9	8.2	0.67	1.20	1.11	51.06	4.13	6.41
39	Perm	62.8	7.2	7.9	1.07	0.34	0.44	81.48	0.58	0.57
41	Sverdlovsk	59.9	7.0	7.8	0.51	0.99	0.93	160.34	0.09	1.24
2	Karelia	67.2	7.1	7.7	0.65	0.94	0.94	81.06	0.15	0.08
22	Arkhangelsk	72.2	7.4	8.4	0.54	0.90	0.98	139.51	0.42	0.96
28	Kirov	67.0	8.4	9.2	0.76	1.06	0.95	40.19	1.00	0.55
35	Udmurtia	57.7	6.2	7.2	0.49	1.24	1.15	276.56	0.79	0.97
3	Karelia	64.7	7.3	8.0	1.13	1.26	1.18	14.33	2.68	1.69
4	Karelia	68.5	7.6	8.5	0.96	0.84	0.90	48.62	0.31	0.32
24	Vologda	63.7	7.9	8.4	1.07	1.60	1.40	65.27	4.98	3.36
27	Kostroma	59.9	6.6	7.8	1.35	1.59	1.57	94.37	3.31	6.96
31	N. Novgorod	53.0	7.1	7.7	1.19	0.81	0.75	167.75	2.52	3.32
5	Leningrad	60.1	7.8	8.9	1.74	1.52	1.52	369.42	2.40	4.95
7	Pskov	51.7	7.9	8.8	1.91	1.40	1.26	567.11	1.54	1.16
30	Tver'	54.1	7.7	8.7	0.81	0.86	0.96	56.54	0.77	0.68
8	Estonia	53.0	7.9	8.1	1.14	0.75	0.78	15.95	1.05	1.16
10	Latvia	50.4	7.7	9.0	1.17	0.95	1.08	26.18	0.15	0.42
29	Moscow	53.2	7.7	8.8	0.95	0.95	1.04	138.28	0.89	1.70

Table 5. Correlation coefficients between of spruce growth and survival and genotype stability parameters.

Parameters	Survival			Diameter			Height		
	Means	b_i	W_i^2	Means	b_i	W_i^2	Means	b_i	W_i^2
Means	1.000	−0.498*	−0.167	1.000	−0.252	0.370	1.000	−0.047	0.206
b_i	—	1.000	0.417*	—	1.000	0.145	—	1.000	0.321
W_i^2	—	—	1.000	—	—	1.000	—	—	1.000

* Significant at 0.05 level.

for survival. Provenance No 23 (*P. obovata*, Arkhangelsk Region, Kholmogory District) from the Northern taiga subzone is different as can be assigned to Group 1 by three indices. Three more provenances have high plasticity index (b_i> 1) for certain parameters: for survival (*P. obovata*, Sverdlovsk Region, No 40) and for height (*P. obovata*, Perm Region, No 39 and hybrid form with properties of *Picea obovata*, Udmurtia, No 35).

For *P. abies* and its hybrid forms the high index (b_i > 1) is observed more often and represents high plasticity of the species. It is especially typical for survival. Five provenances of *P. abies* and its hybrid forms characterize by high plasticity both in survival and growth. These are provenances from Leningrad (No 5), Pskov (No 7), Vologda (No 24), Kostroma (No 27) Regions, Karelia Republic (No 3). They are located in different zones and taiga subzones: in the middle and southern taiga subzones and mix forest zone. However, the area of initial stand habitats of these provenances is quite local and is restricted by 56º30´ – 61º40´ N and 30º30´ – 42º30´ E.

The genotype survival has a clear differentiation ($P < 0.05$) by selected groups of plasticity and by species and forms of spruce (Table 6). The stability of the provenances in the new environmental conditions during the testing of spruces genotypes can be considered as priority in the practical genotypes assessment. Growth (height and diameter) is less impacted by the environment. The provenances maintain hereditarily fixed growth parameters and implement them when the growing conditions change in accordance with the reaction norm.

Table 6. Fisher values (F) and statistical significances (P-values) of main effects of groups of plasticity and spruce species on survival and growth parameters of spruce provenances (one-way ANOVA), F_{crit}=4.351.

Parameters	Spruce species and forms, df = 3		Groups of plasticity, df = 1	
	F	P	F	P
Survival	3.188	0.049	4.558	0.045
Diameter	0.431	0.733	0.223	0.642
Height	0.946	0.439	0.098	0.757

Plastic provenances of *Picea abies* and its hybrid forms are concentrated near the western boundaries of the Russian Plain (Fig. 2). It can be a result of closeness of the spruce refugium located in the territory of Belovezhskaya Pushcha from where spruce migration towards north-east has occurred (Dering & Levandovski 2007).

At the same time, plastic provenances of *Picea obovata* and its hybrid forms are dispersed all over the north-western part of the Russian Plain that can be a result from *P. obovata* propagation to the Russian Plain from Siberia via the Polar Urals (Popov 2005). In the North-Eastern part of the Russian Plain plastic spruce provenances mixed with provenances close to plastic ones, i.e. they are not plastic in all studied parameters (they can be named as partly plastic). Such genomic clustering of parent populations is typical of Eurasian spruce species (Melnikova et al. 2012).

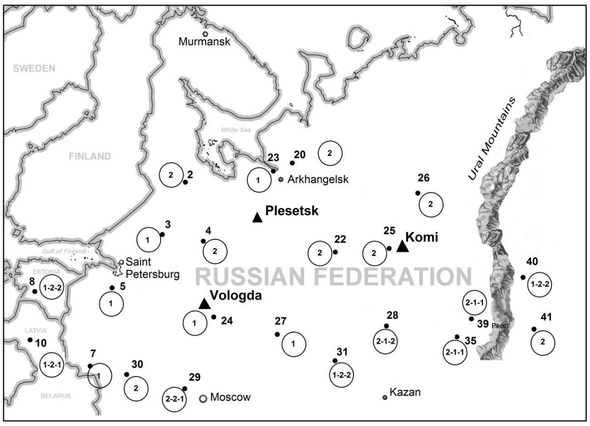

Fig. 2. Spruce provenance plasticity by survival, diameter and height, their location in the Russian Plain (numbers in a circle: 1 – plastic, 2 – non-plastic; three numbers in a circle: rank of plasticity by survival, diameter and height).

According to Garzón et al. (2011), different response to climatic changes can be expected for species and provenances with different phenotypic plasticity. In general, *Picea abies*, due to its better plasticity, would be more responsive to climatic changes in production properties (survival and growth). *Picea obovata* is a more conservative species and would poorly respond to climatic changes. It agrees with a general conclusion made by Kapeller et al. (2012) for *Picea abies*, that southern spruce species from a zone with higher temperatures and less precipitation would be more suitable for use in new environmental conditions.

Gömöry et al. (2012) noted that high-latitude spruce provenances are more resistant and low-latitude spruce provenances are more sensitive to climate change. Persson (1998) considers it as a result of decrease of required cold resistance under climate warming.

In this case, in future, with climate warming in the Northern areas of the Russian Plain, we can expect further *Picea abies* dispersion and its suppression on *Picea obovata*. For species adaptation to climate warming several species generations will required (Beaulieu et al. 2005). It should be taken into consideration that forest ecosystems have high tolerance providing their high resistance to unfavorable environmental impact. In addition, so called adaptive delay (for about 100 years) of species response to climate changes takes place (Savolainen et al. 2004). Therefore, *P. abies* dispersion over the Russian Plain would be slow and first it would cause extension of introgressive hybridization zone. It can cause decrease of *P. abies* phenotypic plasticity due to hybridization with less plastic *P. obovata*.

5. Conclusions

Picea abies (L.) Karst. provenances have better phenotypic plasticity, including the response to the climate changes. In future, on sustainable climate warming, this species could predominate in the Russian Plain and start to force out *P. obovata* (Ledeb.).

Variability of phenotypic plasticity observed for populations of spruce species (*Picea abies* (L.) Karst. and *P. obovata* [Ledeb.]) and for their hybrids forms occurring in the contact zone proves necessity in further study of certain provenances. Selection based on provenances phenotypic plasticity would make it possible to solve some production problems related to adaptation of forest-forming species to climate changes.

Acknowledgements

The authors are grateful to the Northern Research Institute of Forestry, N. V. Ulissova, and D. Kh. Faizulin for contributed field data on provenance observation. A.G. Volkov for help in statistical analysis. The work by N. A. Prozherina was carried out within the framework of the State Task AAAA-A18-118011690221-0 of the N. Laverov Federal Center for Integrated Arctic Research.

References

Beaulieu, J., Rainville, A., 2005: Adaptation to climate change: Genetic variation is both a short- and a long-term solution. The Forestry Chronicle, 81:704–709.

Becker, H. C., 1981: Correlation among some statistical measures of phenotypic stability. Euphytica, 30: 835–840.

Besedina, T. D., Tutberidze, Ts. V., Dobezhina S. V., 2014: Ecological characteristics of the introduced cultivars of *Actinidia deliciosa* in Russian humid subtropics. Nauchnyj zhurnal KubGAU, 100:1275–1286. [in Russian].

Demina N. A., Faizulin D. Kh., Nakvasina, E. N., 2013: Specification of the boundaries of forest seeding of spruce in the European North. Lesnoj Vestnik, 2:23–28. [in Russian].

Dering, M., Lewandowski, A., 2007: Postglacial re-colonization of Norway spruce (*Picea abies* [L.] Karsten) in Poland based on molecular markers In: Conference session abstracts “Norway Spruce in the Conservation of Forest Ecosystems in Europe”, September 3–5, 2007, Warszawa, 37 p.

Eberhart, S. A., Russell, W. A., 1966: Stability parameters for comparing varieties. Crop Science, 6:36–42.

Faizulin, D. Kh., Artemjeva, N. R., Senkov, A. O., 2011: Pine and spruce provenance tests in the middle and southern subzones of the taiga of the European part of the Russian Federation. In: Results of scientific research work of “SevNIILKh” for 2005–2009. Arkhangelsk, p. 23–27. [in Russian].

Garzón, M. B., Alía, R., Robson, T. M., Zavala, M. A., 2011: Intra-specific variability and plasticity influence potential tree species distributions under climate change. Global Ecology and Biogeography, 20:766–778.

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., Merila, J., 2008: Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology, 17:167–178.

Gomez-Mestre, I., Jovani, R., 2013: A heuristic model on the role of plasticity in adaptive evolution: plasticity increases adaptation, population viability and genetic variation. Proceedings of the Royal Society B: Biological Sciences, https://doi.org/10.1098/rspb.2013.1869.

Gömöry, D., Longauer, R., Hlásny, T., Pacalaj, M., Strmeň, S., Krajmerová, D., 2012: Adaptation to common optimum in different populations of Norway spruce (*Picea abies* Karst.). European Journal of Forest Research, 131:401–411.

Gulnyashkin, A. V., Anashenkov, S. S., Varlamov, D. V., 2014: Study results of ecological adaptability of new early ripening hybrids of maize grain farm in Russia. Zernovoe Khozyajstvo Rossii, 4:31–36. [in Russian].

Iroshnikov, A. I. 2002: On the concept and the program of genetic monitoring of forest woody plant populations. Lesovedenie, 1:58–64. [in Russian].

Kang, M. S., Miller, J. D., Darrah, L. L., 1987: A note on relationship between stability variance and ecovalence. Journal of Heredity, 78:107.

Kapeller, S., Lexer, M. J., Geburek, T., Hiebl, J., Schueler, S., 2012: Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: Selecting appropriate provenances for future climate. Forest Ecology and Management, 271:46–57.

Kapeller, S., Schüler, S., 2012: Alternative, adapted seed sources handbook & map of trans-alpine provenance regions. Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Vienna, 8 p.

Krasnova, Y. S., Shamanin, V. P., Petukhovsky, S. L., Kirilyuk, L. M., 2014: Ecological plasticity of grades of the soft springwheat in the conditions of the southern forest-steppe of Western Siberia. Sovremennye Problemy Nauki i Obrazovaniya. 6:1633. [in Russian].

Korzun, O. S., Bruilo, A. S., 2011: Adaptive features of plant breeding and seed crops. GSAU, Grodno, 140 p. [in Russian].

Lindgren, D., Persson, A., 1995: Vitalization of results from provenance tests. In: Pälvinen, R., Vanclay, J., Minna, S. (eds.): Caring for the Forest: Research in a Changing World. IUFRO XX World Congress, August 6–12 1995, Tampere, Finland, 249 p.

Mátyás, Cs., 2006: Migratory, genetic and phenetic response potential of forest tree populations facing climate change. Acta Silvatica et Lignaria Hungarica, 2:33–46.

Melnikova, M. N., Petrov, N. B., Lomov, A. A., la Porta, N., Politov, D. V., 2012: Testing microsatellite primer with different populations of Eurasian spruces *Picea abies* (L.) Karst. and *Picea obovata* (Ledeb.). Russian Journal of Genetics, 48:562–566.

Nakvasina, E. N., Yudina, O. A., Prozherina, N. A., Kamalova, I. I., Minin, N. S., 2008: Provenance test in gene-ecological studies in the European North. Arkhangelsk, 307 p. [in Russian].

Nakvasina, E. N., 2003: Provenance tests of Scots pine (*Pinus sylvestris* L.) as a natural model of imitation of climatic changes. Vestnik Pomorskogo Universiteta, 2:48–53. [in Russian].

Nakvasina, E. N., 2014: Changes in the generic sphere of Scots pine in the imitation of climate warming. Izvestiya Sankt-Peterburgskoj Lesotekhnicheskoj Akademii, 209:114–125. [in Russian].

Nakvasina, E. N., Tarkhanov, S. N., Ulissova, N. V., Sizov, I. I., Bedritskaya, T. V., 1990: Northern forests: state, dynamics, anthropogenic impact. In: Pisarenko, A. I. (ed.): Proceedings of international conference Arkhangelsk, (Russia): USSR State Forest Agency, 2:131–140. [in Russian].

Nakvasina, E. N., Gvozdukhina, O. A., 2005: An assessment of the state and growth of pine and spruce provenance tests in the Arkhangelsk Region. Problems of Forest Science and Forestry. Proceedings of conference Arkhangelsk (Russia): AGTU, p. 58–63. [in Russian].

Nakvasina, E. N., Yudina, O. A., Pokatilo, A. V., 2016: Growth and reproductive reactions *Picea abies* (L.) Karst. × *P. obovata* Ledeb. in simulated climate warming. Arctic Environmental Research, 1:89–96. [in Russian].

O'Neill, G. A., Hamann, A., Wang, T., 2008: Accounting for population variation improves estimates of the impact of climate change on species growth and distribution. Journal of Applied Ecology, 45:1040–1049.

Orlova, L. V., Egorov, A. A., 2010: By taxonomy and geographical distribution of Finnish spruce (*Picea fennica* (Regel) Kom., Pinaceae). Novosti Sistematiki Vysshykh Rastenij, 42:5–23. [in Russian].

Persson, B., 1998: Will climate change affect the optimal choice of *Pinus sylvestris* provenances? Silva Fennica, 32:121–128.

Petrov, S. A., 1984: Recommendations for the use of genetic and statistical methods in the selection of forest species on productivity. Voronezh, 43 p. [in Russian].

Petrov, S. A., 1987: Genetic resources of forest-forming species, ways of their formation and rational use. Lesorazvedenie i lesomelioratsiya, 1:1–30. [in Russian].

Popov, P. P., 2005. Spruce European and Siberian. Science, Novosibirsk, 231 p. [in Russian].

Potokina, E. K., Kiseleva, A. A., Nikolaeva, M. A., Ivanov, S. A., Uljanich, P. S., Potokin, A. F., 2015: Analysis of polymorphism of organelle DNA to elucidate the phylogeography of Norway spruce in the East European Plain. Russian Journal of Genetics: Applied Research, 5:430–439.

Pravdin, L. F., 1975: Norway spruce and Siberian spruce in the USSR. Science, Moscow, 176 p. [in Russian].

Price, T. D., Qvarnström, A., Irwin, D. E., 2003: The role of phenotypic plasticity in driving genetic evolution. Proceedings of the Royal Society B: Biological Sciences, 270:1433–1440.

Prokazin, E. P., 1972: Program and methods of work. The study of available and creation of new provenance trial. VNIILM, Pushkino, 52 p. [in Russian].

Rodin, A. R., Prokazin, A. E. 1996: About study problems of provenance trial of basic forest species. Lesnoe khozjajstvo, 4:16–18. [in Russian].

Rodin, A. R., Prokazin, A. E., 1997: Study of geographic variation of the main forest-forming species. In: Kharin, O. A. (ed.): Forest use and reproduction of forest resources, Moscow, p. 70–75. [in Russian].

Rone, V. M., 1979: Methods of genetic analysis and selection in populations of spruce. Doctoral Thesis in Biology, Institute of General Genetics of USSR Academy of Sciences, Moscow, 36 p. [in Russian].

Savolainen, O., Bokma, F., Garcia-Gil, R., Repo, T., 2004: Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of *Pinus sylvestris* to climatic changes. Forest Ecology and Management, 197:79–89.

Scapim, C. A., Oliveira, V. R., Brassini, A. de L., Cruz, C. D., de Bastos Andrade, C. A., Gonçalves Vidigal, M. C., 2000: Yield stability in maize (*Zea mays* L.) and correlations among the parameters of the Eberhart and Russell, Lin and Binns and Huehn models. Genetics and Molecular Biology, 23:387–393.

Shukla, G. K., 1972: Genotype stability analysis and its application to potato regional trails. Crop Science, 11:184–190.

Shutyaev, A. M., 1990: Basics forest seeds zoning. In: Veretennikov, A. V. (ed.): Increased productivity, sustainability and the protective role of forest ecosystems. Voronezh, Russia, p. 62–66. [in Russian].

Shutyaev, A. M., Giertych, M., 1997: Height growth variation in a comprehensive Eurasian provenance experiment of (*Pinus sylvestris* L.). Silvae Genetica, 46:332–349.

Shutyaev, A. M., Giertych, M., 2000: Genetic subdivisions of the range of Scots pine (*Pinus sylvestris* L.) based on a transcontinental provenance experiment. Silvae Genetica, 49:24–38.

Suvanto, S., Nöjd, P., Henttonen, H. M., Beuker, E., Mäkinen, H., 2016: Geographical patterns in the radial growth response of Norway spruce provenances to climatic variation. Agricultural and Forest Meteorology, 222:10–20.

Tarkhanov, S. N., 1998: Variability of spruce in the provenance tests of the Komi Republic. Ekaterinburg, 194 p. [in Russian].

Wricke, G., 1962. Über eine Methods zur Erfassung der ökologisches Streubreite in Feldversuchen. Zeitschrift für Pflanzenzüchtung, 47:92–96.