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The growth of seven *Abies grandis* provenances in the climatic conditions of the Polish Carpathian Mountains

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Abstract: The introduction of foreign tree species to new areas facilitates an increase in species biodiversity and possibilities for growth of tree stands. Many years of research related to survival rate, basic growth features and evaluation of a sensitivity to climatic conditions of a new habitat is necessary to achieve a successful introduction. The paper presents the results of the research on the adaptation of grand fir to the climatic conditions in the provenance trial located in the lower montane forest belt. The dendroclimatic research has concerned the offsprings of 7 grand fir provenances originated from North America. A total of 24 trees from each provenance were selected and two cores from each tree were taken. Principal component analysis of tree-ring widths was used to classify the provenances. The climate elements described by PC1 and PC2 were identified on the basis of bootstrap correlation function. Survival rate, height and diameter at breast height of trees were also analysed. The features of the studied provenances showed significant differences. The variation of the inter-provenance survival rate and the increase in tree height of particular provenances were determined principally by the genotype. Grand firs trees from Region I exhibited superior survival rates and better dynamic increases in tree height. The variability of these two features had the character of clinal variation because they primarily depended on the elevation and the latitude of the maternal tree stands. Two groups of provenances which were connected with the regions of their natural distribution were characterized on the basis of the features of the short-term rhythm of the radial increments. The provenances of two specific groups revealed different sensitivity to temperature, rainfall, humidity and sunshine. The greatest effect on the variation of radial increments had been produced by the moisture and pluvial factors whilst the solar factor had produced the least effect on it. The air temperature made also a relatively high contribution to their radial increments. Grand fir trees from the Salmon River provenance in British Columbia provided the best trees from the cultivation point of view. The provenances from Vancouver Island and the western slope of the Cascadian Mountains in Washington State have been regarded as the best for introducing and acclimatising to the conditions of the Carpathian Mts.

Keywords: grand fir, dendrochronology, dendroclimatology, survival, growth parameters

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Introduction

The observed climate changes have promoted debate about increasing the introduction of tree species which may more readily adjust to the changing climatic conditions and would not threaten native species. The pro-ecological model of forest management in Poland has significantly limited this process. It should be emphasised that Poland, like the rest of Europe, belongs to an area in which there is a relatively limited number of native tree species. Non-native species show a greater growth potential than native species. It must be stressed that the successful cultivation of a specific species in a given climatic region is no guarantee that it will be successful elsewhere. Data related to the survival and basic growth features of non-native species in a given climatic region can be obtained from the provenance trials and provides crucial information on the likely success of their introduction and acclimatisation. These trials aim at comparing the features of trees originating from different regions in homogeneous habitat conditions on a specific site. In this way the provenances which showed the best survival and reached the best growth parameters in specific soil and climatic conditions are determined. The findings of inter provenance variations enable an evaluation of the adaptation of non-native species to the local habitat conditions to be made (Matyas, 1997). Simultaneously, information about the influence of the environment and genotype on the features of particular provenances is obtained. Some research has indicated that environmental components and genotype influence the density of the wood (McKimmy & Nicholas, 1971). Other research suggests that these features depend mainly on the genetic factor (Isaeva & Cherepnin, 1988) or the influence of the environment (Rink & Thor, 1973).

The introduction of non-native tree species increases the biodiversity of species and the growth potential of stands. Provenance trials should last for many years to enable trees to go through most of their development phases and experience extreme weather conditions. The response of trees to the local climatic conditions is the main indicator of the species plasticity and its ability to adapt (Fritts & Swetnam, 1989).

In addition to Douglas-fir, which has become a permanent component of European forests (Kleinschmit & Bastien, 1992), grand fir has the possibility of enrich the forests of Europe. Grand firs from the Western part of the United States and Canada were introduced to Europe in the first half of the 19th century (Bellon et al., 1977). Initially, they were planted, mainly as decorative trees, in parks and gardens. Forest cultivation of this species was first started at Prussian experimental stations in Germany at the turn of the 19th and 20th century. *Abies grandis* was introduced on a large scale in other Western European countries after the Second World War. The results of many studies indicate the successful introduction of the species in Europe, e.g.: in France (Lacaze, 1967), Britain (Lines, 1974), Belgium (Nanson et al., 1986), Norway (Magnussen, 1986), Ireland (O'Driscoll, 1986), Böhmen (Vančura, 1986), Germany (Dong et al., 1993; Kleinschmit et al., 1996), and in Ukraine (Krynickyj et al., 1999). In Poland research on the adaptability of grand fir was initiated by The International Union of Forestry Research Organisations in 1976 (Bellon, 1990). Significant differences in the climatic and soil conditions on the areas of its natural habitat, in addition to its many races (Müller, 1935, 1936), and provenances (Kleinschmit, 1986; Steinhoff, 1986; Krynickyj et al., 1999) necessitate selecting populations which are best suited for the habitat conditions in the various geographic and climatic areas of Europe.

The tree-ring width is one of the basic characteristics of timber as it provides information about the rate of increase in the thickness of a tree and dendrochronological methods enable the periodic variation and the responsible factors to be determined. Such methods have been used successfully in provenance trials (Oleksyn et al., 1998; Savva et al., 2002, 2003; Eilmann et al., 2013; Wilczyński & Kulej, 2013). The widths of tree-rings are regarded as the measure of a tree's response to the pressure of various environmental factors, including climatic conditions (Fritts 1976; La Marche, 1978; Fritts & Swetnam, 1989). The short-term variability of tree-ring widths indicates the adjustment of the tree to the local climatic conditions, which determine the survival and the growth possibilities. It must be emphasised that the rate of growth of trees and the timber features are influenced by the habitat conditions, the genotype and the tree's age (Zobel & Jett, 1995; Savidge, 1996; Savva et al., 2002; Carrer & Urbinati, 2004).

The research focused on the sensitivity of seven provenances of grand fir originating from the coastal and mountain regions of the western part of the USA and Canada to the climatic conditions existing at the lower montane forest belt of the Polish Carpathian Mountains. The differences in survival, height and diameter at breast height of the individual provenances were established. The identification of the climatic conditions which determine the radial growth was attempted. In addition, the features influenced by the habitat factors and those which were dependent on the provenance were established.

Material and methods

Study area

The four-year-old seedlings of 7 grand fir populations from North America in the provenance trial in

Krynica (Polish Carpathian Mts., 700 m a.s.l) in 1981 year were planted (Fig. 1). Three replicated plots were planted for each provenance. 100 seedlings were planted in each of 21 plots with 2×2 m spacing between individual trees. Prior to 2013 no trees were cut on the plots. Seven populations of grand fir from Regions I and II of its natural habitat as identified by Müller (1935, 1936) (Fig. 1) were studied. The maternal stands of the provenances grew at altitudes from 25 to 1,500 meters above sea level (Fig. 1, Table 1). Four provenances from the coastal area and western slopes of the Cascadian Mountains were representative of Region I, which extends from British Columbia to central Oregon. This region provides the optimum conditions for the growth and development of grand fir. The annual average temperature is 7°C in the north and 10°C in the south with an average total annual precipitation of 3000 mm (Eilmann et al., 2013). Region II, which includes the eastern slopes of the Cascadian Mountains in Washington and Oregon states was represented by three provenances. The region is characterised by a more severe mountain climate and very low precipitation. Grand fir grows more slowly in this region and mature trees are smaller than those in the coastal region. In both regions precipitation occurs mainly in the cool part of the year. The vegetation period is characterised by low precipitation and relatively high air temperatures.



Fig. 1. Location of origin provenances of grand fir planted in Poland (grey dots). R I and R II – two regions distinguished by Müller. TP – indicates the location of the provenance trial in Krynica

Code of provenance	001	003	005	040	007	016	020
Region of provenance origin	Ι	Ι	Ι	Ι	II	Π	II
Name of provenance	Buck Creek	Indian Creek	Bear Mountain	Salomon River	Eagle Creek	Santiam Summit	Crescent Creek
Latitude N	48°15'	48°04'	47°59'	50°20'	47°39'	44°26'	43°28'
Longitude W	121°21'	123°38'	123°02'	125°56'	120°30'	121°52'	121°57'
Elevation (m)	400	140	825	25	1200	1400	1375
Survival (%)	53.5	59.3	50.5	53.5	49.5	41.3	19.7
DBH (cm)	21.3	21.2	22.3	22.2	21.4	20.6	22.8
Mean _{TRW} (mm)	3.99	3.82	3.89	3.99	4.02	4.00	3.83
High (m)	17.5	17.3	18.8	19.3	17.2	14.8	15.2
AC1 _{TRW}	0.65	0.72	0.72	0.73	0.65	0.66	0.61
AC1 _{IND}	0.08	0.32	0.10	-0.16	-0.03	-0.20	-0.13
MS	0.23	0.19	0.21	0.21	0.23	0.21	0.25
r _{bt}	0.65	0.59	0.65	0.55	0.61	0.63	0.62
EPS	0.98	0.97	0.98	0.97	0.97	0.98	0.98
SNR	45	36	44	29	38	42	40
	CL 1				CL 2		
R ² TMP	34.7%				30.9%		
R ² PRE	39.4%				39.6%		
R ² SD	8.5%				11.8%		
R ² RH	47.9%				40.0%		

Table 1. Sample information of grand fir provenances and dendrochronological parameters

DBH – diameter breast height, AC1 - autocorrelation of 1 order of tree-ring width chronology (TRW) and indexed chronology (IND), TRW – mean tree ring width, MS - mean sensitivity, TRW – tree-ring width chronology, IND – indexed chronology, r_{bt} - mean correlation between individual chronologies; EPS – expressed population signal, SNR - signal-to-noise ratio, CL - cluster chronology, R² – multiple determination coefficient, TMP – temperature, PRE – precipitation, SD – sunshine duration, RH – relative humidity.



Fig. 2. The climatic diagrams for the provenance trial in Krynica during the period 1981–2013. Average monthly values (thick lines), monthly maximum and minimum values (thin lines), mean annual values are given in brackets

In the Polish Carpathian Mountains the highest precipitation, temperature and duration of sunshine occur during the vegetation period. The relative humidity is at a minimum during this period because of the high temperature (Fig. 2). The monthly values of the climatic conditions vary significantly. For example, in the analysed period from 1982 to 2013 there were months in which there was no precipitation and others when it was many times greater than the multi-year norm (Fig. 2).

Sampling and data processing

24 trees from each provenance, that is 8 trees from each replicated plot, were selected for dendrochronological analysis. Two increment cores from each tree were taken at a height of one metre. All 168 sampled trees were dominant or co-dominant individual specimens without visible damage. The tree-ring widths were measured using a computer interfaced Biotronik - BEPD3 machine. The tree-rings were dated absolutely and rechecked using the COFECHA program (Holmes, 1983). The two series of tree-ring widths of each tree were averaged creating an individual tree-ring width chronology. The individual treering width chronologies were standardized using the ARSTAN program (Cook & Holmes, 1986) by fitting of the spline function and dividing the values of treering widths by the value of the fit curve for each year. Standardization reduces the non-climatic variances in tree-ring width chronologies (Cook et al., 1990). The standard chronology type (STD) was used because it retains low frequency variation desirable for analysis of long-term climate trends. It should be realised that the annual climatic changes influence the variation in radial growth from year to year and also have a long-term influence (Grissino-Mayer, 1995). These chronologies contain two types of variation and are frequently used in the analysis of the climate-radial growth relationship (Cook, 1990; Grissino-Mayer 1995; DeWeese et al., 2010). The 24 individual standard chronologies were averaged. Thus, the chronologies were developed for each provenance.

Statistical analyses

The short-term growth reactions of firs between 1982 and 2013 of each provenance were characterised using various indicators: MS – mean sensitivity (Douglass, 1920; Fritts, 1976); r_{bt} – mean correlation between individual indexed chronologies; EPS – expressed population signal; SNR – signal to noise ratio (Wigley et al., 1984; Briffa & Jones, 1990) and AC1 – autocorrelation of 1 order of tree-ring and indexed chronologies.

Growth patterns of grand fir provenances (chronologies of tree-ring width indexes) were explored with a principal components analysis (PCA) to assess the shared variance for the time period 1982–2013. The PC analysis transformed the indexed chronologies into a new set of variables - principal components (PC1 and PC2). Component loading plots for PC1 and PC2 were used to display the grouping of chronologies of grand fir provenances. PC1 emphasizes similar features of 7 chronologies and PC2 highlights their differences. The climatic elements described by the first two components were identified on the basis of correlation analysis of PC1 and PC2 scores with climatic parameters. For this purpose the bootstrap correlation function was calculated by the Dendroclim2002 software (Biondi & Waikul, 2004). This program uses 1000 bootstrapped samples to compute the correlation coefficients and to test their significance at the 0.05 level. The dependent variables were the scores of PC1 and PC2. The independent variables were the average monthly temperatures, total monthly precipitation, monthly duration of sunshine and the average monthly humidity for the climatic window from August of the previous year to September of the growth year. In this way the attempts were made to identify the climatic conditions which had a similar, or different influence on the radial growth of the fir provenances.

In addition, the cluster analysis was also used to group the grand fir provenances with regard to their response to temperature, precipitation, relative humidity and sunshine duration. In this case, the series of bootstrap correlation coefficients were grouped, which were calculated between the indexed chronologies of provenances and the monthly climatic variables for 14 consecutive months from August of the year prior to growth to September of the year of the treering formation. In both cases the Ward's agglomeration method and 1-r Pearson's distance were used. For the individual chronology groups the indexed chronologies and the response function were established (Holmes & Lough, 1999). The purpose of the analyses was to establish the influence of individual climatic conditions on the variation of the tree-ring widths on the basis of the multiple determination coefficients.

The climatic data from meteorological station situated 0.5 km from the experimental plot at the same height above sea level were collected.

The survival of trees of each provenance was determined on the basis of the number of live trees in relation to the number of seedlings planted during the establishment of the experimental plot. It must be noted that no trees were cut between 1981 and 2013. 45 trees were selected at random (15 from each replication) and their height determined. However, the diameter at breast height (DBH) was measured for every tree. The influence of genotype and the environment on the survival, height and diameter at breast height of trees from individual provenances were established using the ANOVA two-factor variance analysis.

Results

Growth features of grand fir provenances

The survival of individual provenances varied significantly and ranged from 19.7% to 59.3% as shown in Table 1. However, the average diameter at breast height varied only slightly and ranged from 20.6 to 22.8 cm, similarly the mean tree-ring width ranged from 3.82 to 4.02 mm and the mean height ranged from 14.8 to 19.3 m. The autocorrelation (AC1_{TRW}) of the chronology of tree-ring widths was very high, whereas the autocorrelation of the indexed chronologies (AC1_{IND}) was significantly lower.

In the indexed chronologies the long-term variability was reduced and the short-term variability was reinforced (Fig. 3). The mean sensitivity (MS) of the provenance chronologies ranged from 0.19 to 0.25, which is not considered to be a high value. However, the value of the indicator r_{bt} for the individual provenances was relatively high, ranging from 0.55–0.65. This validates the high homogeneity of the growth reactions of trees from individual provenances. This resulted in high values of the EPS (from 0.97 to 0.98) and SNR (from 29 to 45) (Table 1), which show the high representativeness of the chronologies and very strong climatic signal.



Fig. 3. Seven indexed chronologies of grand fir provenances

Short-term incremental rhythm of grand firs

In order to verify that their growth rhythm was determined by the climatic factor, the series of correlation coefficients (4 climatic parameters \times 14 months=56) were studied using the cluster analysis. These describe the model of climate – radial growth dependence for the seven provenances of grand fir (Fig. 4). The first cluster included provenances from Region I (001, 003, 005), the second cluster grouped provenances 007,



Fig. 4. The bootstrap correlation coefficients calculated between 7 indexed chronologies and monthly values of 4 climatic elements for 14 months – from the prior August (pA) to the September (S) of the current year



Fig. 5. The dendrogram of correlation coefficient series of 7 grand fir provenances as their response to climatic conditions. As variables, the series of bootstrap correlation values calculated between indexed chronologies and monthly temperature, precipitation, sunshine duration and relative humidity of 14 months were used (from prior August to current September) (see Fig. 4)

016, 020 (Region II) and 040 from Region I (Fig. 5). The results indicate that on the trial plot, grand firs of two groups show different sensitivity to temperature, precipitation, humidity and sunshine duration. The division of provenances into two regional groups shows that their genetically coded adjustment to different climatic conditions of the coastal and mountain region of the North America was responsible for their growth rhythm during the Polish provenance trial. The cluster analysis, however, did not enable the climatic conditions, or the seasons, which influenced the



Fig. 6. Loading plot of 7 indexed chronologies and first two principal components

annual variation in the radial growths of the grand fir provenances to be established. Therefore, the principal component analysis (PCA) was employed. The PCA results indicate that all indexed chronologies correlate very closely with the first principal component which accounts for 87% of the variance among all chronologies. The second component accounts for 6% of the variance among the chronologies and divides grand fir provenances into two groups (CL1 and CL2) (Fig. 6). The difference between them is relatively large, which shows that the rhythm of the changes in the radial growth of each provenance group is visibly different. The first group CL1 includes the mountainous provenances from Region II (007, 016, 020 and 040 from the northern part of Region I), their chronologies correlate positively with PC2. The second group CL2 is comprised of provenances from Region I (001, 003 and 005), their chronologies correlate negatively with PC2 (Fig. 6).

Radial growth-climate relationships

In order to identify the climatic elements described by the two components, they were correlated with the various climatic parameters. It was established that PC1 correlated (P < 0.05) with the precipitation and sunshine duration of the prior October, with the temperatures of the prior November and June of the current year and with the temperature, precipitation and humidity of the August of a tree-ring formation (Fig. 7). However, PC2 correlated (P < 0.05) with the temperature and precipitation of the prior September, the sunshine duration of January, the precipitation of March, the temperature, humidity and precipitation of July and with the air humidity of August and the precipitation of September in the growth year. PC1 and PC2, therefore, describe the various climatic elements. The exception was the air humidity of August in the year of the tree-ring formation with which both components correlated (Fig. 7).

The cluster analysis and the principal components analysis identified two regional groups of grand fir populations. For each group a cluster indexed chronology was created (CL1 and CL2) by averaging the provenance chronologies within each group. These chronologies were correlated with the various climatic parameters (Fig. 8), which verified the PC1 and PC2 analysis with the climatic parameters (see Fig. 7).

The first component, which integrates the chronologies, correlated (P<0.05) negatively with the precipitation and positively with the sunshine duration of the previous October (Fig. 7). Identical relationships were established in both cluster chronologies (Fig. 8). In addition, PC1 correlated significantly with the temperature of the previous November, similarly to the two cluster chronologies. Significant negative relationships between PC1 and the temperature of



Fig. 7. The bootstrap correlation coefficients (at the 95% level) calculated between PC1 (black bars), PC2 (white dots) and monthly values of 4 climatic elements for 14 months – from the prior August (pA) to the September (S) of the current year

June and August of the growth year were identified. The cluster chronologies also indicated strong negative relationships with the two climatic parameters. Moreover, PC1 indicated positive relationships with the precipitation and relative air humidity in August of the year of tree-ring formation, similarly to the two cluster chronologies (Fig. 7, 8).



Fig. 8. The bootstrap correlation coefficients calculated between cluster chronology (CL1 – thick line), cluster chronology (CL2 – thin line) and monthly values of 4 climatic elements for 14 months – from the prior August (pA) to the September (S) of the current year. The dots and squares show the significance at the 95% level

The results show that the pluvial and solar conditions of the previous October, the thermal conditions of the previous November and the current June and August and also the pluvial-humid conditions of the current August have a similar influence on the growth reactions in the studied provenances.

However, PC2, which influenced the growth rhythm of the grand fir provenances, correlated positively (P<0.05) with the temperature and negatively with the precipitation of the previous September (Fig. 7). These relationships are reflected in the correlation coefficients of the two cluster chronologies having the opposite sign for these parameters (Fig. 8). The negative correlation of PC2 with the sunshine duration in January was also established. (Fig. 7). This relationship provides a weak confirmation with the results of the cluster chronologies analysis (Fig. 8). Another factor with which PC2 correlated positively was the total precipitation in March. This was confirmed by the different strength of the relationships between the two cluster chronologies and this parameter. The significant negative correlation with the precipitation of March was established only in the chronology of the first group. The different strength of the relationships between the two chronologies and the parameters of temperature and humidity in the current July is reflected in the correlation between PC2 and these factors. The air humidity in August is an interesting aspect. This parameter correlates significantly with PC1 and PC2 (Fig. 7, 8). It is worth emphasising that both chronologies correlate positively with this factor, however, the chronology of cluster 2 correlates much more strongly. The last factor described by PC2 is the precipitation in September of the year in which the tree-ring is formed (Fig. 7). It has been established that the two clusters have a different response to this factor. This has been confirmed by the different correlation of the two chronologies with this parameter (Fig. 8).

The correlation analyses for PC2 and cluster chronologies with climatic parameters show that both groups have a different response to the thermal and pluvial conditions of the previous September, the solar conditions of January, the pluvial conditions of March, the thermal and humidity conditions of July, the humidity conditions of August and the pluvial conditions of September in the year of a tree-ring formation.

The response function analysis of the cluster chronologies shows that the air humidity and precipitation exerted the greatest influence on the variation of radial growths among the studied provenances, whereas the sunshine duration had the least influence. In addition, the air temperature had a relatively high contribution to the variance of their growth rhythm (Table 1).

Survival, growth parameters, and dendrochronological indices

The results of the variance analysis indicate that the survival of the studied provenances of the grand fir at the age of 37 varied significantly (P<0.001). In addition, it was established that this feature is



Fig. 9. Survival, growth parameters and dendrochronological indices of the 7 grand fir provenances growing on the provenance trial in Krynica with respect to the elevation and latitude of the provenance origin

significantly (P<0.001) influenced by the genotype and the environment. The provenances from Region I (Table 1) were best adapted to the conditions of the Carpathian Mountains. The firs originating from Indian Creek (003) in Washington State (59.2%) exhibited the best survival rate. The firs from Region II, especially Crescent Creek (020) provenance in Oregon State (19.7%) had the lowest survival rate.

As with the survival rates, it was only the origin that had a significant influence (P<0.001) on the height of the trees. The provenances from Region I, including the firs from Salmon River (040) attained the greatest mean height, whereas those from Santiam Summit (016) from Region II (Table 1) attained the lowest. The influence of the provenances' genotype on the variance of the breast height diameter, which is a function of the environment (P<0.01), was not established. The firs from Crescent Creek (020) had the largest diameter at breast height while the firs from Santiam Summit (016) had the smallest, both provenances were from Region II (Table 1).

The survival rate exhibited by trees from the studied provenances was strongly related to the geographical location of the provenance origin. It decreased with an increase in elevation and increased with the increase of the geographical latitude of the provenance origin. Similar relationships existed for the height of trees, however, such a relationship was not found for the tree diameter at breast height (DBH) (Fig. 9).

The values of the indicator r_{bt} show a curvilinear relationship with the elevation of the provenance origin with the maximum occurring with provenances at a similar elevation to that of the trial plot. However, the mean sensitivity (MS) decreased with the latitude and increased with the elevation of the original provenance (Fig. 9).

Discussion

Survival and growth parameters of grand fir provenances

The variance of trees is the result of the influence of the genotype and the environment. The environmental conditions in which the studied provenances grew were homogeneous. Therefore the variations in the tested provenances of grand fir can only be explained by the influence of the genotype and the local environmental conditions. The mean values of the analysed features can therefore be defined as the diagnostic or qualifying features of an individual provenance. The great variation in the survival rates of trees from the various provenances needs emphasising. The greatest rate of survival was displayed by grand fir from Indian Creek, Washington State,

(Region I), the lowest by those from Crescent Creek from Oregon State (Region II). The difference between the survival rates of trees from these two provenances was 39.5%. The high survival rate of grand fir from Indian Creek validates the findings of other researchers: in the Polish lowlands (Bellon, 1990; Bellon et al., 2005); in Germany (Rau & Weisgerber, 1986; Rau et al., 1990) and in Czech (Vančura, 1986). Szymański (1964) stated that the survival rate is a measure of the adaptability of a provenance, especially in difficult climatic conditions. The survival rate of the studied provenances shows a clinal character variation. This was verified by the strong decrease in the percentage survival rate with an increase in the elevation and its increase with the increase of the latitude of the provenance origin. The firs from Region I according to Müller were the provenances with the best adaptability. This was confirmed by earlier research results (Kulej, 2010).

The populations with the best survival rates show the lowest sensitivity to short-term climatic impulses. The studied provenances indicate significant variation in height, which was related to the latitude and elevation of the maternal stands. The mean height of provenances increased with an increase in latitude and decreased with the elevation. At the age of 37 the firs from Region I: Salmon River, Bear Mountain, Buck Creek and Indian Creek achieved the greatest height, whereas the provenances from Region II: Santiam Summit and Crescent Creek attained the lowest height. Similar results were obtained by the grand fir research undertaken in Czech (Vancura, 1986; Vančura & Beran, 1995), in Germany (Kleinschmit, 1986; Rau & Weisgerber, 1986; Steinhoff, 1986; Rau et al., 1990; Kleinschmit et al., 1996), in Ireland (O'Driscoll, 1986), in Belgium (Nanson et al., 1986), in Norway (Magussen, 1986), and in Canada (Xie & Ying, 1993). At the age of 37 the grand firs from Crescent Creek in Region II, Salmon River and Bear Mountain in Region I achieved the greatest diameter at breast height; whereas the provenances from Santiam Summit in Region II and Indian Creek in Region I had the smallest diameter. The mean diameter at breast height, contrary to the survival rate and the height attained, did not show a relationship with the provenance origin. The greatest homogeneity of short-term growth reactions was displayed by the provenances whose maternal stands grew at an elevation similar to that of the trial plot. However, the mean sensitivity of the trees of individual provenances to short-term environmental impulses, especially to the annual changing climatic conditions, decreased with the latitude and increased with the elevation of the provenance origin.

In addition to Douglas-fir, grand fir is one of the most important and productive non-native timber species grown in Europe (Lines, 1974; Aldhous & Low, 1974; Herman & Lavender, 1999). However, its volume increment is considerably lower than in North America (Stage, 1969; Pfister et al., 1977). The research of the same grand fir provenances conducted in Germany established that the provenances from the central and eastern slopes of the Cascadian Mountains and Idaho State (007, 016, 020) begin the process of lignification later than the provenances from Vancouver and the western parts of Washington and Oregon States (001, 003, 005). The lowland provenances (001, 003) are more sensitive to early frost whereas the provenances from the Cascadian Mountains (007, 016, 020 from Region II) appeared to be totally resistant to frost. In addition, the provenances 001 and 003 acclimated more slowly and less effectively than those from the Cascadian Mountains and they de-acclimated more quickly (Larsen, 1978). With reference to the drought resistance in Germany, the grand fir provenances from the eastern slopes of the Cascadian Mountains (Region II) appeared to be the least sensitive. However, the firs from the coastal part of Washington and Oregon States in Region I were the most sensitive to droughts (Scholz & Stephan, 1982). Positive results from the introduction of A. grandis were achieved in Norway (Magnussen, 1986) and in Holland (Kranenborg, 1986). This research indicates the high breeding value of the provenances from Washington State and revealed the low resistance to negative temperatures of the provenances from the southern coastal areas of Region I. Grand fir in Great Britain has the greatest productivity in Europe. However, significant differences in growth and resistance of individual provenances indicate the necessity of selecting suitable provenances for the intended local conditions (Lines, 1974). The research related to the increase in height of grand fir in Ukraine indicates its significant advantage over the native common fir (Krynickyj et al., 1999). The results of these research projects indicate the benefits of introducing grand fir to the forests of Europe.

Radial growth-climate relationships

An understanding of the climate-growth relationship of the two groups of provenances was obtained by comparing the results of the analysis of the relationship between the principal components, cluster chronologies and climatic parameters. On the basis of the indexed chronologies, which are characterised by a strong climatic noise, two groups of provenances were identified. The first group was composed of the provenances from Region I according to Müller (Bear Mountain, Buck Creek, Indian Creek). The second group was composed of the provenances from Region II (Eagle Creek, Santiam Summit, Crescent Creek) and the population of grand fir from Salmon River from Vancouver Island. Thus, the sensitivity of

the two regional groups of provenances to the climatic conditions of the trial plot was to a large extent dependent on genotype. A number of climatic factors to which both groups of provenances displayed different sensitivities were identified. The first was the thermal-pluvial factor of September of the year preceding the growth. The weather conditions of September influence the quantity and quality of the vegetative buds, that is the shoots and needles, which are the organs by which the substances needed for growth are created. In addition, the weather in September influences the quality of the buds of generative organs, the flowers and cones (Chałupka, 1975). An abundance of flowers and seeds has a negative influence on the increase of the tree thickness (Eis et al., 1965; Chałupka et al., 1975, 1976). The dependence of the radial growth on the abundance of seeds and cones was displayed most strongly in the southern sector of the stem, where there are usually most cones (Chałupka et al., 1975, 1976).

Therefore the conditions could have had a different influence on the number and type of buds on the firs from the both groups of provenances. The significant influence of the climatic conditions in the previous year on the growth of the grand fir was proved by Eis et al. (1965). They showed the negative relationship between the abundance of the cone harvest and the radial growth of grand fir. Additionally, Eis (1973) indicated that the abundance of blooms was influenced by the climatic conditions in the previous and current year. In the year of abundant flowering, the weight of newly-formed needles, their length and density on the shoots were reduced (Morris, 1951). It should be noted that a warm September led to a decrease in the radial growth of the firs from the warmer and lower areas (001, 003 and 005) in the following year. Such conditions favoured the lengthening of the trees' vegetation period, so that the trees could be threatened by the danger of early frost. In addition, excess sunshine during the winter could result in a physiological drought, which is dangerous for trees. It was established that the two selected groups of provenances displayed different sensitivity to this climatic factor. The sunshine in January had a beneficial influence, solely on the firs coming from the higher and cooler areas (007, 016, 020 and 040). The two groups had different sensitivity to snowfall occurring at the end of winter. Heavy snowfall led to a longer winter season and a shorter vegetation period, which had an unfavourable influence on the growth activity of the firs from the mountainous regions (007, 016, 020 and 040). These provenances also suffered from high temperatures in July in the year of tree-ring formation. Our research revealed the positive influence of heavy rainfall in September of the growth year on the radial growth of the firs from Region I (001, 003 and 005), which is very significant as it shows that the cambium of these trees is still active in September, providing there is sufficient rainfall.

In addition to the described differences in the studied grand fir provenances, many similarities in the climate-radial growth relationships were found. It was established that not only the genotype but environmental factors also influenced the variability of radial growth in all provenances. The studied grand firs reacted similarly to the solar and thermal conditions of late autumn in the year preceding the growth. It can be assumed that the shortage of light and low temperature in autumn caused more rapid hardening and lignification of the trees' shoots, regardless of their origin. In this way the danger of damage from early frost and general frost was reduced. The grand firs displayed a similar sensitivity to the temperatures of June and August in the year of a tree-ring formation. Excessively high temperature in these months was harmful for the trees of all provenances as they caused excessive evaporation and transpiration, which could result in a harmful water balance in the trees. In addition, the rainfall in August was beneficial for the growth in all firs because the heavy rainfall and humidity in August could stimulate the activity of their vascular cambium. The influence of the relative air humidity in August in the year of a tree-ring formation on the growth of firs is another interesting aspect as the growth reactions of the two provenances groups differed. This was confirmed by the high correlation of the second principal component with the relative humidity in August. However, it was established that this factor had a similar influence on the growth activity in all provenances as indicated by its high correlation with the values of the first component. The analysis of the chronology correlation for the two groups of provenances with this climatic factor leads to the conclusion that the growth of all populations indicated a positive correlation with the air humidity in August. However, the correlation was much stronger in the provenances from the higher and cooler areas of Region II. The shortage of rain in August had a negative influence on the radial growth of the provenances from both regions. The level of the water table frequently drops in August following the culmination of precipitation in July. This situation occurs in the studied area because August frequently experiences a significant shortage of rainfall, as shown in the climatic diagrams.

Conclusions

The provenances of grand fir from Region I and II displayed significant variations of the analyzed features in the habitat conditions of the Carpathian Mts. in Poland. The intra-provenance survival variability

and the height growth of the provenances are mainly determined by a genotype. In the conditions on a trial plot, the provenances from Region I of their natural habitat showed significantly better growth in height and a superior survival rate. The variability of the two features which differentiate the studied provenances is characterised by a clinal variability as it is dependent on the altitude above the sea level and the latitude of the provenance origin. The difference in the diameter at breast height of the studied provenances, at the current stage of research, is caused mainly by the local environmental conditions. The sensitivity of the individual grand fir provenances to the local climatic conditions of the trial plot displays, in addition, a spatial variability, which is related to the provenance origin. The first group, homogenous with regard to the climate-radial growth relationship, was composed of the provenances from Müller's Region I, which is characterised by a warm, ocean climate with high precipitation. The second group was composed of provenances from Region II, which is characterised by a severe, mountain climate with low precipitation and a wide temperature range. This group included provenance 040 from the Salmon River, the most northern natural habitat of grand fir, which has a cool climate and high rainfall. The two groups display different sensitivity to the climatic conditions of the trial plot situated in the lower level of the Polish Carpathian Mountains. At the current stage of research, Abies grandis can be regarded as a species with the huge potential for productivity in the conditions of the Polish Carpathian Mountains. However, a definite conclusion will require further research, if considering the age of the studied firs. In addition, for the introduction of grand fir on a larger scale, the appropriate selection of provenances must be made to ensure successful introduction and acclimatisation.

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