

SHORT REPORT

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Adaptation of Norway spruce populations in Europe: a case study from northern Poland^S

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Abstract

Background: The productive potential of European species of forest tree assumes particular importance in the context of populations adapting to accelerating climatic change. Genotype-environment interaction ($G \times E$) was studied to determine *Picea abies* (L.) H.Karst. (Norway spruce) inter-population variation, characterising their adaptability to the growing conditions in north-eastern Poland. The data were analysed from 22 populations evaluated in four experimental sites based on 5-year height. To identify best-adapted as well as specifically adapted populations, GGE biplots were performed.

Findings: Analysis of multi-environment trial (MET) data revealed significant differences between four experimental sites, as well as interactions between populations and sites. However, it proved possible to identify specifically adapted populations achieving high values for the trait at specific sites only, although some performed relatively well across several sites.

Conclusions: The productive potential of the Norway spruce populations in north-eastern Poland is associated with specific adaptation of given populations to growth conditions at the experimental sites. However, in the set of populations studied can also be found some capable of average but stable growth in all experimental sites.

Keywords: *Picea abies*, GGE biplot, Genotype \times environment interaction, Stability, Multi-environment trials, Growth rate, Adaptation

Findings

Introduction

The observed increase in the rate of climate change and accompanying weather anomalies in Europe necessitate ongoing adaptation processes in forest trees, as well as generating changes in the productive potential of stands (Hanewinkel et al. 2012; IPCC 2015; Lindner et al. 2014). The adaptability of trees to new conditions is dependent on genetic diversity, which is largely controlled by population size, the nature and direction of observed climate change, and the direction and intensity of selection (Alberto et al. 2013). Among Europe's native tree species, *Picea abies* (L.) H.Karst. (Norway spruce) is characterised by broad

adaptability, including the potential to adjust to the predicted water deficit in Central Europe (Lévesque et al. 2013; Zang et al. 2014).

Many studies have considered the potential of Norway spruce populations to adapt to climate change (Ununger et al. 1988; Krajmerová et al. 2009; Kapeller et al. 2012; Nilsson et al. 2012; Ulbrichová et al. 2015). However, the level of knowledge of the productive potential of Polish populations of Norway spruce are still inadequate for forecasting capacity to adapt to foreseen climate change (Matras 2002, 2009).

The results of phylogenetic studies based on molecular markers suggest separate evolutionary origin of Polish populations of Norway spruce with southern populations descended from Alpine refugia while north-eastern populations are from Scandinavian refugia (Lewandowski and Burczyk 2002; Nowakowska 2009; Dering and Lewandowski 2009).

Evaluation of the genotype \times environment interaction ($G \times E$) in a multi-environment trials (MET) makes it

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possible to characterise the genetic conditioning behind the productive potential of forest trees in relation to site conditions (Kang and Gauch 1996). The use of the GGE biplots (graphical method) in MET-based analysis allows the most-representative sites to be identified. Their discriminating ability can also be defined, along with the genotypes best adapted to grow in groups of experimental sites (MET). In addition, it is possible to characterise the stability of genotypes with respect to traits studied, i.e. in terms of rankings or relative performances of genotypes (Yan and Kang 2002). Among the broad range of possible analyses, the methods presented to assess the $G \times E$ are being used more and more in METs involving forest tree species (Murillo 2001; Kim et al. 2008; Ding et al. 2008; Correia et al. 2010; Sixto et al. 2015; Ukalski and Klisz 2016; Zhao et al. 2016).

We attempted to assess the influence of genetic and site factors on the productive potential, as assayed by height and survival 5 years after field planting, of populations of Norway spruce from north-eastern Poland. The assessment of the $G \times E$ was made based on GGE biplots, with the data used concerning measurements of the heights of trees in the MET.

Materials and methods

Experimental design

Twenty-two populations of Norway Spruce (21 from north-eastern and one from southern Poland) were sampled for a series of four field trials (Table 1), each using a randomised complete block design with four replicates. All populations studied are selected seed stands—phenotypically the best Norway spruce stands in north-eastern Poland. Incorporating population 1 (from southern Poland) alongside a group of north-eastern populations was intended to reference the performance of local populations against one from outside of the region, meaning that it served as an outgroup. Seed collection in each stand was done on 50 randomly selected trees in 2009, on transects with a minimum distance of 25 m between trees. However, the origin of the metapopulation (local or from foreign seed source) has not been ascertained by phylogenetic study. Seeds were collected from healthy trees in a year of heavy seed production. From each tree was collected no less than 1 kg of cones. It allowed gathering over 20 g seeds per tree, meaning at least 1 kg of seed per stand.

Table 1 Mean values and coefficients of variation (CV%) of tree heights at the individual-tree level and survival in 22 populations of spruce at four experimental sites: *CBL* Czarna Bialostocka, *CDW* Czerwony Dwor, *GOL* Goldap, and *SCB* Szczebra Czarna sites

Population	Mean height [cm] (CV [%])					Mean survival [%]				
	CBL	CDW	GOL	SCB	Across sites	CBL	CDW	GOL	SCB	Across sites
1	99 (28)	106 (30)	127 (32)	89 (34)	107 (35)	70	49	62	61	62
5801	108 (25)	92 (33)	113 (27)	98 (32)	103 (30)	81	94	88	83	86
5802	114 (38)	102 (29)	121 (32)	83 (31)	106 (37)	82	63	79	70	74
5821	97 (28)	97 (28)	116 (31)	84 (37)	100 (33)	85	67	90	67	78
6429	126 (30)	93 (32)	122 (34)	85 (41)	109 (37)	83	84	89	68	81
6522	123 (31)	101 (30)	105 (28)	89 (34)	106 (33)	88	73	87	68	79
6523	131 (30)	98 (30)	112 (32)	87 (37)	110 (35)	92	81	79	62	78
6540	98 (28)	107 (30)	113 (31)	82 (36)	101 (33)	83	87	86	66	80
27102	123 (34)	95 (28)	108 (32)	75 (36)	102 (37)	86	84	88	71	82
32160	117 (26)	113 (31)	112 (33)	89 (38)	108 (33)	84	68	88	71	78
33253	116 (30)	90 (30)	110 (33)	87 (34)	103 (34)	89	57	83	66	75
33256	98 (27)	107 (29)	118 (34)	78 (35)	101 (34)	86	91	83	68	81
33257	93 (27)	123 (29)	112 (32)	85 (33)	101 (34)	73	47	92	70	72
33259	99 (28)	94 (29)	99 (33)	82 (34)	94 (32)	80	76	75	66	74
50257	111 (34)	96 (29)	120 (30)	80 (34)	104 (35)	86	82	92	66	81
50258	136 (31)	104 (29)	121 (30)	81 (30)	112 (36)	88	87	87	74	83
50262	117 (40)	106 (31)	124 (29)	82 (35)	110 (37)	85	85	90	54	78
50263	119 (34)	92 (31)	106 (37)	79 (35)	100 (38)	85	83	77	72	79
50264	111 (35)	105 (37)	109 (33)	78 (32)	101 (37)	78	77	85	70	77
50265	120 (32)	115 (31)	108 (33)	86 (33)	108 (35)	86	82	75	63	76
52690	123 (28)	96 (35)	105 (32)	84 (33)	104 (34)	91	84	86	70	82
52692	137 (28)	115 (27)	119 (33)	82 (34)	115 (35)	82	88	80	62	72
Multi-population mean	115 (33)	102 (32)	114 (32)	84 (35)	105 (35)	84	77	84	67	78

The seedlings were produced in Kołaki Forest Nursery (N 53° 18', E 22° 04'). Sowing was carried out manually in March 2010, one seed per container cell. For producing the seedlings, HIKO V120/40 containers were used (cell volume, 120 cm³/7.32 in.³). Seedlings were kept in polyhouses until June 2010 then they were transferred to open-air conditions. A late frost in April 2011 led to the death of a number of apical shoots so some seedlings were culled from the planting stock at the nursery stage. During all nursery stages, the containers were grouped on pallets with populations distributed randomly. Up to the planting stage, seedlings were not removed from the container in order to avoid mistakes between populations. After 1 year growing in the nursery, planting material was transferred directly to the experimental sites. To acclimatise the seedlings to local growing conditions, planting material was stored close to planting places.

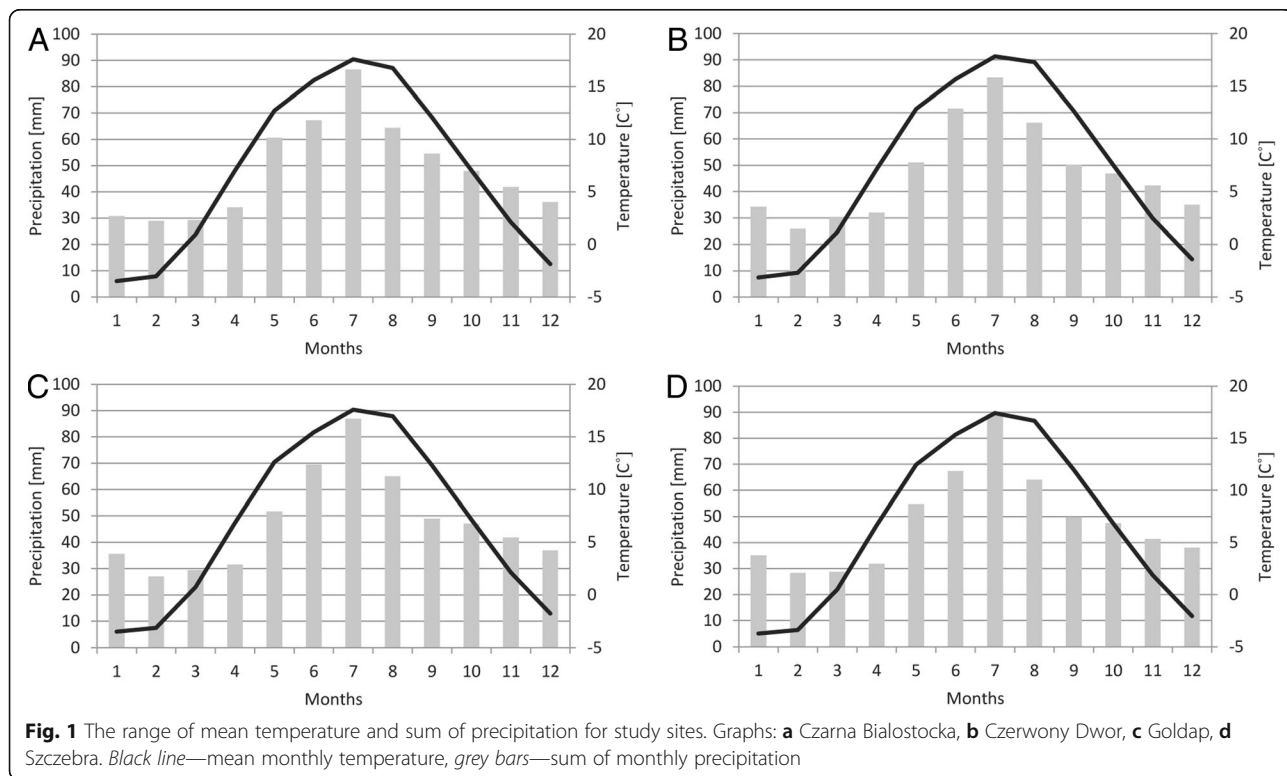
Planting was done in 2011 in north-eastern Poland, at the four localities: Czerwony Dwór (CDW) (N 54° 17' E 21° 59'), Goldap (GOL) (N 54° 19' E 22° 40'), Szczebra (SCB) (N 53° 56' E 22° 54') and Czarna Białostocka (CBL) (N 53° 20' E 23° 19') (Fig. 1). The climate is cool temperate with a mean annual temperature from 6.8 to 7.4 °C (respectively: SCB, CDW) and annual precipitation from 569 to 582 mm (respectively: CDW, CBL), mostly distributed in June–November [climate data from National Oceanic and Atmospheric Administration (NOAA) agency, weather stations in Białystok, Suwałki and Kętrzyn, reference period

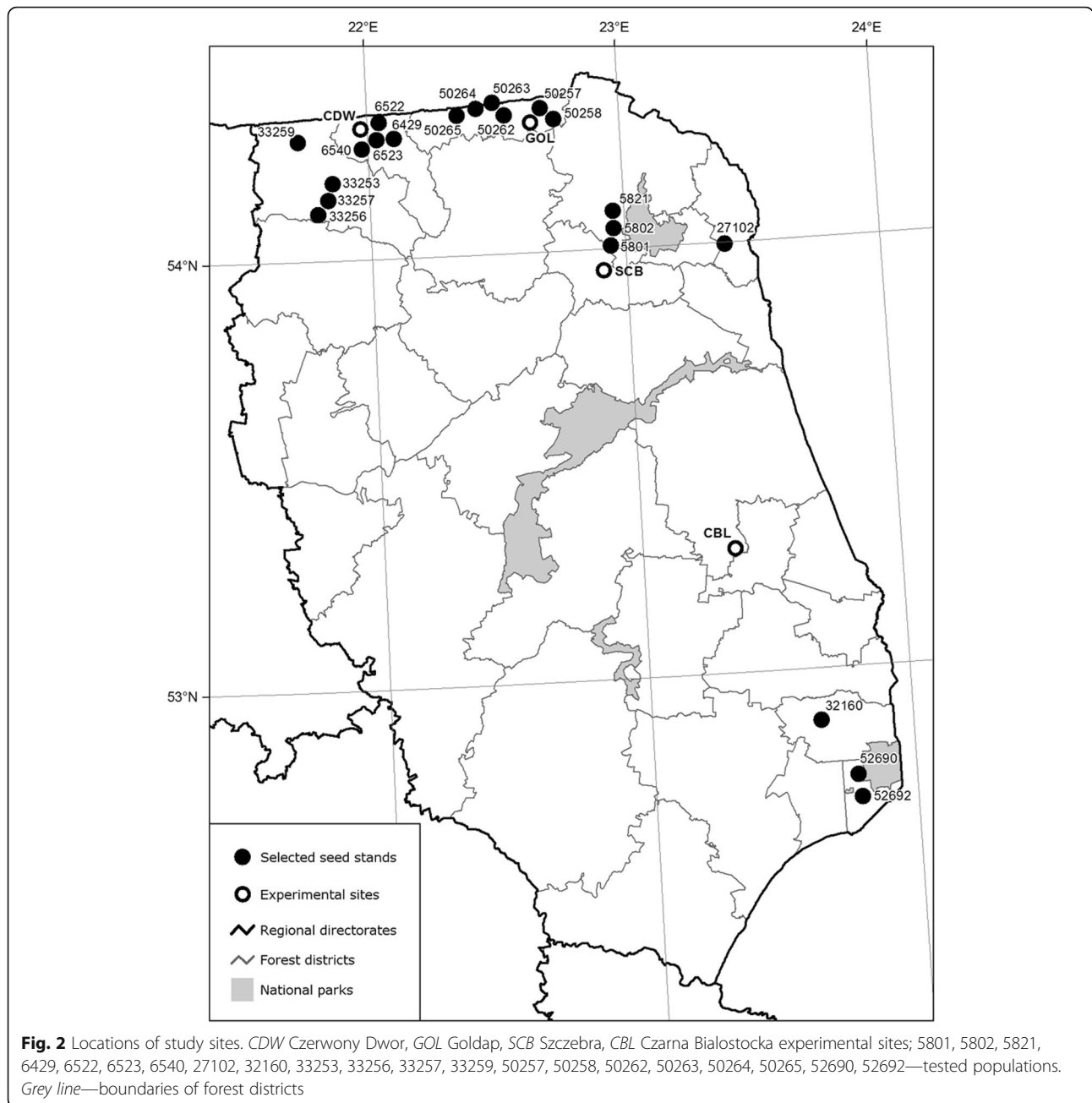
1973–2014] (NOAA/NCEI/CWC <http://www.noaa.gov/>) (Fig. 2). The soils were loamy sand (SCB), spodic (CDW, GOL), or rusty (CBL). The ground in all cases was previously occupied by managed forest stand dominated by 80–100-year-old trees of *Pinus sylvestris* L. (Scots pine) and Norway spruce. After clear-cutting a year earlier, the ground was cultivated 3 months before planting. The experimental sites were established using 10-tree × 10-tree population plots, at 1.5 × 1.5 m spacing. In the CBL, GOL and SCB sites, each test population was represented by 400 trees (100 per plot × four replicates) but in CDW by 300 trees (100 per plot × three replicates). Only population 1 was represented by 300, 200, 400 and 300 trees (respectively: CBL, CDW, GOL, SCB). The reference population (1) for the trials was the Istebna selected seed stand in southern Poland (N 49° 34' E 18° 50'). In 2015, following 5 years of growth, the heights of all surviving trees were measured in each site (Table 1).

The impact of the environment and genotype on height growth

According to a linear model with genotype and block fixed effects, analysis of variance was performed for each site separately. Based on Tukey HSD test, homogeneous groups were determined for the sites where the genotype effect was significant (*p* < 0.05).

The modelling approach in MET analysis is recently based on mixed model framework (Piepho 1998; Balzarini





2002). Environments are deemed to be a random effect, as they were chosen to represent a roughly random sample of a population of environments. The effect of genotypes is often treated as a fixed effect, in that the genotypes may represent the entire population in a genetic improvement programme. When at least one of the two main factor effects is regarded as random, the $G \times E$ interaction effect is also deemed to be random (Saxton 2004). On this basis, we fitted a linear mixed model for classifying the effects site, population, block and $G \times E$ interaction, in the following form (Searle et al. 1992, Piepho 1998):

$$y_{ijk} = \mu + r_k(e_j) + g_i + e_j + ge_{ij} + \varepsilon_{ijk} \quad (1)$$

where y_{ijk} is the trait value observed for the experimental plot for the i th genotype ($i = 1, \dots, G$) in the j th site ($j = 1, \dots, E$) and in the k th block ($k = 1, \dots, R$), μ is the general mean, g_i is the fixed effect of the i th genotype, e_j is the random effect of the j th site, ge_{ij} is the random effect of the genotype \times site interaction, $r_k(e_j)$ is the random effect of the k th block in the j th site, and ε_{ijk} is the random residual containing the effect of a block-within-site \times genotype interaction (i.e. plot effect) and some tree-

within-plot experimental error. The data obtained for the 22 spruce populations at the four sites did not represent a fully balanced classification. The best linear unbiased predictors (BLUP) were calculated to create, in effect, a completed data set (Piepho 1998; Balzarini 2002; Piepho and Möhring 2006; Piepho et al. 2008). *F* statistics for testing random effects were determined using the Hocking's approach (Hocking and Speed 1975).

GGE and GREG biplots

To identify stable populations in terms of height growth at the experimental sites, the GGE biplot was used (Gabriel 1971; Yan et al. 2001). The significance of the individual $G \times E$ interaction effects was examined using the Bonferonni test (Dunn 1961), with a 0.01 probability threshold experiment-wise. In turn, GREG biplot (Cornelius et al. 1996; Cornelius and Seyedsadr 1997) was used to determine the similarity between sites, along with the AEC method (Yan and Hunt 2001; Yan 2002). The choice of the GREG biplot was dictated by the fact that first and second principal components for interaction effects (PC1 and PC2, respectively) explained 9.95% more of the variation than did the GGE biplot, as well as the fact that the interaction in this model comprises the effects of *E* and the $G \times E$, a combination that better characterises the interrelationships between the experimental sites (Ukalski and Klisz 2016).

The similarities between all of the pairs of experimental sites were determined in two ways. In the first method, the value of α_{ij} angles between vectors OA_i and OB_j were determined (where OA_i and OB_j are vector lengths between the centre of the coordinate system and position of sites *A* and *B*, respectively). In the second method, Pearson correlation coefficients were calculated for each pair of sites on the basis of the principal component values utilising $G \times E$ interaction effects.

Statistical analyses and presented biplots were performed using SAS/STAT 13.1 software (SAS Institute Inc 2013) with procedures GLM, MIXED (Littell et al. 1996), PRINCOMP (Khattree and Naik 2000), and GPLOT.

Results and discussion

Analysis of variance

Between-population differences were confirmed for height growth only for the CDW site, while for survival only for the CDW and GOL sites. Details regarding the analyses of variance are given in Additional file 1: Table S1.

For height growth, no significant across-site differentiation among the populations was found but there was strong among-site variation as well as a $G \times E$ interaction (Table 2). The *F* value for genotype effect was less than 1, because $Q(G) < 0$ for the quadratic form associated with the genotype fixed effect. This meant the estimate of the genotypic variance across sites was negative,

so we assumed the variance to be zero. Accordingly, we found that the overall variation in height was explained by the effects of site (*E*) (72%) and $G \times E$ interaction (28%). Low variation explained by the across-site genotype effect may be related to modest local genetic variation within the Norway spruce metapopulations of north-eastern Poland (Lewandowski and Burczyk 2002). However, it is still surprising in the context of the modest variation of environmental conditions among the experimental sites (low in the case of climatic conditions and modest in the case of soil). The aforementioned results are in accordance with the results of ANOVA performed at the individual-population level separately for each site (Additional file 1: Table S1). Significance of genotypic variation and of $G \times E$ had been demonstrated previously in research on tested clones of Norway spruce from central and southern Sweden (Bentzer et al. 1988), as well as in work involving Japanese red pines (*Pinus densiflora* Siebold & Zucc.) in South Korea (Kim et al. 2008). Studies of European provenances of Norway spruce carried out in 11 localities in northern Denmark and southern Sweden pointed stability in all the test environments (Karlsson et al. 2001).

The principal components analysis (PCA) showed that the division of effects ($G + E + GE$) with GGE biplot was as follows: the PC1 explained 51.08% of the variation ($G + E + GE$), while PC2 explained 25.85%. This made 76.93% in total.

Similarity of environments

Use of principal components PC1 and PC2 for the four sites allowed for the designation of the average environment (AE). This was then used, in association with the centre of the coordinate system, to run an AE axis (Fig. 3).

The location of sites relative to the position of the AE axis shows that the average height of spruce trees at CDW was almost identical to the height overall mean. Where the comparisons among the other sites were concerned, two—SCB and GOL—were rotated through 90° in the direction of the location of site CBL. A new AE point for these three sites was designated. It emerged that, at the CBL site, the heights of spruce trees were greater than the overall mean, as was also the case for the GOL site, albeit with the differences in comparison with the mean being slight in this case. In contrast, at the SCB site, heights of spruce trees were much below the overall mean.

The vector length of the site is determined by a line drawn through the biplot origin and the site marker and is a measure of discriminating ability of the site. Thus, the sites CBL and CDW, which had the longest vectors, were the most discriminating for genotypes. The line that passes through the plot origin and is perpendicular to the AE axis is a measure of representativeness of the sites (Yan and Hunt 2001). Therefore, site CDW was the most representative (as it had a near-zero length of projection from marker of a site onto the AE axis) and CBL was the least.

Table 2 Results of analysis of variance for tree heights in 22 populations of spruce at four trial sites, along with the percentage of the variation explained (Q(G) is a quadratic form associated with genotype fixed effect; F statistics are calculated according to Hocking's approach)

Source of variation	df	Mean square	Expected mean square	Error term	F	P	% (G + E + GE)
Genotype (G)	21	248.34	Var(ERROR) + 3.69 Var(GE) + Q(G)	0.989*MS(GE) + 0.011*MS(ERROR)	0.81	0.700	0
Site (E)	3	16,825	Var(ERROR) + 3.73Var(GE) + 22Var(Block (Site)) + 82.13Var(E)	MS(Block (Site)) + MS(GE) – MS(ERROR)	6.9	0.006	72
Block (site)	11	2339.99	Var(ERROR) + 22Var(Block (Site))	MS(ERROR)	11.12	<0.001	–
Genotype × site (GE)	63	309.44	Var(ERROR) + 3.73Var(GE)	MS(ERROR)	1.47	0.020	28
Experimental error (ERROR)	231	210.49	Var(ERROR)				

On the basis of the comparison of angles between vectors for the sites, it was noted that the sites most similar to each other were GOL and SCB (Fig. 2). Location of CBL site in the diagram suggests that the Norway spruce genotypes show the opposite interaction ($G \times E$) than GOL and SCB sites. The vector for site CDW creates obtuse angles with the others, albeit ones close to right angles (Fig. 3); while the correlation coefficients indicate non-significant correlation with the remaining three sites (Table 3).

Stability of populations

The GGE biplot (Fig. 4) was used to define the population of spruce at each site characterised by the greatest effect of $G \times E$. The GGE biplot has a polygon formed through the

connection of the positions of populations located furthest from the centre of the coordinate system. All remaining populations are contained within the polygon created. The lines creating the sectors are at right angles to the sides of the polygon or else form extensions of them (Yan 2001). The 22 populations of spruce and four sites are found to be distributed across seven sectors. Sites CDW and GOL fall within a single sector. A high mean for height at these two sites characterised population 33257, which at the same time showed marked instability. In turn, at site CDW, population 33257 attained very superior heights, though it achieved only very low ones at site CBL. It was in a second sector containing population 52692 that site CBL was located. There, the latter population, with its good growth,

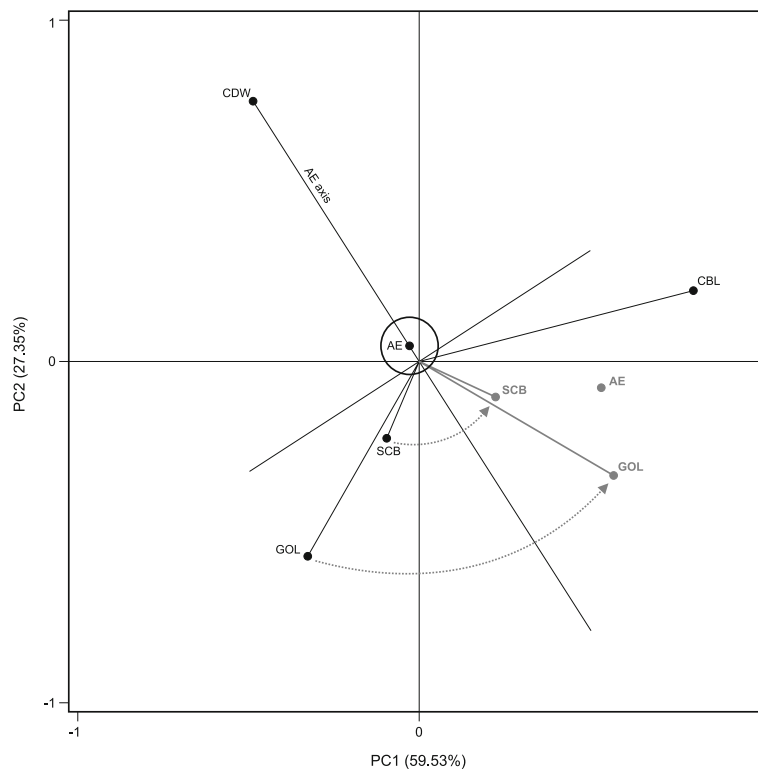
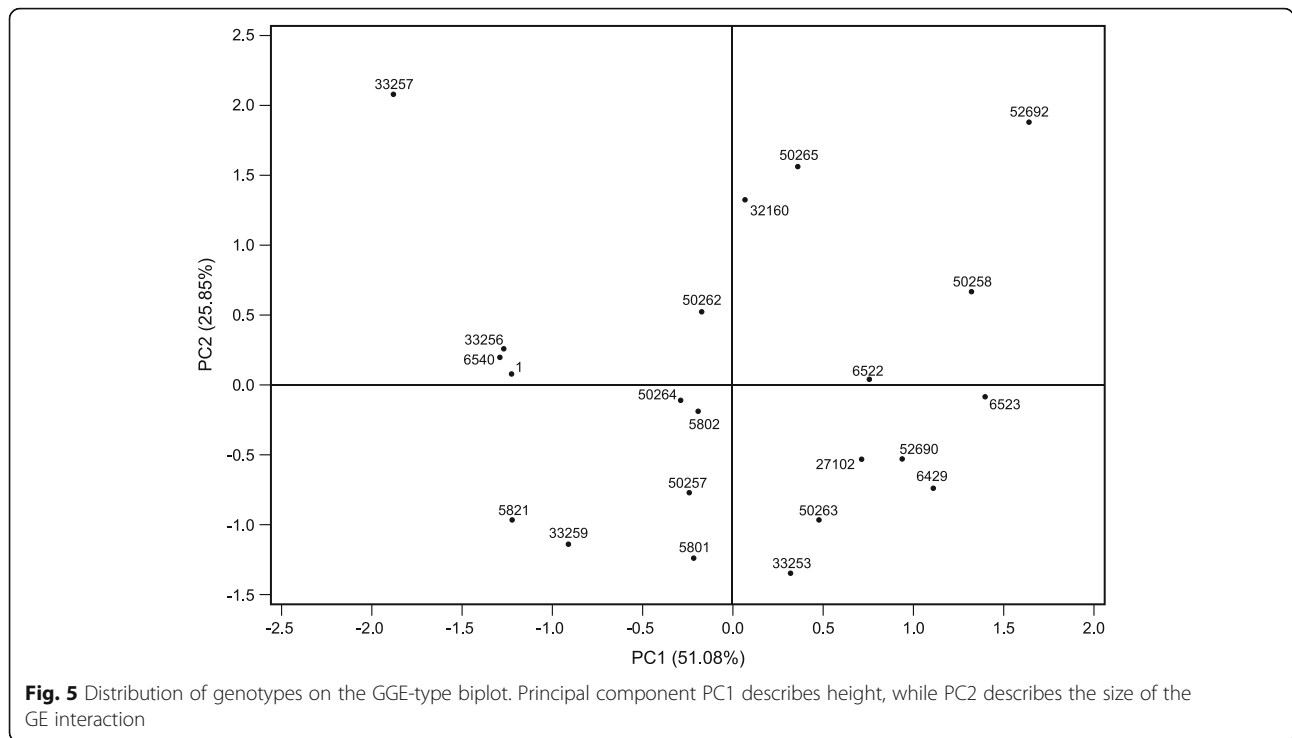


Fig. 3 View of AEC on the GREG-type biplot based on principal components for the environments. AE in the circle is the 'average environment' for SCB, GOL and CBL designated for comparison



adaptation to growth at experimental sites CBL and CDW. Population 1 (national standard from southern Poland) shows some lack of adaptation to the growing conditions in northern Poland. Site CDW seems to be the most-representative site, while CBL and SCB are characterised by the greatest discriminating ability.

Additional file

Additional file 1: Table S1. Mean plot values of tree heights and survival in 22 populations of spruce at four experimental sites: CDW – Czerwony Dwor, GOL – Goldap, SCB – Szczebra, CBL – Czarna Białostocka sites. ANOVA was performed for each site separately. Homogeneous groups were determined based on Tukey HSD test. Means with the same letter within the column are not significantly different at $p < 0.05$. (DOCX 20 kb)

Abbreviations

AE: Average environment; AEC: Average environment coordination; BLUP: Best linear unbiased predictor; CBL: Czarna Białostocka experimental site; CDW: Czerwony Dwór experimental site; E: Effect of environment; G: Effect of genotype; G × E: Genotype-environment interaction; GGE: Genotype and genotype-by-environment interaction biplot; GOL: Goldap experimental site; GREG: Genotype regression biplot; MET: Multi-environment trial; PC: Principal components; PC1: First principal component; PC2: Second principal component; PCA: Principal components analysis; SCB: Szczebra experimental site

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Authors' contributions

MK is responsible for the data collection, preparation of manuscript, text corrections, coordinating work; SzJ is responsible for the initial preparation, data collection, text corrections; KU is responsible for the proposal and performance of statistical analysis and contribution to interpretation of results; JU is

responsible for the description and performance of statistical analysis and correction of manuscript; PP is responsible for the data collection, text corrections. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

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