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Variation in growth of Norway spruce in the IUFRO 1972 provenance experimental series

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Abstract

Provenance experiments traditionally provide information on genetic variation within tree species in adaptation ability and other traits important for commercial forestry. In this study we investigated variation in growth among 20 populations of Norway spruce (*Picea abies* (L.) H. Karst) at four common-garden sites of the IUFRO 1972 provenance experimental series at the age close to half of rotation. Because stand density varied among sites, we analyzed stand density-adjusted basal area (BA) and quadratic mean diameter (D_q). The examined provenances varied significantly in both analyzed traits. We identified provenances that performed consistently better or worse than average across all four sites. Among the well-growing and possibly adaptive seed sources were those from the uplands of the eastern and central Poland, Sudety Mts, and from the region of Istebna in Beskid Mts. Performance of the other populations from Beskid Mountains was average to poor, and all high-altitude populations were poor-growing. The results of this study help to verify the knowledge of genetic variation pattern among Norway spruce populations in Poland, and to guide management decisions regarding spruce planting material.

Keywords: *survival; Picea abies; population; productivity*

Introduction

Identification of proper forest planting material becomes a challenge in a changing world. However, information about genetic variation in growth and adaptation within the species may help to resolve this problem. Common-garden trials have been traditionally used for identifying patterns of genetic variation in the traits of interest within tree species, mostly in the context of commercial tree improvement programs (White, et al. 2007, Zobel and Talbert 1984). To this end the review of only the most recent literature shows that provenance experiments still provide valuable information on variation of adaptive traits and growth in a number of forest tree species (e.g. Barzdajn, et al. 2016, Di Matteo and Voltas 2016, George, et al. 2017, Hofmann, et al. 2015, Kerr, et al. 2015, Lee, et al. 2015, Miguez-Soto and Fernandez-Lopez 2015, Stojnic, et al. 2015, Szeligowski, et al. 2016), and may offer material for further selection (Skroppa and Steffenrem 2016). The interest in provenance experiments has been renewed in the light of tree populations' responses to projected changes in climate (Aitken, et al. 2008, IPCC 2014, Matyas 1994). Information gained in such trials helps to assess within-species responses and adaptation capacity to projected alterations of temperature and precipitation regimes, and to select proper planting material for future climates (e.g. Montwe, et al. 2015, Saenz-Romero, et al. 2017, Sofletea, et al. 2015, Suvanto, et al. 2016, Wang, et al. 2006). Existing provenance experiments, especially the long-term multi-site series, provide information valuable for both points of interest. From the perspective of commercial forestry the results of provenance tests are most meaningful when obtained at ages close to, or exceeding half of rotation age.

Norway spruce (*Picea abies* [L.] H.Karst.) is ecologically and commercially important tree species in Europe. However, its importance might be compromised, because of the negative influence of interacting factors such as climate change, especially altered precipitation regimes, air pollution, and infestations with pests and pathogens on spruce growth and health (Cienciala, et al. 2017, Jonard, et al. 2012, Šrámek, et al. 2008, Vacek, et al. 2015). Therefore it is especially important to recognize the pattern of variation within the species in order to identify the most adaptive and best-growing seed sources

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across the range of environments for further use in forest plantations, and to design proper programs of conservation of spruce genetic resources.

The aim of this study was to examine variation among Polish populations of Norway spruce at the age close to half of rotation. We analyzed the most recent available data collected at four sites of the Norway spruce IUFRO 1972 provenance series. These are likely the last data possible to report in such a manner from this experimental series, because of deteriorating condition of trees in this trial. The questions we addressed in this study were: 1) how do provenances differ in productivity, and 2) whether the performance of populations was stable across planting sites. The second question helped to assess population adaptability.

Materials and Methods

Planting material and research trials

Maternal stands of the populations that were included in the study were selected as permanent research plots between 1965 and 1967 (Kocięcki 1968). Between 1966 and 1971 seeds were collected from 20 of these stands (Table 1, Figure 1). Common garden trials were planted with seedlings of these provenances as the IUFRO 1972 series at 42 locations in 10 European countries and in Canada (Krutzsch 1992, Lacaze and Kocięcki 1979, Matras 1993). Five of those sites were established in Poland, but one of them (Istebna) was destroyed by fire at early age (Giertych 1984, Lacaze and Kocięcki 1979, Matras 2002); thus, further data are available from only four research trials in Poland, as follows (Figure 1, Table 1):

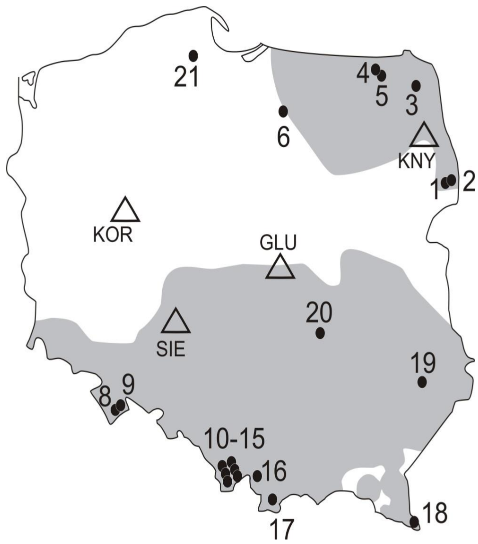

Figure 1
Distribution of 20 tested provenances of Norway spruce (dots) and four trial sites (triangles) in Poland. Provenance numbers correspond to those given in Table 1. Natural distribution of the species is shown in gray according to the Distribution map of Norway spruce (Picea abies) EUFORGEN 2009, www.euforgen.org

Table 1
Mean values (and standard errors) of basal area (BA) and trees per hectare (TPha) for the 20 provenances of Norway spruce tested at four experimental sites in Poland.

site			Głuchów (GLU)				Knyszyn (KNY)				Kórnik (KOR)				Siemianice (SIE)			
age			40				42				44				43			
Provenance*		Altitude (m a.s.l.)	BA (m^2 ha^{-1})	s.e.	TPha	s.e.	BA (m^2 ha^{-1})	s.e.	TPha	s.e.	BA (m^2 ha^{-1})	s.e.	TPha	s.e.	BA (m^2 ha^{-1})	s.e.	TPha	s.e.
1	Zwierzyniec-Pogorzelce	160	44.0	(1.8)	1822	(77)	24.8	(5.7)	1076	(289)	12.1	(4.5)	459	(170)	21.2	(4.6)	1080	(278)
2	Zwierzyniec-Krzyże	180	47.9	(2.4)	1618	(214)	33.0	(4.1)	1323	(252)	18.2	(5.4)	597	(176)	25.4	(5.1)	1160	(279)
3	Wigry	170					34.8	(10.3)	1434	(346)	0	0	0	0	18.7	(4.1)	809	(250)
4	Przerwanki	180					28.8	(4.0)	1404	(127)	9.9	(3.8)	353	(141)	21.3	(3.4)	1062	(240)
5	Borki	180	44.4	(2.4)	1674	(129)	36.6	(2.8)	1713	(178)	15.0	(5.7)	317	(132)	20.7	(4.6)	1056	(335)
6	Nowe Ramuki	160	51.7	(4.3)	1926	(150)	27.5	(6.1)	965	(240)	16.6	(5.6)	511	(199)	26.0	(3.3)	1358	(156)
8	Międzygórze	580	46.8	(2.8)	1733	(245)	34.2	(5.2)	1583	(176)	29.3	(5.5)	635	(112)	19.0	(2.0)	975	(106)
9	Stronie Śl.	820	39.0	(2.4)	1600	(98)	37.7	(2.6)	2028	(136)	23.2	(4.7)	582	(144)	14.3	(1.6)	772	(156)
10	Wisła	710	45.5	(3.3)	1644	(127)	17.9	(7.7)	915	(260)	21.1	(6.4)	441	(140)	16.9	(2.5)	809	(147)
11	Istebna-Bukowiec	630	46.9	(5.2)	1467	(116)	32.7	(3.7)	1360	(262)	25.4	(6.6)	547	(137)	19.9	(3.8)	944	(185)
12	Istebna-Zapowiedź	600	41.9	(2.7)	1541	(114)	33.3	(5.6)	1286	(230)	9.9	(5.4)	212	(128)	17.6	(2.4)	840	(163)
13	Rycerka-Zwardoń	620	43.6	(2.8)	1630	(207)	34.2	(4.4)	1787	(248)	12.4	(4.6)	370	(148)	13.4	(4.0)	630	(188)
14	Rycerka-Praszywka700	700	42.1	(2.3)	1644	(172)	32.3	(1.9)	1583	(212)	17.3	(7.4)	370	(152)	13.7	(3.2)	735	(230)
15	Rycerka-Praszywka950	950	39.5	(2.8)	1748	(118)	29.4	(6.5)	1379	(195)	12.8	(5.9)	317	(123)	18.5	(4.2)	1086	(281)
16	Orawa	1,050	40.8	(4.1)	1609	(216)	28.0	(3.9)	1614	(223)	17.3	(5.0)	494	(168)	18.8	(2.1)	951	(166)
17	Witów	1,420					24.4	(1.5)	1422	(190)	11.3	(4.8)	547	(194)	17.4	(0.9)	1074	(104)
18	Tarnawa	750	35.9	(2.0)	1407	(142)	28.8	(3.4)	1459	(152)	5.1	(2.4)	159	(70)	13.1	(2.7)	679	(181)
19	Zwierzyniec Lub.	260	46.8	(4.4)	1526	(97)	35.4	(3.7)	1484	(70)	28.1	(4.9)	600	(122)	29.0	(2.7)	1630	(180)
20	Bliżyn	310	40.5	(1.7)	1378	(135)	34.6	(3.6)	1744	(312)	17.1	(6.4)	529	(197)	28.0	(2.7)	1525	(214)
21	Kartuzy	200	43.5	(2.6)	1778	(115)	27.2	(3.2)	1546	(94)	21.0	(4.4)	476	(175)	21.3	(3.9)	1117	(221)
mean			**43.0**	**(0.8)**	**1616**	**(36)**	**30.7**	**(1.0)**	**1456**	**(52)**	**16.6**	**(1.3)**	**437**	**(34)**	**19.7**	**(0.8)**	**1015**	**(50)**

*seeds were not collected from the provenance 7, but the original enumeration of maternal stands was retained as in Kocięcki (1968)

The Głuchów site (GLU 51º 44' N, 20º 05' E, alt. ~158 m a.s.l.) was established in 6 randomized blocks in spring 1975. The provenances 3-Wigry, 4-Przerwanki, and 17-Witów were missing from this site. Three of the blocks were planted with non-transplanted 3-year-old seedlings (3/0), and the other three with transplanted seedlings (2/1). In addition, the blocks with transplanted seedlings had missing provenances 1-Zwierzyniec-Pogorzelce, 6-Nowe Ramuki, 8-Międzygórze, and 19-Zwierzyniec Lub. The 100 trees per provenance-plot were planted in 1.5 × 1.5 m spacing (4,444 trees ha^{-1}). The site was thinned in 1995 (tree age 20 years) to 2,244 trees ha^{-1}.

The Knyszyn site (KNY, 53º 19' N, 23º 03' E, alt. 156 m a.s.l.) was established in 4 randomized blocks in spring 1975 with 3-year-old transplanted (2/1) seedlings. The 169 trees per provenance-plot were planted in 1.65 × 1.45 m spacing (4,180 trees ha^{-1}). The provenances 19-Zwierzyniec Lub. and 20-Bliżyn were planted at the half-size plots. The site was thinned in 1999 (tree age 28 years) to about 3,774 trees ha^{-1} (Matras 2002).

The Kórnik site (KOR, 54º 14' N, 17º 11' E, alt. ~80 m a.s.l.) was established in 7 randomized blocks in spring 1976 with 4-year-old transplanted (2/2) seedlings. The 36 trees per provenance-plot were planted in 1.5 × 1.5 m spacing (4,444 trees ha^{-1}). The provenance 3-Wigry was planted at only three replications (blocks), however, no trees of this population survived to the time of the last measurement used in this study. The site was thinned in 1986 (tree age 16 years) to 2,222 trees ha^{-1}. Since then only trees that were killed by bark beetle (*Ips typographus* L.) were removed.

The Siemianice site (SIE, 51º 11' N, 18º 07' E, alt. ~180 m a.s.l.) was established in 5 randomized blocks in spring 1975 with 3-year-old non-transplanted seedlings. The 144 trees per provenance-plot were planted in 1.5 × 1.5 m spacing (4,444 trees ha^{-1}). The site was thinned in 1991 (tree age 20 years) to 3,086 trees ha^{-1} (Barzdajn 1982, Barzdajn 1994).

Measurements and analysis

For the analysis we used the last available data on tree diameter at 1.3 m from each experimental site. The basal areas (BA) of individual trees were summed at the plot level, and expressed on per hectare basis (m^2 ha^{-1}, Table 1). We also calculated quadratic mean diameter at the plot level ($D_q = \mathrm{sqrt}(\Sigma DBH^2/n)$; where DBH is diameter at 1.3 m, n is number of trees). We have chosen to report this diameter, because it represents the diameter of a tree with average BA. The age of trees when these data were collected varied slightly among the sites between 40 and 44 years (Table 1).

Tree diameters and stand basal area are affected by stand density (Table 1). In this experiment differences in stand density were partially related to the thinnings, because the initial planting density was almost uniform among sites (except the Knyszyn site). Although those thinnings at ages below 28 years, were made mostly to prevent the density-dependent mortality we could not determine the exact causes of mortality, and thus variation in stand density among sites. To account for the influence of different stand densities on tree diameters and basal areas we used the analysis of covariance with stand density at the plot level as a covariate, according to the model:

$$Y_{ijk} = \mu + S_i + P_j + Cov + Cov \times S_{ij} + \varepsilon_{ijk} \qquad \text{(eq. 1)}$$

where: Y_{ijk} is the observation at the plot level (BA or D_q), μ is the overall mean, S_i is the effect of site, P_j is the effect of provenance, *Cov* is a covariate (stand density), $Cov \times S_{ij}$ is the effect of covariate × site interaction, and ε_{ijk} is the error term. The significant $Cov \times S_{ij}$ interaction term ($P \leq 0.0001$, Table S1 – Supplementary Information) for both BA and D_q indicated that the slopes of the relationships between the independent variable and stand density varied by site. Therefore, values predicted with the equation 1 were used for further analysis of stand basal area (adjusted BA) and tree diameter (adjusted D_q). The analysis of covariance was performed in the JMP 9.0.0 software (SAS Institute Inc. Cary, NC, USA).

Because the field design contained missing data (not all provenances were represented at all sites; Table 1) the mixed linear model was used for analysis. First, the full model containing all terms was fit:

$$Y_{ijkl} = \mu + S_i + B(S)_{j(i)} + P_k + PS_{ik} + \varepsilon_{ijkl} \qquad \text{(eq. 2)}$$

where Y_{ijkl} is the observation at the plot level, μ is the overall mean, S_i is the random effect of site, $B(S)_{j(i)}$ is the random effect of block within the site, P_k is the fixed effect of provenance, PS_{ik} is the random effect of provenance × site interaction, and ε_{ijkl} is the error term. Subsequently the reduced models were fit to test for the significance of the main effects and the interaction

Table 2
Results of the log-likelihood ratio tests between models testing for significance of particular model effects for adjusted basal area (BA) and adjusted quadratic mean diameter (D_q).

model*	LRT** for significance of:	Df	AIC	BIC	logLik	deviance	Chisq	Chi df	Pr(>Chisq)
adjusted BA									
full model m4	interaction term	24	2836.8	2932.7	-1394.4	2788.8	0.0	1	1.0
reduced m3		23	2834.8	2926.7	-1394.4	2788.8			
reduced m3	block nested within site	23	2834.8	2926.7	-1394.4	2788.8	49.14	1	<0.00001
reduced m2		22	2882.0	2969.9	-1419	2838.0			
reduced m2	site effect	22	2882.0	2969.9	-1419	2838.0	353.5	1	<0.00001
reduced m1		21	3233.5	3317.369	-1595.75	67166.3			
reduced m3	provenance effect	23	2834.8	2926.7	-1394.4	2788.8	87.6	19	<0.00001
reduced m3b		4	2884.4	2900.4	-1438.2	2876.4			
Adjusted D_q									
model*	**LRT** for significance of:**	**Df**	**AIC**	**BIC**	**logLik**	**deviance**	**Chisq**	**Chi df**	**Pr(>Chisq)**
full model m4	interaction term	24	2202.7	2298.6	-1077.4	2154.7	0.0	1	1.0
reduced m3		23	2200.7	2292.6	-1077.4	2154.7			
reduced m3	block nested within site	23	2200.7	2292.6	-1077.4	2154.7	60.7	1	<0.00001
reduced m2		22	2259.5	2347.3	-1107.7	2215.5			
reduced m2	site effect	22	2259.5	2347.3	-1107.7	2215.5	11.0	1	0.00097
reduced m1		21	2268.4	2352.2	-1113.18	6051.7			
reduced m3	provenance effect	23	2200.7	2292.6	-1077.4	2154.7	71.2	19	<0.00001
reduced m3b		4	2233.9	2249.8	-1112.9	2225.9			

*model number according to notation used in the Supplementary Information
**LRT stands for the log-likelihood ratio test

Table 3
Variance components for the random effects from the linear mixed-model analysis of adjusted basal area (BA) and adjusted quadratic mean diameter (D_q).

	Adjusted BA			Adjusted D_q		
Random effect	Variance Component	St. Error	% of total variance	Variance Component	St. Error	% of total variance
site	138.684	115.61	66.3	0.4917	0.99	3.1
block(site)	13.842	5.60	6.6	3.4676	1.35	21.8
Residual	56.698	4.22	27.1	11.9595	0.89	75.1
Total	209.224		100	15.9187		100

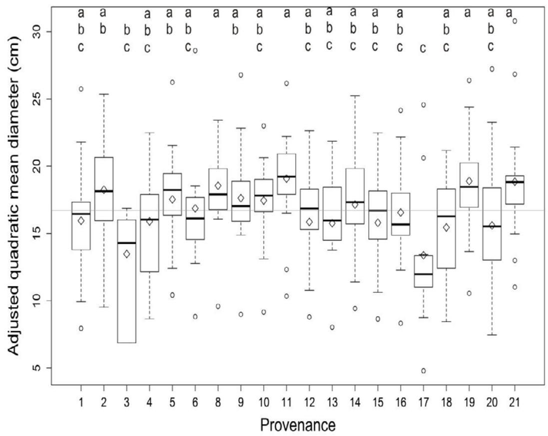

Figure 3
Boxplot of adjusted quadratic mean diameters for 20 tested provenances of Norway spruce. Values for provenances sharing the same letter are not statistically different at the α = 0.05.

term with the log-likelihood ratio test (Table 2 and Supplementary Information).

Goodness of fit of the selected model was diagnosed by examination of the AIC and the distribution of residuals. Provenance least square means were compared with the Tukey-Kramer HSD test. Model fitting was performed with the '*lmer*' procedure in the 'lme4' package in R (R Core Team 2017; Supplementary Information).

Stability of the adjusted BA was tested with the Spearman's rank correlation among the sites.

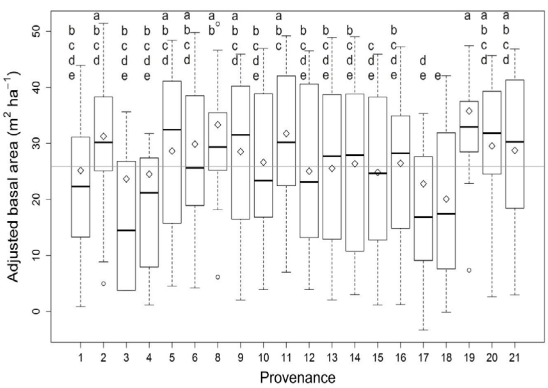

Figure 2
Boxplot of adjusted basal area for 20 tested provenances of Norway spruce. Values for provenances sharing the same letter are not statistically different at the *α* = 0.05.

Results

The slope of the relationships between stand density (trees per hectare) and stand basal area or tree diameter varied significantly among the sites (Table S1), indicating that separate equation for each site should be used to account for differences in stand density when analyzing BA and D_q.

The provenance × site interaction term was not significant for the adjusted BA nor for the adjusted D_q (Table 2). Thus, in both traits the reduced model 3, which did not include the interaction term was the best (Table 2 and Supplementary Information), although the fit for the adjusted D_q was poorer than for the adjusted BA (Fig. S1 and S2, Suppl. Info). The random site effect accounted for over 66 % of variation in adjusted BA, but only for the 3 % of total variation in adjusted D_q (Table 3).

Provenance effect was significant for both examined traits ($P \leq 0.0001$, Table 2). The provenance 19-Zwierzyniec Lub. had significantly greater adjusted BA than half of the remaining populations (Figure 2), and the second provenance from the top, 8-Międzygórze, significantly differed from the populations 17-Witów, 18-Tarnawa, and 15-Rycerka Praszywka 950 (Figure 2). As regards the adjusted D_q, the best four provenances differed significantly from the two poorest ones (3-Wigry and 17-Witów, Figure 3).

The Spearman's rank correlation between sites was positive and significant for the adjusted D_q, except for the relationships between KOR and GLU, and KOR and SIE (Table 4). For the adjusted BA, all site-site rank correlations were significant, except those involving the KNY site (Table 4). These differences in the ranking of populations at the Knyszyn site were apparent when examining the graph of rank positions for the adjusted BA (Figure 4). Two populations showed the stably high rank positions (significantly above average, α = 0.05)

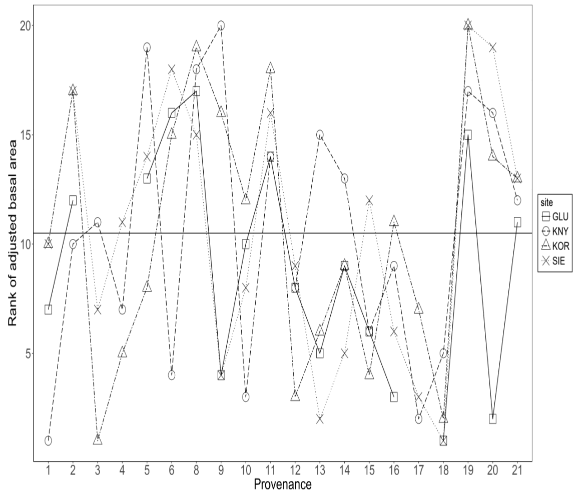

Figure 4
The plot of rank positions for 20 provenances at four experimental sites according to the adjusted basal area.

Table 4
Rank correlations for the adjusted basal area (BA) and the adjusted quadratic mean diameter (D_q) between the experimental sites.

	adjusted BA		adjusted D_q	
site-site	Spearman ρ	Prob>|ρ|	Spearman ρ	Prob>|ρ|
GLU-KNY	0.16	0.5288	0.61	**0.0100**
GLU-KOR	0.59	**0.0125**	0.48	0.0537
GLU-SIE	0.63	**0.0067**	0.66	**0.0042**
KNY-KOR	0.42	0.0634	0.62	**0.0035**
KNY-SIE	0.25	0.2796	0.58	**0.0077**
KOR-SIE	0.63	**0.0031**	0.36	0.1213

– 19-Zwierzyniec Lub. and 8-Międzygórze, whereas only one – 18-Tarnawa – showed a stably low ranking position at all sites. There was also a number of provenances that performed well (11- Istebna Bukowiec, 20-Bliżyn, 5-Borki, 6-Nowe Ramuki and 2-Zwierzyniec-Krzyże) or poorly (13-Rycerka-Zwardoń, 14-Rycerka Praszywka700 and 15-Rycerka Praszywka 950) in at least three out of four locations (Figure 4). The group of poor-performing seed sources should also include the provenance 17-Witów, which was tested at three sites only. However, for those groups the differences of the ranks from the average were not statistically significant, due to variation of ranks among sites. A few of the provenances were especially reactive to site conditions and varied widely in performance across sites: 1-Zwierzyniec Pogorzelce, 3-Wigry, 5-Borki, 6-Nowe Ramuki, 9-Stronie Śl., 10-Wisła, and 20-Bliżyn (Figure 4).

Discussion

Provenance experiments provide information necessary to recognize patterns of genetic variation within tree species in adaptation ability and other traits important for commercial forestry. In this study we investigated variation in productivity, expressed as stand basal area, among 20 populations of Norway spruce at four common-garden trial sites at the mid-rotation age.

In this study we were not able to directly address the adaptive ability of provenances to particular site conditions. However, given the fact that the initial planting density was almost uniform among sites (except the Knyszyn site), and that the thinnings which were made between 14 and 23 years back before the measurements mostly prevented the density-dependent mortality, it is likely that the variation in stand density we observed (Table 1) resulted from non-adapted trees dying out, and from mortality related to other causes throughout stand development, such as, for example attacks by the European spruce bark beetle (see below). Thus, the data on stand density-adjusted basal area should also reflect the adaptive ability of examined populations. However, because the exact causes of mortality were not recorded at the thinnings nor later on, it is impossible to determine how those other factors affected population adaptability.

Basal area is a better indicator of stand productivity than tree diameter alone. However, because it is strongly affected by stand density, in our analysis we used the density-adjusted basal area. We found that site differences were responsible for a large amount of total variation in adjusted stand basal area, and that variation among provenances was significant. However, the provenances changed their ranks of adjusted BA among sites (Figure 4), which indicates that the provenance × site interaction was likely not negligible, despite that the formal test did not confirm statistical significance of the interaction term. We were able to identify two seed sources that performed well across all sites, one that performed poorly, and at least seven that had highly variable performance across sites. Three of those provenances with variable response were promising at most sites. Thus, our results help to identify seed sources of Norway spruce that should be recommended for broader use in commercial plantings.

It is interesting to compare our results with the earlier results at the same experimental series to show how reliable could be the recommendations given at earlier ages compared to the current one. Similar results regarding mostly good performance of provenances 19-Zwierzyniec Lub. and 20-Bliżyn, and the instability of provenance 1-Zwierzyniec Pogorzelce across the sites in Poland and other countries (Germany, Slovakia and Belarus) were found for height growth at early age (Giertych 1984). In this same study the provenances of Istebna region (numbers 10, 11 and 12) performed well across most Polish sites and at many sites abroad (Giertych 1984). In the current study good growth could only be claimed for the provenance 11-Istebna Bukowiec. The other populations from Beskidy Mountains (Rycerka region – populations 13, 14 and 15) were average to poor-performing both at the early age and in the current study. However, the early study by Giertych (1984) does not mention the other populations that showed promising results based on the current study – those originating from north-eastern Poland (5 and 6), Sudety Mts. (8), and the uplands of the eastern and central Poland (19 and 20) (Figure 1).

Comparison of our current results with the reported data on basal area from the Siemianice site at age 20 years (Barzdajn 1994) and on stand volume per hectare from the Knyszyn (age 23 years) and Głuchów sites (age 26 years; Matras 2002) revealed that the rankings of provenances based on those earlier results were not reliable for prediction of their current rank positions. Considering the top five provenances at both ages, only two of them were maintained within this group at the GLU and SIE sites, and only one at the KNY site. Similarly, in the group of bottom five provenances at both ages there were one, two and three provenances at those sites, respectively. At the SIE site the two populations 6-Nowe Ramuki and 5-Borki improved their ranks by 15 and 12 positions, respectively, and the provenance 9-Stronie Śl. fell down by 16 rank positions between the earlier and the current age. At the KNY site the provenance 10-Wisła fell down by 12 rank positions, and population 9-Stronie Śl. moved up by 14 rank positions. The changes in rank positions with age were smaller at the GLU site. Even for the most recent data from Polish sites at the age of 30 years the rankings of provenances at particular sites varied by as much as 14 rank positions up or 16 rank positions down between earlier and current analysis (Matras 2009). Thus, comparison with earlier results obtained at the same sites shows that identification of well growing sources would need to be postponed to the ages closer to that in the current study. Earlier identification would be wrong because large changes in rank positions could take place even from the assessment at seemingly "safe" age of about 20-30 years. Those changes, especially during the last 10-14 years, were likely related to the damage by the European spruce bark beetle, but the exact causes could not be determined.

Our results allow making some recommendations regarding the tested provenances of Norway spruce. The two seed sources 17-Witów and 18-Tarnawa, representing high altitude stands definitely should not be recommended for the broader use, beside perhaps the local use for gene conservation purposes. On the other hand, the two sources from the uplands of the eastern and central Poland – 19-Zwierzyniec Lub. and 20-Bliżyn are very promising and likely worth promoting at all locations suitable for spruce planting in Poland. It is worth noting that in those regions Norway spruce does not grow in pure stands, but rather occurs as important admixture species, occupying suitable sites (Tyszkiewicz 1968). In addition to good growth in our study, provenance 19 had the greatest wood density at the SIE site (Szaban, et al. 2014). Performance of spruce from the Istebna region, which was among the best based on the earlier results of this series and other provenance experiments (Giertych 1976, Giertych 1984, Matras 2002, Matras 2004), was variable in our experiment. This confirms that spruce populations from that region are not uniform (Giertych 1978), and care should be taken when making recommendations regarding those seed sources. On the other hand, most earlier reports were from the early ages, thus it is also possible, that spruce from that region shows advantage at early stages of growth and does not maintain it at the later age. Spruce from the Sudety Mountains (8) showed a good growth across the experimental sites. Similarly, the provenance from Pomerania (21) – from outside the natural range of the species, showed a consistent performance slightly above the average. These results indicate that valuable sources of planting material for Norway spruce in Poland could be found also in regions other than northeastern Poland, Beskidy Mts. and Sudety Mts., which were traditionally considered (Załęski, et al. 2000).

Although the IUFRO 1972 provenance experiment with Norway spruce was established at many sites (Krutzsch 1992, Lacaze and Kocięcki 1979), so far the results have not been synthesized in a consistent way. Up to date, the most comprehensive summaries of findings from this series was published by Matras (2002, 2004, 2009), where he gathered data on tree height or diameter or stand volume measured at ages ranging from 7 to 30 years at four Polish sites and 28 sites in other countries. According to that analysis, the rankings of populations varied the most for the sites established in Quebec, Canada and in Finland from those in other European countries (Matras 2002, 2004, 2009). However, as mentioned above, even at the sites located in Poland the rank shifts were quite substantial between different ages, thus it is hard to generalize the comparisons between the results obtained in this study and those earlier results from other sites of this series of provenance experiments.

The two of our experimental sites – Głuchów and Kórnik – were located outside the area that is considered the natural distribution range of Norway spruce in Poland (Figure 1). Extensive damage by the European spruce bark beetle was observed at these two sites during last years (W. Buraczyk, D. J. Chmura – pers. observation). Indeed, the damage at the GLU site was so intense that the site was liquidated in 2015 (W. Buraczyk – pers. information). Although the number of sites would need to be greater to allow firm conclusions, these observations indicate that planting of Norway spruce outside its natural distribution might be associated with high risk of failure before reaching half of the regular rotation age for this species in Poland. The risks and benefits would need to be carefully weighted for making decisions about planting spruce outside its natural range.

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References

Aitken SN, S Yeaman, JA Holliday, T Wang and S Curtis-McLane (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1(1):95-111 https://doi.org/10.1111/j.1752-4571.2007.00013.x

Barzdajn W (1982) Growth and morphological characteristics of Polish Norway spruce (Picea abies L. Karst.) grown on comparative culture in Experimental Forest District Laski. Roczniki Akademii Rolniczej w Poznaniu 140:1-49

Barzdajn W (1994) Dwudziestoletnie doświadczenie proweniencyjne ze świerkiem (Picea abies [L.] Karsten) serii IUFRO 1972 w Leśnym Zakładzie Doświadczalnym Siemianice. I. Cechy wzrostowe (The twenty-year-lasting experiment with provenances of spruce (Picea abies [L.] Karsten) within the IUFRO-1972 serues in the Siemianice Forest Experiment Station. I. Growth features). Sylwan 138(11):25-25

Barzdajn W, W Kowalkowski and DJ Chmura (2016) Variation in growth and survival among European provenances of Pinus sylvestris in a 30-year-old experiment. Dendrobiology 75:67-77. http://dx.doi.org/10.12657/denbio.075.007

Cienciala E, J Tumajer, V Zatloukal, J Beranova, S Hola, I Hunova and R Russ (2017) Recent spruce decline with biotic pathogen infestation as a result of interacting climate, deposition and soil variables. Eur. J. For. Res. 136(2):307-317. https://dx.doi.org/10.1007/s10342-017-1032-9

Di Matteo G and J Voltas (2016) Multienvironment evaluation of Pinus pinaster provenances: Evidence of genetic trade-offs between adaptation to optimal conditions and resistance to the maritime pine bast scale (Matsucoccus feytaudi). For. Sci. 62(5):553-563. https://dx.doi.org/10.5849/forsci.15-109

George J-P, M Grabner, S Karanitsch-Ackerl, K Mayer, L Weißenbacher, S Schueler and A Mäkelä (2017) Genetic variation, phenotypic stability, and repeatability of drought response in European larch throughout 50 years in a common garden experiment. Tree Physiol. 37(1):33-46. https://dx.doi.org/10.1093/treephys/tpw085

Giertych M (1976) Summary results of IUFRO 1938 Norway spruce (Picea abies (L) Karst) provenance experiment. Height growth. Silvae Genet. 25(5-6):154-164

Giertych M (1978) Plastyczność polskich ras świerka (Picea abies (L) Karst.) w świetle międzynarodowego doświadczenia IUFRO z lat 1964-1968 (Adaptability of Polish spruce (Picea abies (L) Karst.) in the light of the IUFRO 1964-1968 international provenance experiment). Arb. Kórn. 23:185-205

Giertych M (1984) Świerk istebniański w świetle międzynarodowych doświadczeń proweniencyjnych (Istebna spruce in the light of international provenance trials). Sylwan 128(12):27-42

Hofmann M, W Durka, M Liesebach and H Bruelheide (2015) Intraspecific variability in frost hardiness of Fagus sylvatica L. Eur. J. For. Res. 134(3):433-441. https://dx.doi.org/10.1007/s10342-015-0862-6

IPCC (2014) Climate Change 2014: Synthesis Report. Summary for Policymakers. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: Intergovernmental Panel on Climate Change, 31 p

Jonard M, A Legout, M Nicolas, E Dambrine, C Nys, E Ulrich, R van der Perre and Q Ponette (2012) Deterioration of Norway spruce vitality despite a sharp decline in acid deposition: a long-term integrated perspective. Glob. Change Biol. 18(2):711-725. https://dx.doi.org/10.1111/j.1365-2486.2011.02550.x

Kerr G, V Stokes, A Peace and R Jinks (2015) Effects of provenance on the survival, growth and stem form of European silver fir (Abies alba Mill.) in Britain. Eur. J. For. Res. 134(2):349-363. https://dx.doi.org/10.1007/s10342-014-0856-9

Kocięcki S (1968) Study on permanent areas with spruce in mature stands. In: Population studies of Norway spruce in Poland. Tyszkiewicz S (ed) Warsaw: Forest Research Institute, pp 78-99

Krutzsch P (1992) IUFRO's role in coniferous tree improvement - Norway spruce (Picea abies (L.) Karst.). Silvae Genet. 41(3):143-150

Lacaze JF and S Kocięcki (1979) Zmienność populacji polskiego świerka na powierzchniach we Francji i w Polsce (Variation in Polish spruce population on areas in France and in Poland). Sylwan 123(6):1-21

Lee SJ, T Connolly, SM Wilson, DC Malcolm, J Fonweban, R Worrell, J Hubert and RJ Sykes (2015) Early height growth of silver birch (Betula pendula Roth) provenances and implications for choice of planting stock in Britain. Forestry 88(4):484-499. https://dx.doi.org/10.1093/forestry/cpv018

Matras J (1993) Growth of Norway spruce in IUFRO 1972 experiment. Proceedings of the Norway spruce provenances and breeding. IUFRO (S2,2-11) Symposium, Riga, Latvia 1993

Matras J (2002) Growth and development of Polish provenances of Norway spruce (Picea abies Karst.) in the IUFRO 1972 experiment. Prace IBL, seria A 947(4):73-97

Matras J (2004) Genetic value of the Silesian Beskid populations of Norway spruce Picea abies (L.) Karst. in the IUFRO 1972 provenance experiment. Dendrobiology Suppl. 51 71-80

Matras J (2009) Growth and development of Polish provenances of Picea abies in the IUFRO 1972 experiment. Dendrobiology Suppl. 61:145-168

Matyas C (1994) Modeling climate change effects with provenance test data. Tree Physiol. 14(7-9):797-804. https://doi.org/10.1093/treephys/14.7-8-9.797

Miguez-Soto B and J Fernandez-Lopez (2015) Variation in adaptive traits among and within Spanish and European populations of Castanea sativa: selection of trees for timber production. New For. 46(1):23-50. https://dx.doi.org/10.1007/s11056-014-9445-5

Montwe D, H Spiecker and A Hamann (2015) Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. Tree Genet. Genomes 11(2). https://dx.doi.org/2910.1007/s11295-015-0854-1

Saenz-Romero C, JB Lamy, A Ducousso, B Musch, F Ehrenmann, S Delzon, S Cavers, W Chalupka, S Dagdas, JK Hansen, SJ Lee, M Liesebach, HM Rau, A Psomas, V Schneck, W Steiner, NE Zimmermann and A Kremer (2017) Adaptive and plastic responses of Quercus petraea populations to climate across Europe. Glob. Change Biol. 23(7):2831-2847. https://dx.doi.org/10.1111/gcb.13576

Skroppa T and A Steffenrem (2016) Selection in a provenance trial of Norway spruce (Picea abies L. Karst) produced a land race with desirable properties. Scand. J. Forest Res. 31(5):439-449. https://dx.doi.org/10.1080/02827581.2015.1081983

Sofletea N, AL Curtu, ML Daia and M Budeanu (2015) The dynamics and variability of radial growth in provenance trials of Norway spruce (Picea abies (L.) Karst.) within and beyond the hot margins of its natural range. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 43(1):265-271 https://doi.org/10.15835/nbha.43.1.9861

Šrámek V, M Vejpustková, R Novotný and K Hellebrandová (2008) Yellowing of Norway spruce stands in the Silesian Beskids – damage extent and dynamics. Journal of Forest Science 54(2):55-63. https://doi.org/10.17221/795-jfs

Stojnic S, S Orlovic, D Ballian, M Ivankovic, M Sijacic-Nikolic, A Pilipovic, S Bogdan, S Kvesic, M Mataruga, V Danicic, B Cvjetkovic, D Miljkovic and G von Wuehlisch (2015) Provenance by site interaction and stability analysis of European beech (Fagus sylvatica L.) provenances grown in common garden experiments. Silvae Genet. 64(4):133-147 https://doi.org/10.1515/sg-2015-0013

Suvanto S, P Nojd, HM Henttonen, E Beuker and H Makinen (2016) Geographical patterns in the radial growth response of Norway spruce provenances to climatic variation. Agric. For. Meteorol. 222:10-20. https://dx.doi.org/10.1016/j.agrformet.2016.03.003

Szaban J, W Kowalkowski, Z Karaszewski and M Jakubowski (2014) Effect of tree provenance on basic wood density of Norway spruce (Picea abies [L.] Karst.) grown on an experimental plot at Siemianice Forest Experimental Station. Drewno 57(191):135-143. https://dx.doi.org/10.12841/wood.1644-3985.061.10

Szeligowski H, W Buraczyk, S Drozdowski, M Studnicki and L Bolibok (2016) Variability of Scots pine (Pinus sylvestris L.) provenances in the IUFRO 1982 series experiment in Rogow Forest District. Sylwan 160(3):230-237

Tyszkiewicz S (1968) The occurence of spruce in Poland. In: Population studies of Norway spruce in Poland. Tyszkiewicz S (ed) Warsaw: Forest Research Institute, pp 8-14

Vacek S, I Hunova, Z Vacek, P Hejcmanova, V Podrazsky, J Kral, T Putalova and WK Moser (2015) Effects of air pollution and climatic factors on Norway spruce forests in the Orlick, hory Mts. (Czech Republic), 1979-2014. Eur. J. For. Res. 134(6):1127-1142. https://dx.doi.org/10.1007/s10342-015-0915-x

Wang T, A Hamann, A Yanchuk, GA O'Neill and SN Aitken (2006) Use of response functions in selecting lodgepole pine populations for future climates. Glob.

Change Biol. 12(12):2404-2416
https://doi.org/10.1111/j.1365-2486.2006.01271.x
White TL, WT Adams and DB Neale (2007) Forest genetics. Cambridge, MA, USA: CABI Publishing, 682 p. https://doi.org/10.1079/9781845932855.0000
Załęski A, B Zajączkowska, J Matras and J Sabor (2000) Leśna regionalizacja dla nasion i sadzonek w Polsce (Forest regionalization for seeds and seedlings in Poland). Warszawa: Centrum Informacyjne Lasów Państwowych, 112 p
Zobel B and J Talbert (1984) Applied forest tree improvement. New York: John Wiley & Sons