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The vulnerability of silver fir populations to damage from late frosts

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Abstract. The aim of the study was to determine the vulnerability of selected silver fir populations to damage from late frost in the climatic conditions of south-eastern Poland. To determine the vulnerability of apical and lateral shoots to damage caused by late frosts, we observed four test plots in 2009 and 2014, each containing progenies of selected seed stands. Our statistical analyses were based on a model incorporating the following variables: site, year, type of frost damage, population as well as the possible interaction between these variables. Significant differences between the populations were found in terms of their sensitivity to damage from low temperature occurring during the growth period. Furthermore, we indirectly demonstrated differences in the severity of late frost on the experimental plots, as well as the intensity and variability of late frost shoot damage. Based on these results, we divided the studied populations into two groups of low (EF, KRA1 and NAR) and high (LES2 and BAL2) sensitivity to late frost damage.

Keywords: adaptation, environmental stress, frost damage, testing program, *Abies alba*

1. Introduction

In choosing forest trees, testing the progeny of selected populations and genotypes in field experiments plays a key role in understanding their adaptive potential in the context of predicted and observed climate changes (Ledig, Kitzmiller 1992; Hanewinkel et al. 2012). Testing populations of forest trees helps to determine their adaptivity, direction and scope of change, as well as to evaluate the flexibility of the provenance in a variable environment (Aitken, Whitlock 2013). The earliest attempts to define the genetic variability of adaptive traits of forest trees based on experiments of Scots pine provenances were made by Philippe Pierre Andre de Vilmorin in the first half of the nineteenth century (see Langlet 1971). However, the first field experiments using a layout for provenance trials with replications were set up in Sweden in the first half of the 1930s (Langlet 1934). In Poland, provenance plots using a classic layout were established 30 years later. However, these experiments tested only part of the seed base (Barzdajn 2009). The oldest provenance plots of silver fir were established in Rogów in 1961 (Gunia 1986; Szeligowski et al. 2011). The results of measurements and observations conducted by Gunia (2006) and Bąk (2007) show a great degree of variability in the analysed population in terms of growth and qualitative characteristics.

The system of field trials involving different environmental conditions to test populations representing a wide range of natural species allows us to gain a better understanding of the character of the genetic variation of adaptive traits than under conditions of natural growth (Aitken, Hannerz 2001).

According to the premises of the program testing the progeny of forest trees, 37 progeny testing plots of 78 populations and 298 mother trees of silver fir from all four regions of testing were established in Poland as of 2015, covering the entire range of this species in the country (Fig. 1). In test region IV (south-east 2), one population set is being tested

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(progeny of 15 selected stands) in parallel with the national standard, regional standard and local standards (Fig. 2). The experimental layout includes four trial plots having different conditions of altitude, exposure and soil fertility (Fig. 3). The study subjects are assessed for their adaptation to adverse growing conditions, among other factors, which in the present experiment is expressed by a reduced susceptibility to bud and needle damage due to freezing temperatures. The results presented are among the first on the assessment of the sensitivity of firs to late frosts. The testing program focused on quantitative traits (Sabor et al., 2004) in studying the adaptation of the progeny of selected seed stands and mother trees to different growth conditions. For this reason, the field trials assess only spring bud burst, whereas susceptibility to frost damage is assessed only in the event of its occurrence. Artificial freezing tests combined with their verification in field trials have not been included in the testing program, even for such a low temperature sensitive species as silver fir (Dolnicki 2003). The location of the silver fir progeny test plots in south-eastern Poland takes into account the risk of frost in mountainous areas because of the configuration and cover of the terrain (Koźniński 1974). This was confirmed by the periodic occurrence of late frosts at all test plots.

Studies on silver fir conducted to date were mainly concerned with learning about the physiological mechanisms of acquiring frost resistance and how this changes over time (Dolnicki 2003; Sarvaš 2004). The issue of the variability in a silver fir population of its susceptibility to damage from late frosts is still insufficiently explored (Ivankovic et al. 2007). The aim of this work is to select populations of silver fir that can best adapt to the growing conditions of south-eastern Poland and are characterised by a significantly higher resistance to late frosts in their first years of growth.

2. Materials and methods

The tested progeny of selected fir stands represent populations from eight districts of the Regional Directorate of State Forests in Krosno (Table. 1). The trial plots were established in 2009 in the districts of Cisna (CIS) – N49°09’60’’, E22°27’57’’; Komańcza (COM) – N49°22’82’’, E22°00’97’’; Bircza (BIR) – N49°38’24’’, E22°29’34’’ and Lesko (LES) – N49°29’51’’, E22°17’36’’ (Fig. 2), each with an area of 225 m^2 in a randomised block design with four replications. All experimental plots were established under the cover of European larch planted two years earlier. Habitat conditions at the test plots are varied (respectively: CIS – LGśw, COM – LGśw, BIR – Lwyżśw LES – Lwyżśw), but meet the trophic requirements of the test species. In terms of regionalisation, the natural-forest areas are situated in the Carpathian region, in the mesoregions of the Przemyskie Uplands (BIR), Dukla (COM), the Low Bieszczady (LES), the High Bieszczady (CIS) (Zielony, Kliczkowska 2012). Seedlings with a covered root system (1.5 / 1.5 K) were used to establish the crop and were planted in 1.5 × 1.5 m^2. Each population was represented by 400 seedlings (100 for each replication).

Table 1. Characteristics of tested populations

Population ID	Forest Base Material	Regional Directorate of State Forest	Forest District	Provenance region
BAL2	11626	Krosno	Baligród	806
BIR1	27146	Krosno	Bircza	804
KRA1	11270	Krosno	Krasiczyn	804
KRA2	11271	Krosno	Krasiczyn	804
LES1	30320	Krosno	Lesko	806
LES2	30326	Krosno	Lesko	806
LES3	30327	Krosno	Lesko	806
LES5	30329	Krosno	Lesko	806
LUT1	30205	Krosno	Lutowiska	806
LUT2	30212	Krosno	Lutowiska	806
LZD	MP/2/45114/06	Kraków	LZD Krynica	803
NAR	10995	Krosno	Narol	606
RYM1	36145	Krosno	Rymanów	806
RYM2	36146	Krosno	Rymanów	806
STU	10691	Krosno	Stuposiany	806

Late frosts occurred twice (in 2009 and 2013) in the seven years since the tested crops were planted, causing damage to the apical and lateral shoots of the fir. Variability in the degree and nature of the damage was observed in terms of both the experimental plots as well as the tested populations. The type of damage was determined immediately after the frost occurrence. A three-degree scale was used to assess damage during field observations to determine the extent of damage to the shoots (intact trees, damaged lateral shoots, damaged apical shoot). In this study, we analysed the observations of damage to the lateral shoots and apical shoot.

In order to determine the proportion of trees experiencing different types of damage, we determined the frequency of such damage for individual provenances. To determine the variation in the type of damage among the test plots and tested populations of fir, we used the general linear model, combining a cross classification with a hierarchical one (Oktaba 1980): plot × year × type of damage × population and the effect of nested blocks in the interaction of site × year:

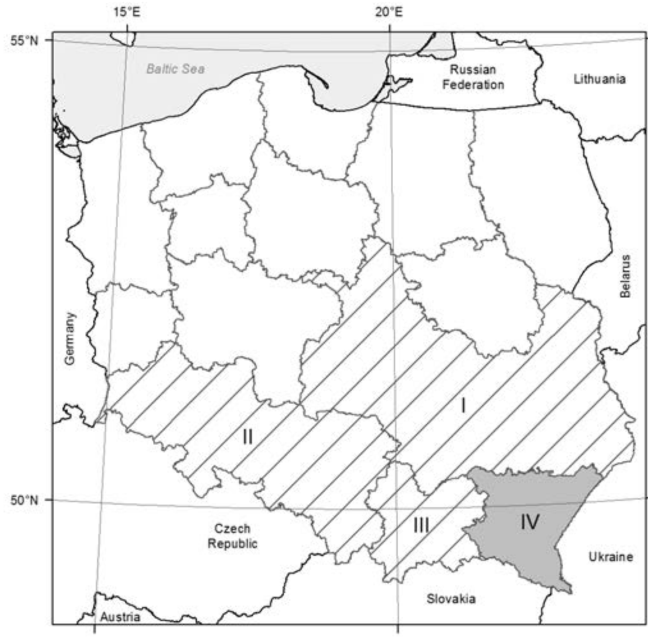

Figure 1. Testing regions for Selected Seed Stands of silver fir: I – Middle Eastern, II – South Western, III – South Eastern 1, IV – South Eastern 2

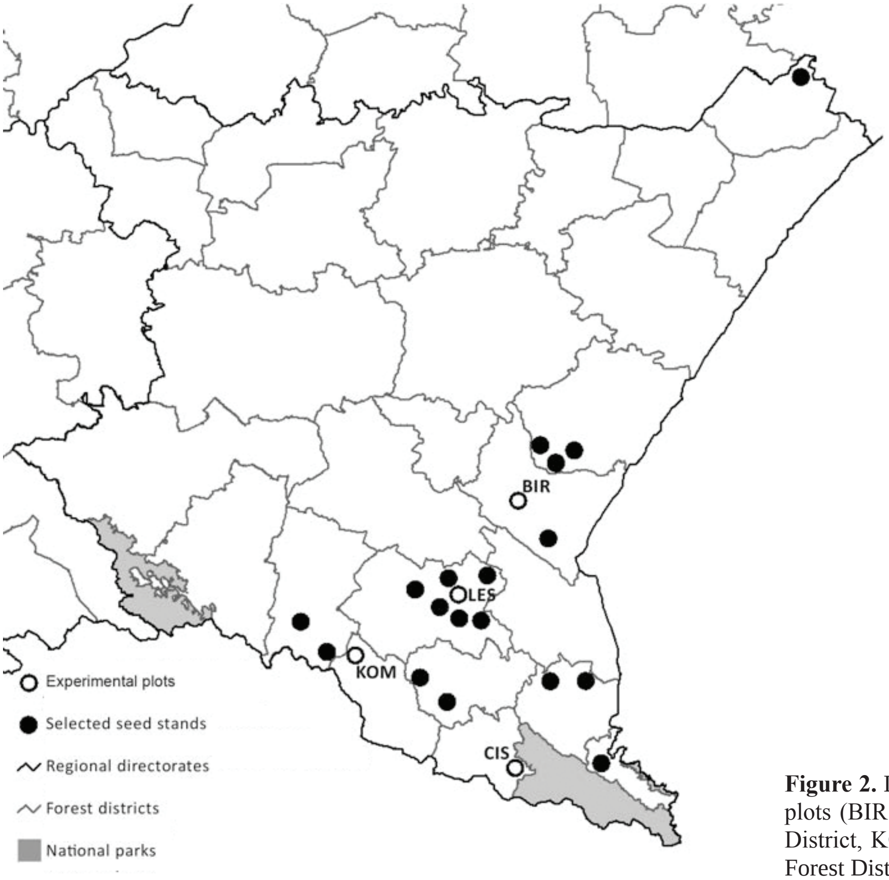

Figure 2. Location of tested population and experimental plots (BIR – Bircza Forest District, LES – Lesko Forest District, KOM – Komańcza Forest District, CIS – Cisna Forest District)

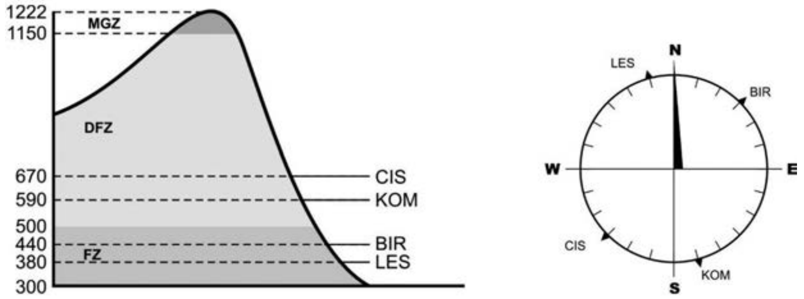

Figure 3. Elevation gradient and geographical directions of exposure of experimental plots. MGZ – mountain grassland zone, DFZ – lower mountain decidous forest zone, FZ – foothills zone. Other designation as in Figure 2.

$$F_{ijklm}=\mu + S_i + Y_j + FT_k + P_l + SY_{ij} + SFT_{ik} +YFT_{jk}+ SP_{il} + YP_{jl} + FTP_{kl} + SYFT_{ijk} + SYP_{ijl} +SFTP_{ikl} + YFTP_{jkl} + B_m(SY_{ij}) + E_{ijklm}$$

where:

F_{ijkm} – percentage of frost damage of site *i*, in year *j* and type of damage *k*,
μ – overall average,
S_i – effect of site *i*,
Y_j – effect of year *j*,
FT_k – effect of type of damage *k*,
P_l – effect of population *l*,
SY_{ij} – interaction of site *i* and year *j*,
SFT_{ik} – interaction of site *i* and type of damage *k*,
SP_{il} – interaction of site *i* and population *l*,
YP_{jl} – interaction of year *j* and population *l*,
FTP_{kl} – interaction of type of damage *k* and population *l*,
YFT_{ik} – interaction of year *j* and type of damage *k*,
$SYFT_{ijk}$ – interaction of site *i*, year *j* and type of damage *k*,
SYP_{ijl} – interaction of site *i*, year *j* and population *l*,
$SFTP_{ikl}$ – interaction of site *i*, type of damage *k* and population *l*,
$YFTP_{jkl}$ – interaction of year *j*, type of damage *k* and population *l*
$B_m(SY_{ij})$ – effect of nested block *m* in the interaction, site *i* and year *j*,
E_{ijklm} – random error.

The analysis was based on data obtained from the Bliss transformation. Homogeneous groups were determined using Tukey's Honestly Significant Difference (HSD) test. Statistical analyses were performed using the GLM procedure of SAS (SAS Institute 2011).

3. Results

The analysis of variance confirmed significance differences in the rates of the occurrence of frost damage among the tested populations ($p = 0.002$), sites ($p < 0.001$), the years 2009 and 2014 ($p < 0.001$), and the second and third types of damage ($p < 0.001$). At the same time, the significance of the interaction was confirmed for: type of damage × population, type of damage × site, type of damage × year and site × year (in all cases $p < 0.001$). The analyses conducted also confirmed the significance of the interaction between type of frost damage and year of occurrence and the tested populations with the site, respectively: $p = 0.001$ and $p < 0.001$ (Table 2).

The analysis of variance demonstrated a significant difference in the frequency of the incidence of the second and third types of damage, which was confirmed in the majority of the tested populations. Only the LZD population (the national standard) was characterised by the same number of trees with damaged lateral shoots and apical shoot (Fig. 4). For most of the remaining tested populations, the third damage type (damaged apical shoot) was observed significantly more frequently than the second damage type (damaged lateral shoots). The difference in the frequency of damage types between the LES1 and NAR populations was not statistically significant.

The analysis of the frequency of the occurrence of both frost damage types observed in 2009 and 2014 showed a different trend for damage to the apical shoots and lateral shoots. The frequency of the second damage type (damaged lateral shoots) was similar in both late frost years for most of the tested populations. The proportion of damaged trees in 2009 was significantly greater than in 2014 only for the LZD population (the national standard). At the same time, the trees of the KRA1 population had the least frequently observed second damage type (Fig. 5). The opposite trend was found for the frequency of the third damage type (damaged apical shoot). All populations showed a significantly greater frequency of damage to the apical shoot from the late frost of 2009 compared to the 2014 frost. In the case of the 2009 late frost, the third damage type was least like to have been observed on the trees of the LZD population. The late frosts of 2014 most heavily damaged the LES2 population, but the difference in the frequency of damage to the remaining populations (except for LZD) was not statistically confirmed. In 2014, the frequency of damage to the apical shoot of the tested populations was more evenly distributed and no significant differences were found among populations.

Table 2. Analysis of variance

Source of variation	Sum of squares	Deegres of freedom	Mean square	F-statistic	p-value
Type of frost damage	6.58	1	6.58	367.09	<0.001
Population	0.62	14	0.04	2.47	0.002
Site	3.29	3	1.10	61.26	<0.001
Year	36.32	1	36.32	2026.32	<0.001
Type of frost damage × population	1.07	14	0.08	4.27	<0.001
Type of frost damage × site	0.84	3	0.28	15.6	<0.001
Type of frost damage × year	34.46	1	34.46	1922.28	<0.001
Population × site	0.81	42	0.02	1.07	0.352
Population × year	0.32	14	0.02	1.27	0.218
Site × year	3.3104	3	1.10	61.55	<0.001
Type of frost damage × population × site	0.93	42	0.02	1.24	0.145
Type of frost damage × population × year	0.80	14	0.06	3.17	0.001
Type of frost damage × site × year	3.75	3	1.25	69.69	<0.001
Population × site × year	0.31	42	0.01	0.42	0.999
Block (site × year)	1.46	24	0.06	3.39	<0.001
Error	13.23	738	0.02		

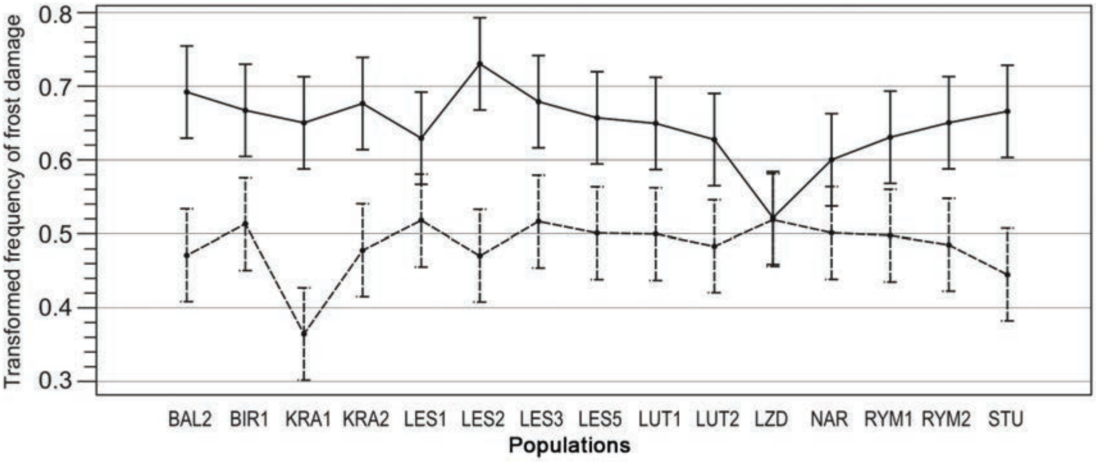

Figure 4. Transformed average for frequency of late frost damage of silver fir populations (both years); error bars means HSD Tukey; continuous line – 3rd damage type; dotted line – 2nd damage type.

4. Discussion

The risk of frost damage depends both on the increase in average annual temperature and the impact of climate change on the incidence (frequency and scale) of short-term temperature fluctuations (Beuker et al., 1998). Populations of conifer species growing in variable mountain environments exhibit greater interpopulation variation than populations growing in a more homogeneous environment (Aitken, Hannerz 2001), so the selection of mountain populations of silver fir for resistance to frost damage can probably improve their adaptive potential (Dolnicki, Kuchciński 2003). According Sabora (1999), the genetic value of silver fir from the Polish Carpathians region provides the basis for attempting to select a population that is best able to adapt to growing in mountainous areas characterised by the frequent

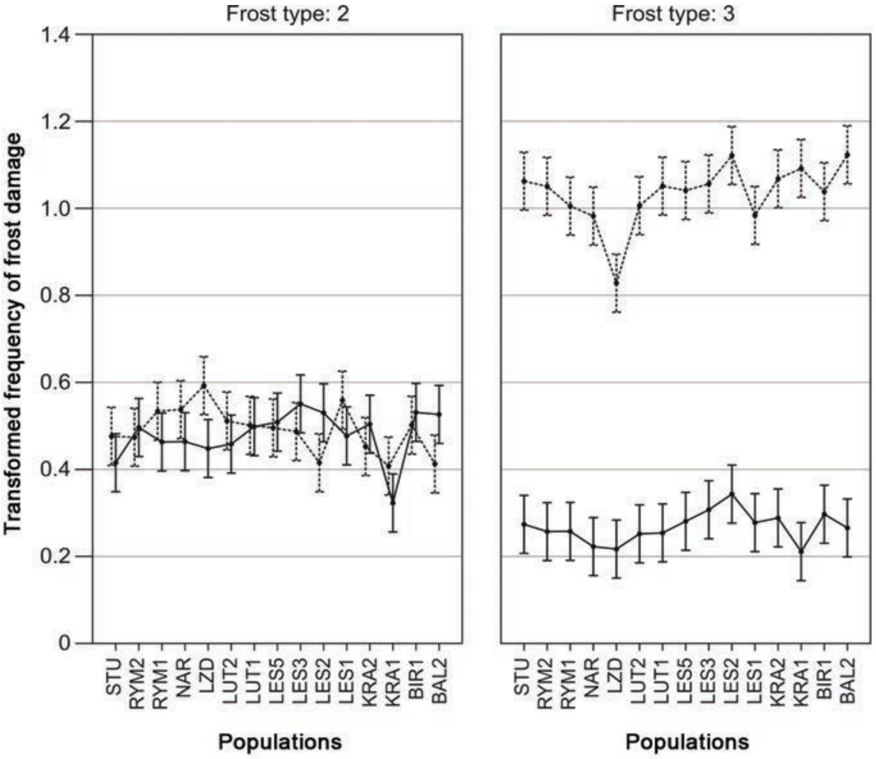

Figure 5. Transformed average for frequency of late frost damage (2nd damage type – side shoots, 3rd damage type – apical shoots) of silver fir populations in subsequent years; error bars means HSD Tukey. Continuous line means late frost in 2014; dotted line means late frost in 2009.

occurrence of late frosts. Assessing the adaptive potential of this species to environmental conditions differing from its place of origin is based on observations conducted in provenance areas and in experimental plots testing the progeny of excluded seed stands and mother trees (Barzdajn 2009; Kowalkowski 2013; Skrzyszewska 2013). So far, Poland has not conducted research on the population's genetic variability in terms of frost hardiness under controlled growth conditions. Past studies on the adaptive potential of silver fir populations from Poland examined characteristics providing indirect evidence of its susceptibility to damage, such as height, survivability and the phenology of bud development (Kempf, Sabor 2009; Skrzyszewska 2010; Szeligowski et al. 2011). Genetic variability of frost hardiness has been directly confirmed for other conifer species by studies based both on field trials as well as artificial freezing tests (Dormling 1982; Hannerz 1994; Simpson 1994; Aitken, Adams 1997; Beuker et al. 1998; Dolnicki, Kraj 1998; Andersson, Fedorkov 2004; Langvall 2011). The results of these studies suggest that the silver fir also has an adaptive potential, conditioned genetically, of resistance to tissue damage caused by periodic frosts during the growing season. The temperature limit, below which trees are damaged by frost, depends on many factors: the seasonal variation of the frost hardiness of trees, the duration of sustained frosts, sun exposure and the pace of temperature drops (Hannerz 1994). Bearing in mind the location of the experimental plots (Fig. 3), it should be assumed that these factors strongly differentiate the impact of late frosts on the type and intensity of the resulting damage. The lack of monitoring of local weather conditions does not allow the assumptions listed above to be directly verified and the use of multi-year meteorological data in mountainous regions does not provide the basis for determining the actual intensity of the frosts (Aitken, Adams, 1997). The variability of the intensity of late frosts related not only to the sites of the experimental plots, but also to the year in which they occurred. Evidence of this is seen in both the significantly different numbers of damaged trees as well as the proportion of trees with damaged lateral shoots and apical shoot (Fig. 5). A significantly lower proportion of trees with a damaged apical shoot in 2014 compared to 2009 could have occurred because of both a lower intensity of the frost in 2014, as well as a lower susceptibility of the trees to damage related to the acclimatization of the tested population. The diverse response of trees to frost could also have been influenced by the ambient conditions occurring prior to the growing season, responsible for the timing of bud development (Dormling 1982). Comparing the proportion of apical shoot damage among the tested populations in both analysed years allows the statistically significant differences between populations and between the years of frost to be observed. In 2009, the LZD population, serving as the national standard in the progeny testing program, was the most resistant to this type of damage. Susceptibility to frost damage at a juvenile age is one of the important characteristics that may affect the viability of the crops. Reduced susceptibility of LZD tree stand progeny to late frosts may indicate a high degree of adaptivity in this population. The interpopulation variation of frost hardiness observed in the first year of growth of the trees was greatly reduced after six years. It is true that the LZD population continued to be characterised by a low degree of apical shoot damage, but similar values were also reached by populations from locations which were the farthest away from the test sites: KRA1 and NAR (Fig. 5). This pattern is confirmed by the general theory characterizing local provenances as suboptimal populations (Matyas. Yeatman 1992). Perhaps this observed trend was associated with a later seedling bud burst of the LZD population in 2009, while in 2014, the remaining populations acquired resistance to late frosts, reaching a height above which the phenomenon of frost no longer affects the development of apical buds. During research into the frost hardiness of spruce, Danusevicius and his team (1999) observed a greater degree of frost damage in older trees. They explained this pattern by the greater surface of the assimilation apparatus in older (higher) plants leading to a loss of water.

The authors of this study believe that due to the ambiguity of Anderson and Fedorkova's (2004) results which discuss the influence of seedling height on susceptibility to frost damage, the study should take into account both quantitative traits as well as the adaptive potential of seedlings. For this reason, the test results of the progeny of selected silver fir tree stands and mother trees should also relate to both quantitative traits as well as their adaptive potential. Selection for adaptivity aims to define the best trees in terms of resistance to damage from frost and population, as well as to define the target environmental conditions for their use (Aitken, Hannerz 2001). The presented approach to selecting silver fir for mountainous conditions is justified due to the wide variability of environmental conditions.

5. Conclusions

- The population of silver fir in the south-eastern testing (second) region most susceptible to damage from late frosts in the first year of growth was the tree stand selected from the Forest Experimental Station (LZD) in Krynica.
- After six years of growth in the south-eastern testing (second) region, the progeny of tree stands selected from the Forest Districts of Krasiczyn and Narol (No. RLMP LP respectively 11270 and 10995) exhibited the lowest susceptibility to damage from late frosts.
- Assessing the course of a reaction to environmental stimuli of silver fir populations under mountain climate conditions characterised by frequent occurrences of late frost requires the continuous monitoring of microclimate conditions occurring at the experimental plots.

Conflicts of interest

The authors declare that no potential conflicts of interest exist.

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Authors' contribution

M.K. – data collection and its statistical analysis, preparation of the manuscript, coordinating the work; Sz.J. – initial preparation, data collection, text corrections; J.U. – statistical analysis of the data, text corrections; P.P. – data collection, text corrections; J.M. – concept and premises of the study; M.M. – cartographic editing, text corrections.

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