DOI: 10.1515/frp-2017-0034
Available online: www.lesne-prace-badawcze.pl

Leśne Prace Badawcze / *Forest Research Papers*
Grudzień / December 2017, Vol. 78 (4): 303–314

ORIGINAL RESEARCH ARTICLE

e-ISSN 2082-8926

Comparing natural regeneration of Norway spruce *Picea abies* (L.) Karst. in the Kaszuby Lake District and in the other regions of northern Poland

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Abstract. The paper investigates the biometric characteristics natural Norway spruce (*Picea abies* (L.) Karst.) regeneration in the Kaszuby Lake District, which is beyond the acknowledged Norway spruce range, with the natural regeneration in the Augustów Forest situated deep within the natural range, Warmia, at the edge of the natural range and in the West-Pomerania Lake District far beyond the natural range.

For each region, four tree stands with similar light conditions on the forest floor were selected, including two cambisols and two brunic arenosols. All sites contained naturally regenerating spruces 16–17 years of age.

The features of the forest stand and the biometric features of the saplings were determined for the selected stands on circular research plots. Altogether, the characteristicts of 400 saplings (100 in each region) were measured and analyzed using basic descriptive statistics. ANOVA with the Tukey's multiple comparison test was performed to compare the features of forest stands and the natural regeneration of spruce in each region. The degree of interrelation between regeneration features was described by Pearson's, 'r' factor or Spearman's rank correlation coefficient. A discriminatory analysis was carried out to determine the set of regeneration features differentiating regions from each other.

The features of regeneration that differed between regions the most were: height of regeneration, basal diameter, mean height increment, and mean basal diameter increment of the saplings. The parameters for Warmia and the West-Pomerania Lake District were similar. The Augustów Forest showed the lowest values for the regeneration parameters, while the Kaszuby Lake District produced the highest values. The regeneration in the Kaszuby Lake District was markedly different from all other regions as indicated by more dynamic growth. Additionally, this population shows a great distinctness, indicating adaptation to local environmental conditions, which may be proof for the insular presence hypothesis of spruce in this region.

Due to their good quality, spontaneously developing natural regenerations in the Kaszuby Lake District should be supported by appropriate cutting and silvicultural measures.

Keywords: *Picea abies*, Norway spruce, natural regeneration, natural range, silviculture

1. Introduction

It is generally believed that Norway spruce *Picea abies* (L.) Karst. that grows in the region of Kaszuby Lake District, occurs outside of its natural range in Poland (Boratyńska 1998); however, this opinion has been increasingly criticized (Modrzyński 1999, Lewandowski et al., 2014). Nonetheless, Norway spruce plays an important economic role in this region (Szydlarski 1999) and it is dynamically regenerating (Szydlarski, Modrzyński 2015). When conducting a detailed study on Norway spruce natural regeneration in the Kaszuby Lake District, the authors found it interesting, from a scientific and practical viewpoint, to compare the observed Norway spruce regeneration with that in other northern Poland's regions, both within and beyond the limits of its natural range. The results obtained could be a contribution to the knowledge on the natural range of Norway spruce in Poland, as well as to the development of more coherent approach to this species in forest management practice.

Received: 20.06.2017, reviewed: 14.09.2017, accepted: 11.10.2017.

2. Material and methods

Research on Norway spruce natural regeneration was carried out in the Kaszuby Lake District, the Augustów Forest, the region of Warmia and in the West-Pomerania Lake District. Figure 1 shows geographical locations of the regions under the study and the border of the natural range of Norway spruce in Poland's lowlands.

Consistent with the natural-forest regionalization (Zielony et al. 2010), the Kaszuby Lake District is located in the Baltic Region (I), where it forms the Mesoregion of the Kaszuby Lake District (I.18) (Forest District Kartuzy). The Augustów Forest covers a large part of the Augustów Plain (Kondracki 2001), and as stated in the natural-forest regionalization, is located in the Mazury-Podlasie Region (II): the Mesoregion of the Augustów Forest (II.11) (Forest District Szczebra). In Warmia, the study was conducted in the area of the Staropruska Lowland (Kondracki 2001). According to the natural-forest regionalization, the Staropruska Lowland is located in two Regions: the Baltic Region (I), the Warmia Mezoregion (I.22) and in the Mazury-Podlasie Region (II), the Sępopolska Lowland Mesoregion (II.1) (Forest Districts: Górowo Iławeckie and Wichrowo). In the West-Pomerania Lake District, research was carried out in the Mesoregions: the Drawskie Lake District (I.12) and the Polanowska Upland (I.15) (Forest Districts: Szczebra Połczyn and Polanów), both located in the Baltic Region (I).

In each of the regions, there were selected four forest stands, including two growing on brown earth (Cambisols) and two on rusty soils (Brunic Arenosols), on fresh forest sites (fresh mixed-coniferous forest, fresh mixed deciduous forest, fresh deciduous forest), with similar light conditions in the forest bottom (as determined on the basis of measurements), with natural regeneration of Norway spruce at the age of 16—17 years.

The characteristics of forest stands and site conditions on research plots in each region are presented in tables 1 and 2.

In each of the selected stands, there were randomly established 5 circular research plots consisting of concentric measurement circles: 'stand' – with a radius of 10 m and the area of 314 m^2, where the stand characteristics were evaluated and 'regeneration' – with a radius of 2 or 3 m (depending on regeneration density), where the biometric features of 5 trees (Norway spruce saplings), randomly selected along the north-south transect, were assessed.

Within the 'stand' plots, the diameter at breast height (DBH) of all trees, with the thickness of ≥ 7 cm was measured (by species). Based on the cross-sectional area (calculated per 1 ha), the species' composition of the stand and the canopy type were determined.

Within the 'regeneration' plots, the following were determined: regeneration coverage, regeneration quality (1 – unsatisfactory, 2 – satisfactory, 3 – good), the height and the most recent height increment, as well as additional lower height increments: stem diameter near the ground (basal diameter) and at the height 1.3 m, the number of whorls on the stem up to 1.3 m height and the length of two branches in the last whorl. After cutting the trees, the rings were counted on the cross-section at the ground level, in order to determine the age of trees.

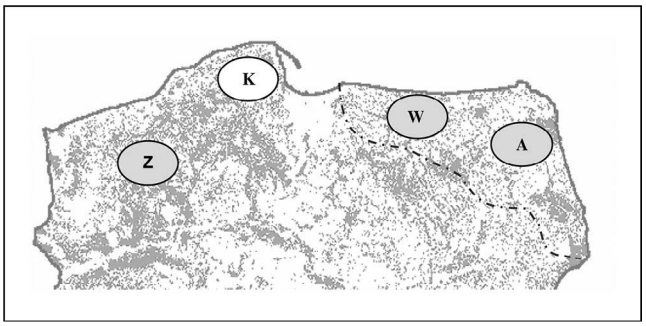

Figure 1. Localization of the investigated regions, with marking (dashed line) of the approximate south-western border of the natural range of Norway spruce in the lowland

Explanation of symbols: K – Kaszuby Lake District, Z – West-Pomerania Lake District, W – Warmia, A – Augustów Forest

Within the 'regeneration' circular plots, the photosynthetically active radiation (PAR) was measured in units [$\mu mol \cdot m^{-2} \cdot s^{-1}$], using the Basic Quantum Meter (BQM, Spectrum Technologies Inc.). The measurements were performed in 5 points: the centre of the circle and its circumference (N, W, S and E). The measurement results were averaged for each plot included for the biometric assessments.

Based on the measurements of sapling biometric features, there were determined the following: age and height of the natural regeneration, the age when 1.3 m height was accomplished, the number of saplings per 1 m^2, regeneration quality (estimated), the stem diameter at root collar (basal diameter), DBH, the radius of the last whorl and the current height increment.

On the basis of the results of the measurements, the synthetic regeneration indicators were calculated: the current height increment in the years 1996–2000, average tree height and basal diameter increments, light factor, slenderness coefficient and the average increment of the radius of the last whorl.

The value of the light factor was calculated as the quotient of the height increment in the most recent year and the mean length of the lateral shoot in last whorl, and the value of the slenderness index – as the quotient of tree height [m] and tree basal diameter [cm].

Independent statistical analysis (relative light intensity and regeneration age), as well as all the measured and cal-

Table 1. Characteristics of investigated sample plots in Kaszuby Lake District (K), West-Pomerania Lake District (Z), Warmia (W) and Augustów Forest (A), in terms of localization (forest district, forest inspectorate, forest compartment), type of forest site (TSL), type of soil (BR – cambisol, RD – brunic arenosol) and stand composition

Region	Forest district (forest inspectorate), forest compartment	Type of forest site	Soil type	Composition and age of stands
K	Kartuzy (1), 52 m	LMśw	BR	8 Św 82 l, 1 So 82 l, 1 Brz 66 l
K	Kartuzy (3), 63 b	LMśw	RD	8 Św 97 l, 2 So 97 l
K	Kartuzy (3), 28 g	BMśw	RD	6 Św 82 l, 3 So 101 l, 1 Św 61 l
K	Kartuzy (1), 208 b	Lśw	BR	9 Św 82 l, 1 Bk 82 l
Z	Połczyn (1), 452 i	Lśw	BR	7 Św 90 l, 1 So 90 l, 1 Bk 90 l, 1 Js 90 l
Z	Polanów (1), 507 c	LMśw	RD	5 Św 60 l, 3 So 60 l, 1 Brz 60 l, 1 Db 60 l
Z	Polanów (1), 117 f	LMśw	RD	6 So 57 l, 2 Md 57 l, 2 Św 57 l
Z	Połczyn (1), 392 d	Lśw	BR	8 Św 65 l, 1 Bk 65 l, 1 Brz 65 l
W	Górowo Ił.(1), 241 a	LMśw	BR	4 Db 90 l, 4 Św 90 l, 1 So 90 l, 1 Św 120 l
W	Górowo Ił.(1), 206 b	LMśw	RD	3 Db 80 l, 1 Św 80 l, 3 So 80 l, 2 Św 60 l, 1 Db 100 l
W	Wichrowo (1), 82 d	BMśw	RD	8 Św 90 l, 2 Św 70 l
W	Górowo Ił. (1), 292 f	LMśw	BR	6 Św 65 l, 3 Brz 65 l, 1 So 100 l
A	Szczebra (1), 210 a	BMśw	BR	8 So 108 l, 2 Św 78 l
A	Szczebra (1), 211 f	BMśw	RD	I: 9 So 178 l, 1 Św 118 l, II: 6 Św 88 l, 4 So 88 l
A	Szczebra (1), (98 c	BMśw	RD	9 So 88 l, 1 Św 78 l
A	Szczebra (1), 277 b	LMśw	BR	8 Św 88 l, 1 So 88 l, 1 Brz 88 l

Górowo Ił. = Górowo Iławeckie
Explanation: LMśw- fresh mixed deciduous forest, BMśw – fresh mixed coniferous forest, Lśw – fresh mixed decidous forest; Św – Norway spruce, So – Scots pine, Brz – birch, Bk – beech, Db – oak.

Table 2. Average annual temperature and sum of annual precipitation for the investigated plots in each region

Independent variables in regions	Unit of measure	Kaszuby Lake District [K]	West-Pomerania Lake District [Z]	Warmia [W]	Augustów Forest [A]
Annual temperature	ºC	7.4	8.7	7.6	6.9
Annual precipitation	mm	705	716	609	571

culated dependent variables were analysed statistically to determine differences between the regions studied.

Most of the analysed features, both directly measured and calculated (indicator values), showed a normal distribution of variables, taken into account in further statistical analyses. The values of the regeneration features: the age when the height of 1.3 m is reached, the radius of the last whorl, and the current annual increment required logarithmic transformation ($\log_e x$) to make data conform to the normal distribution. The feature 'number of trees per unit area' [specimens/m^2] was adjusted to normal distribution after transformation into the cyclometric function arcus cotangent (Acot).

For all the variables, the basic descriptive statistics were calculated: the mean, range, standard deviation and coefficient of variation. The normality of distribution was determined using the Shapiro-Wilk test. In order to compare the features of the examined Norway spruce stands and Norway spruce natural regeneration in the regions under the study, ANOVA and post-hoc Tukey's test were performed, preceded by the Levene's test for homogeneity of variances. In a given region, if variables indicated populations with not normal distribution or not homogenous variances, the nonparametric Kruskal-Wallis test was used to compare variables. The Pearson's 'r' coefficient or Spearman's rank

Simulation of growth and increase in the average height of Norway spruce natural regeneration in the period of 1–51 years is illustrated in figure 4.

According to the analysed growth model, the culmination of the increase in the average height of Norway spruce natural regeneration is:

- the earliest, in the Warmia region – tree age range: 18–25 years (on average 21.5 years), height increment: 7.4 cm/year – the lowest among the regions under the study,
- next in order, in the West-Pomerania Lake District – age range: of 22–25 years (on average 23.5 years), height increment: 8.3 cm/year,
- the latest, in the regions of the Kaszuby Lake District and the Augustów Forest, where the peak of the average height increment occurs at almost the same time: 31±41 years, (on average 36 years) and 32–42 years (on average 37 years), respectively. The average height increment values

in the two regions differed significantly and were: 12.7 cm/year in the Kaszuby Lake District (the highest in the studied regions) and 7.8 cm/year (similar to the region of Warmia and West-Pomerania Lake District) in the Augustów Forest.

In all the regions examined, the culmination of the current height increment took place before the average growth of Norway spruce culminated (fig. 5). The current height increment (on average 16 cm) reached its peak comparatively the earliest in the West-Pomerania Lake District – at the average regeneration age of 12 years. In the Kaszuby Lake District, the peak of the current height increment (on average 20 cm) occurred in Norway spruce natural regeneration at the average age of 13 years, in the Augustów Forest – at 15 years (11 cm), and in the Warmia region at the age of 19 years (the average current height increment – 17 cm).

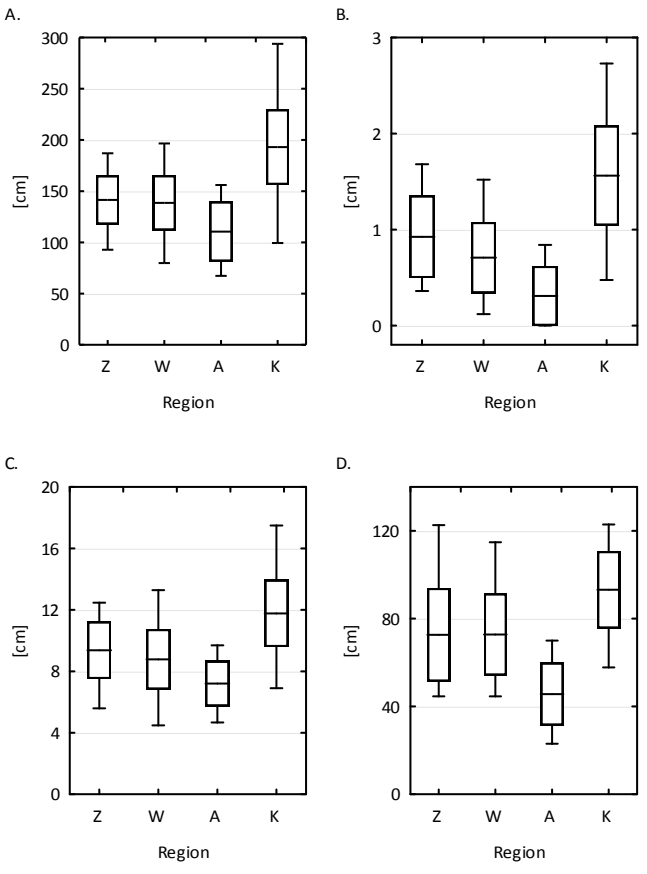

Figure 2. Features of the regeneration distinguishing significantly Kaszuby Lake District from other regions: A – height, B – breast-height diameter, C – mean height increment, D – current height increment in the period 1996–2000. Symbols of regions as in table 1.
Marks: ¯ Mean, □ Mean±SD, ⊥ Min–Max

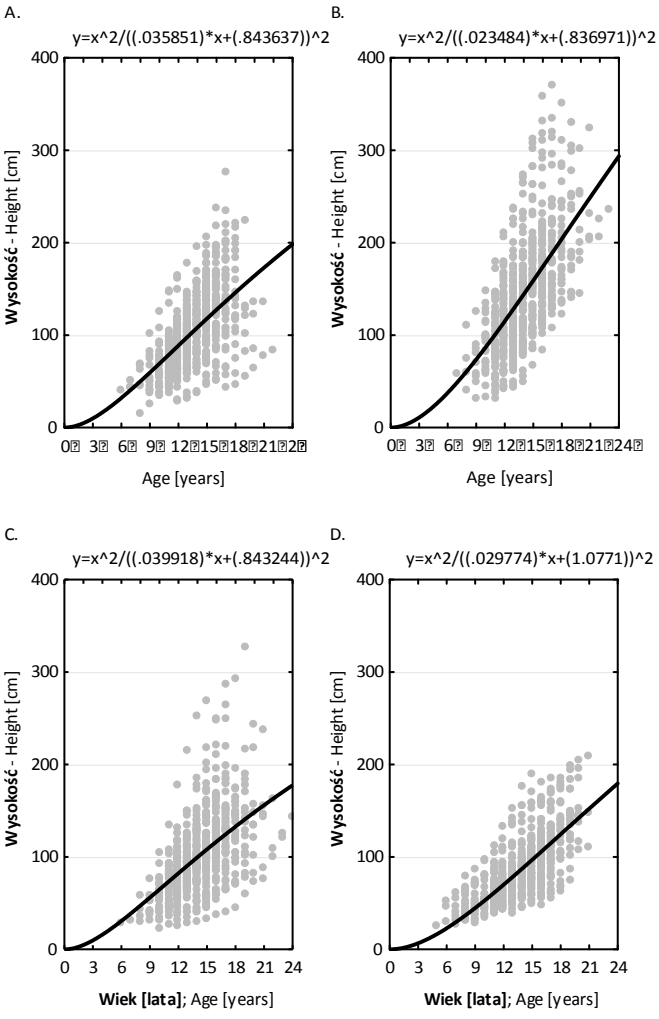

Figure 3. The dependence of the height of natural regeneration on its age in regions: A – West-Pomerania Lake District, B – Kaszuby Lake District, C – Warmia, D – Augustów Forest

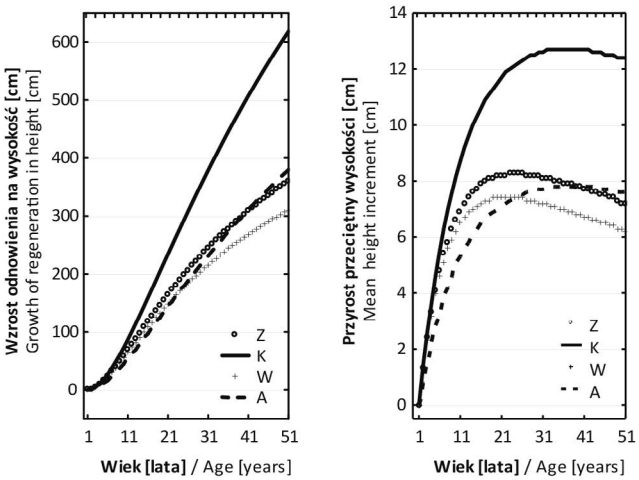

Figure 4. Growth in height and mean height increment of regeneration for the regions Z, K, W, A

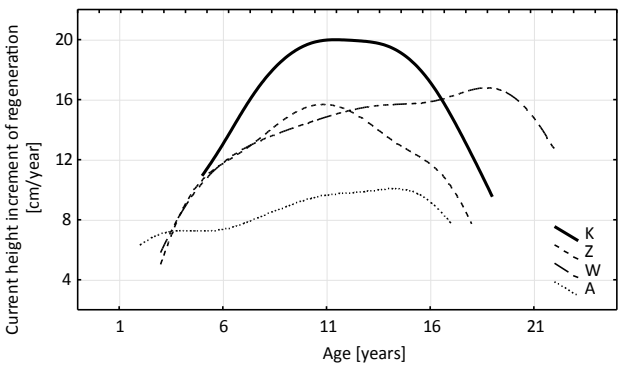

Figure 5. Current height increment of regeneration in the regions Z, K, W, A

Tukey's HSD (honest significant difference) test showed that ($p \leq 0.1$):

- among the regions examined, Norway spruce natural regeneration in the Kaszuby Lake District and in the Augustów Forest differed between each other with respect to the current height increment, the last whorl radius, slenderness, the number of trees per unit area, the light factor, regeneration quality and the average annual growth of the last whorl;
- the populations observed in Warmia and the Augustów Forest differed with respect to the age of reaching the height of 1.3 m, the basal diameter and its average increase;
- tree slenderness was the only feature that distinguished Norway spruce natural regeneration in the Kaszuby Lake District from that in the West Pomerania-Lake District.

In order to establish a set of features significantly differentiating natural regeneration observed in the regions studied, the discriminant analysis was performed with the use of the mean results from circular research plots concerning all the features of Norway spruce natural regeneration: 7 directly assessed and 8 calculated (index values) (table 4 and 5).

The analysed features (excluding: average regeneration age, regeneration quality and light factor, as well as environment/stand characteristics, such as: the soil type and light intensity) had a statistically significant ($p \leq 0.01$) effects on differences between the regions.

The discriminant analysis of all the regeneration features under the study, treated jointly, exposed 4 features (tab. 7) that strongly differentiated the regions studied.

The first discriminant function (height) explains over 47.7% of the inter-group variance, and the second (basal diameter) – 38.5%. Overall, both discriminant functions explain over 86.2% of the inter-group variance. Both functions are significant (chi-square test 199.63 and 113.32, $p < 0.001$ in both cases). The first discriminant function distinguished primarily the region of the Augustów Forest and the Kaszuby Lake District from other regions, while the second discriminated the region of Warmia, the Kaszuby Lake District and the Augustów Forest (descending order). Both the first and the second function did not distinguish the region of the West-Pomerania Lake District from other regions. The spatial distribution of the regions determined on the basis of the first and second discriminant function and using the discussed variables is illustrated in Figure 6.

The Kaszuby Lake District and the Augustów Forest are clearly distinct regions, in terms of the average values of all the examined regeneration features, in contrast to other two regions studied, where those are analogous and none of the regions can be definitely distinguished. On the other hand, Warmia and the West-Pomerania Lake District taken together, differ from the region of the Kaszuby Lake District, as well as from the Augustów Forest.

4. Discussion

The study addressed the issue of the influence of geographical location on the features of Norway spruce natural regeneration in Poland's northern regions. Site soil and climatic factors are directly associated with the geographical location. Seeing that the obtained results demonstrated regional diversity in the studied features of Norway spruce natural regeneration, it can be presumed that climate had a decisive effect on the natural regeneration, as soil conditions on the study plots established in the regions were analogous.

The study areas were located in 2 natural-forest regions: the Baltic Region (I) (study plots established in the West Pomerania Lake District, the Kaszuby Lake District, and a considerable part of Warmia) and the Mazury-Podlasie Region

Table 7. The features of regeneration most of all differentiating the regions (standardized variables)

Feature of regeneration	Wilks' Lambda	Partial Wilks' Lambda	F to remove	*p*-value	Tolerance	1-Tolerance (R-sqr.)
Height	0.0756	0.7637	6.4968	<0.001	0.0113	0.9887
Basal diameter	0.0726	0.7955	5.3973	0.002	0.0129	0.9871
Mean height increment	0.0838	0.6887	9.4927	<0.001	0.0092	0.9908
Mean basal diameter increment	0.0856	0.6748	10.1213	<0.001	0.0135	0.9865

(II) (study plots established in the eastern part of Warmia and the Augustów Forest).

The Baltic Region is characteristic of the comparatively higher sum of annual precipitation (including the growing season), which affects clearly better conditions for the growth of Norway spruce natural regeneration, in contrast to the Mazury-Podlasie Region, with significantly lower annual precipitation and mean temperature. Not without significance is also the fact that the Baltic Region is located at a higher altitude (the Kaszuby Lake District spreads at 200–300 m above sea level), and its soil-site conditions are similar to those in the areas within the lower montane zone located in southern Poland, where Norway spruce has optimal growth conditions (Modrzyński 1999).

Our results showed that the Augustów Forest differed the most from other regions studied, and the majority of Norway spruce features examined here showed the lowest values. Also, the Kaszuby Lake District was different, and here, the majority of Norway spruce biometric features showed the highest values. In comparison with the latter, significantly lower values were obtained for Norway spruce natural regeneration located towards the west and the east (the West-Pomerania Lake District, Warmia, respectively). These results are only partly consistent with the statements of other authors that better growth of Norway spruce stands is observed in the areas located west of the border of Norway spruce range (Karpiński 1971, Żybura 1990, 1993).

Among others, the fact that research was carried out at the time when in the Augustów Forest, the harvesting age for Norway spruce was raised that could possibly have the disadvantageous effects on the natural regeneration of Norway spruce. The impediment of the increment of the regeneration height and a decrease of its quality could be due to neglecting opening-up cuttings for some time.

Our research also shows that in terms of the local population of Norway spruce, the Kaszuby Lake District is a largely separate region. This may indicate an advanced process of adaptation of Norway spruce population to the specific conditions of this region, as according to Kowalski and

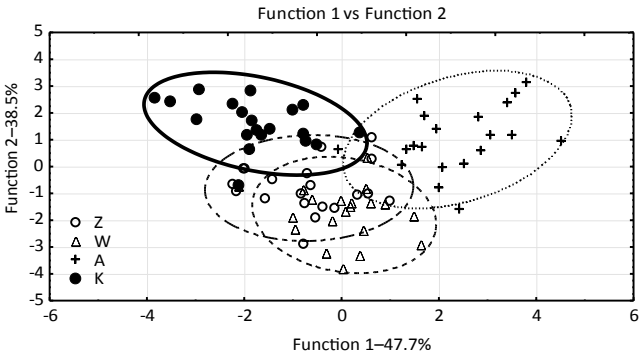

Figure 6. Discrimination of the regions carried out based on means from all features of the regeneration

Włoczewski (1972) and Modrzyński (1989, 1995), Norway spruce has a great potential for ecological adaptation. It is also a confirmation of the insular presence hypothesis of Norway spruce (most likely the north-eastern provenance) in this region.

Genetic studies carried out by the Institute of Dendrology of the Polish Academy of Sciences in Kórnik (Lewandowski et al. 2012a, 2012b, 2014), with regard to the origin of Norway spruce in the northern parts of Poland (including the Kaszuby Lake District) show that in contemporary forest stands, there occur Norway spruces of north-eastern, Carpathian and Alpine origins (with diverse percentage shares). A characteristic feature of this phenomenon in Pomerania is the fact that the share of Norway spruce of north-eastern origin decreases towards the west. In the stands located to the west of the Kaszuby Lake District, no more than Norway spruces of Carpathian or Alpine origin were found – except for the natural occurrence of Norway spruces from the north-eastern range observed in the Forest District Karnieszewice, near Koszalin (Latałowa, van der Knaap 2006; Lewandowski 2016 – personal communication).

In the area of, for example, the Forest District Kartuzy, the shares of Norway spruce of different origins were: Alpine – 59%, Carpathian – 30%, and north-eastern – 11% (Le-

wandowski et al. 2014). Potentially, Norway spruce could naturally enter this area, though its densities were somewhat low or else it occurred in patches.

Adaptation of Norway spruce population from the Kaszuby Lake District to local conditions is also confirmed by the results of the genetic evaluation of the value of Norway spruce from the areas beyond the accepted natural range in Poland, carried out by Giertych (2000). As said by this author, Norway spruce populations from the areas of Połczyn Zdrój and Szczecinek (West Pomeranian Lake District) are flexible and generally grow well outside the areas of their origin. On the other hand, the population from the area around Kartuzy usually grows much worse outside the region of the Kaszuby Lake District, which is also confirmed by the results of research conducted by Matras (2002).

5. Conclusions

Based on the results obtained and their discussion, the following review and conclusions were formulated:

1. The diversification of the regions studied was influenced the most by the following features of Norway spruce natural regeneration: height, basal diameter, average height increment and average basal diameter increase.

2. In northern Poland, the biometric features of Norway spruce natural regeneration with the strongest effects on regional differences change along the east-west axis, and generally, these changes show increasing trends in the west. However, this is mainly due to the clear superiority of the Kaszuby Lake District region. The values of the regeneration features examined in the West-Pomerania Lake District are evidently lower than those in the Kaszuby Lake District; however, they are higher than those observed in Warmia and the Augustów Forest

3. In comparison with other studied regions, the natural regeneration of Norway spruce in the Kaszuby Lake District was characterized by the highest trees with the greatest DBH, as well as the highest average height increment and the average current height increment. The regeneration quality was alike in all the regions under the study.

4. The natural regeneration of Norway spruce in the Kaszuby Lake District clearly differed from other regions. The distinction of Norway spruce population in the Kaszuby Lake District, notwithstanding internal genetic variability due to Norway spruce origins, deserves to be emphasized, as it indicates that this population has undergone a process of ecological adaptation to local conditions. This fact should be taken into account for the Norway spruce cultivating in this region.

5. Due to high dynamics and good quality, Norway spruce spontaneous natural regeneration in the Kaszuby Lake District should be supported by forest management activities appropriate for this species.

Conflict of interest

The authors declare the lack of potential conflicts.

Acknowledgements and source of funding

The study was partially financed by the Scientific Research Committee under a supervisory grant: 6 P04F 068 21.

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Authors' contribution

M. Sz. – literature review, methodology, data collection and processing, manuscript preparation; J. M. – concept and control of research, participation in interpretation of the results, manuscript preparation; M. St. – assistance in field work, preliminary evaluation of data and manuscript preparation; M.M., K. M. – assistance in field work and preliminary data preparation.