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Adaptive genetic potential of European silver fir in Romania in the context of climate change

G. Mihai, M.-V. Bârsan, A. Dumitrescu, A. Alexandru, I. Mirancea, P. Ivanov, E. Stuparu, M. Teodosiu, M. Daia

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Abstract. Five provenance tests with twenty-six European silver fir autochthonous populations were used in order to assess the response of populations to climate change. Height growth and diameter at breast height of trees at age 31 years were considered as response variables and eight climate variables as predictors. Climatic variables for the trial sites and for origin location of provenances were calculated from 1961 to 2010. The experiments revealed a large genetic variability within species level and a plastic response to climate change, which certainly has a genetic basis. The transfer to warmer climate has resulted in an increase of the provenances growth, in the trial sites situated on the lower vegetation layer. But growth is significantly influenced by mean annual temperature and annual precipitation of planting site and also by the differences in mean annual temperature, annual precipitation, monthly mean temperature in July and July precipitation between provenance site and test site. These are the climatic factors which should be associated with risk in case of the transfer of forest reproductive materials. The provenance origin should be especially considered if the species will be planted outside of its current climate optimum. The best provenances in terms of total height and diameter at 1.30 m came from origin climate close to site climate, small transfer distances. Based on growth response functions and RCP4.5 scenario, we could project the shifts in species distribution for 2050s and 2100s and identify vulnerable populations.
Keywords Silver fir, transfer functions, response functions, local adaptation, phenotypic plasticity, climate changes impact

Authors. Georgeta Mihai (gmihai_2008@yahoo.com), Alin Alexandru, Ionel Mirancea, Paula Ivanov, Elena Stuparu, Maria Teodosiu - "Marin Drăcea" National Institute for Research and Development in Forestry, Department of Forest Genetics and Tree Breeding, Bucharest, Romania; Marius-Victor Bîrsan, Alexandru Dumitrescu - National Meteorological Administration (Meteo Romania), Department of Climatology, Bucharest, Romania; Mihai Daia - National Forest Administration (RNP-Romsilva), Department of Forest Regeneration, Bucharest, Romania.
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Introduction

Researchers in the last decades have revealed a clear change in global climate, which cannot remain without effects on forest ecosystems. The most pessimistic climate change scenarios indicate increase of 4°C and higher in average annual air temperature until the end of the century, as well as changes in the rainfall regime and in the frequency of some extreme events (Salinger 2005). In Romania, the annual air temperature is projected to increase by 1.2°C during 2021-2050 compared to 1991-2020 (Cheval et al. 2017), and by over 2°C in 100 years, i.e., 1961-1990 vs. 2061-2090 (Bojariu et al. 2015).

There is a high degree of uncertainty regarding climatic influences on forest growth, health and stability. It is still widely accepted that phenology and species composition will be substantially modified, and the productivity and stability of forest ecosystems will be reduced. Forest species adapt on the long term by natural selection, migration to other habitats or phenotypic plasticity (Price et al. 2003). The real potential for adaptation depends upon the existence of a wide genetic diversity in tree population, upon the adaptive genetic variation, respectively. Genetic diversity, as the first level of biodiversity, offers the guarantee that forest species can survive, can adapt and evolve under the influence of changing environmental conditions.

Therefore, assessment of adaptive genetic potential of local species is essential for increasing forest productivity and stability in the context of climate changes. Proper choice of tree species and provenances with high plasticity are decisive for increasing the adaptability of tree populations to rapid environmental changes. The report of the European Forest Institute (EFI 2008) calls the regeneration strategy, including artificial regeneration, and forest tree breeding as one of the most important measures in a strategy to adapt forests to climate change. In addition, scientific evidence reveals that natural adaptation mechanisms of forest trees to buffer effects of climate change may not be sufficient to keep forests' ecosystem and economic functions intact (Savolainen et al. 2004, Jump et al. 2006, Aitken et al. 2008). The transfer of forest reproductive material adapted to environmental changes or the "assisted migration" is considered one of the measures that can facilitate adaptation of forest species and maximize forest productivity (Kremer 2007, Lindner 2000).

European silver fir is one of the most important forest tree species comprising 4% from national forest area in Romania and 7% from total regenerated area (NSI 2015). European silver fir is an extremely demanding species to site conditions (Șofletea & Curtu 2001), and also less tolerant to environmental changes than other species, like European larch, white pine (Weisgerber & Sindelar 1992, Rehfeldt 1994a, Ficko et al. 2011). It is a main component of mountainous forests in Romania and has manifold ecological, economical and soil protective functions. Both anthropic and environment pressures on European silver fir populations increased in the last decades and focus on adaptive traits has become a new priority.

In order to predict the impact of future climate change on tree phenotypes, the environmental and genetic effects need to be considered and quantified. It is generally hypothesized that tree populations are best adapted to their local climate conditions. Therefore, the best growth performance is expected at small climate transfer distances, whereas at larger climatic distances, trees are expected to perform poorly due to lack of adaptation (Kapeller et al. 2012).

To obtain climate-related responses different approaches can be used. In this study, we used two primary approaches: population transfer functions and population response functions. Both have been used to predict the response of forest trees populations to climate change, and to make recommendations about provenance selection as seed sources, breeding population establishment, and reforestation for uncertain

future climates (Schmidtling 1994, Aitken et al. 2008, Farjat et al. 2015).

The objectives of this study were: (1) to examine the genetic variability and patterns of adaptation of European silver fir populations, (2) to develop models to predict the adaptability of populations to climate changes, (3) to determine the potential impact of the climate change on tree growth, (4) to provide practical information for the use and transfer of forest reproductive material in Romania.

Materials and methods

Genetic material and experimental design

In 1980, seven field trials were established with 6-year old seedlings from 26 European silver fir autochthonous populations. Two of the field trials exhibited poor survival and could not be continued beyond age 20 years. Therefore, only five trials were considered in this study. The trials were established in different geographic regions, two of them (Bautar and Domnesti) being located outside of the natural range of species in Romanian Carpathians, in the mountain beech layer, in climatically warmer sites and three within the natural range, in the mixed mountain layer. The tested populations are from seven geographic regions and nine sub-regions respectively, which were defined as provenance regions for European silver fir in Romania (Parnuta et al. 2012). Locations of the field trials and of the provenances are presented in Figure 1. In all sites the field layout was a randomised square lattice with 4 replications and 25-tree per plots at 1.0 m × 2.0 m spacing.

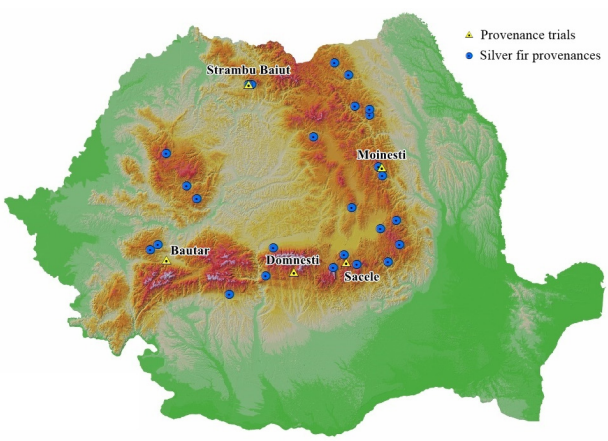

Figure 1 Location of European silver fir provenances and the comparative trials

Data analysis

For analyses we consider the height growth (H31) and diameter at breast height (D31) of trees at age 31 years as response variables. Height and diameter growth can be considered adaptive traits because they are under natural selection more than other traits and also have high heritability (Mihai et al. 2014, Mihai & Mirancea 2016).

Climatic conditions for the trial sites and the origin location of provenances were represented by four temperature variables: the annual mean temperature (TMA), the mean temperature of the coldest month (TM_{JAN}), the mean temperature of the warmest month (TM_{JUL}), the annual mean temperature during vegetation season (TM_{VEG}), and four precipitation variables: the annual mean total precipitations (PMA), the mean precipitation of the coldest month (PM_{JAN}), the mean precipitation of the warmest month (PM_{JUL}) and the annual mean total precipitation during growing season (PM_{VEG}). Also, the De Martonne index was calculated for each trial site (Marcu 1983).

For all analyses we used as basic data the monthly values of the climatic parameters. Climatic variables of the five trial sites were obtained by averaging the monthly observations for the period 1981-2010. Climatic variables of the location of provenances were calculated over a twenty year period,

from 1961 to 1980. The climatic variables were estimated using an improved version of the ROCADA daily gridded dataset (Dumitrescu & Birsan 2015), a state-of-the-art homogenized climatic dataset over Romania at a spatial resolution of 0.1° × 0.1°. In order to better assess the spatial variability of the parameters, this dataset has been spatially downscaled by spatial interpolation techniques (Dumitrescu et al. 2016, 2017) to a resolution of 1 km x 1 km. Future (projected) climatic data were derived from the Regional Climate Model (RCM) CLMcom-CCLM4-8-17 forced by the Global Circulation Model (GCM) MPI-M-MPI-ESM-LR run1 (http://mpimet.mpg.de/en/science/models/mpi-esm/), following the RCP (Representative Concentration Pathway) 4.5 Scenario (Thomson et al. 2011), at a spatial resolution of 0.11° × 0.11°. RCP 4.5 is a scenario that presents a moderate change in temperature and precipitation, stabilizing radiative forcing at 4.5 W/m^2 in 2100 without ever exceeding that value. The projected climate periods analyzed in this article are 2021-2050 and 2071-2100.

Statistical analysis

Analyses of variance were performed for each trial site and among sites using GLM procedure (SPSS programme version 19). The total amount of variation was divided into provenances, provenance regions, sites components, and interaction between them. All effects were considered as random except for the trials location, which was considered as fixed. Data for H31 and D31 were examined and found to conform to the normal distribution and homogeneity of variance assumption.

The ANOVA were performed as described in the following mixed model:

$$Y_{ijkln} = \mu + R_k + S_l + B_i + P_j + SP_{lj} + BP_{ij} + e_{ijkln}$$

where: Y_{ijkln} = response (H31 or D31), μ = the overall mean, R_k , S_l , B_i , P_j , SP_{lj}, BP_{ji} and e_{ijkln} are effect due to k^{th} region, l^{th} site, i^{th} repetition (block), j^{th} provenance, interaction due to l^{th} site and j^{th} provenance, interaction due to i^{th} repetition and j^{th} provenance, and random error associated with ijklnth trees.

Phenotypic plasticity of the provenances for each trait was evaluated by calculating the ecovalence and its variance. Ecovalence represents the contribution of each provenance to the total provenance x site interaction sum of squares. For this reason, provenances with low ecovalence values have smaller deviation from the mean across environments and are thus more stable. Ecovalences were computed by the following formulas (Wrike 1962):

$$W_i = \Sigma_j (X_{ij} - X_{i.} - X_{.j} + X_{..})^2$$

where: W_i - ecovalence of provenance i, X_{ij} - mean of provenance i in environment j, $X_{i.}$ - mean of provenance i across environments, $X_{.j}$ - environment mean, $X_{..}$ - overall mean.

Populations transfer functions were then developed using H31 and D31 as dependent variables and difference between the climate of each provenance location and of the trial site as predictors (Matyas 1994, Rehfeldt et al. 1999b, Andalo et al. 2005). Transfer functions are test site specific (Wang et al. 2010) and therefore we calculated them for each trial site. Because the relationship between growth and climate did not follow linearity (Rehfeldt et al. 1999a) we modeled the response to transfer using quadratic regressions. Three types of climate transfer models were constructed: (1) based on temperature, (2) based on precipitation and (3) both temperature and precipitation (Table 1). Since there were four temperature variables and four precipitation variables, a total of 136 models were developed. For variables selection, we used the stepwise selection method of SPSS software. The best models were selected based on R^2 coefficients.

In order to account the environmental effects of trial sites on the performances of tested provenances, the growth response functions were also developed. For modelling populations response functions the quadratic regressions were considered appropriate. Thus, the

Table 1 Types of quadratic models used

Transfer model	D_Tij variable	D_Pij variable
$Y_{ij} = \beta_0 + \beta_1 D_Tij + \beta_2 (D_Tij)^2$		
$Y_{ij} = \beta_0 + \beta_1 D_Pij + \beta_2 (D_Pij)^2$		
$Y_{ij} = \beta_0 + \beta_1 (D_Tij)^2 + \beta_2 (D_Pij)^2$		
$Y_{ij} = \beta_0 + \beta_1 D_Tij + \beta_2 (D_Pij)^2$		
$Y_{ij} = \beta_0 + \beta 1 (D_Tij)^2 + \beta_2 D_Pij$	D_TMA / D_TM_{JAN} /	D_PMA / D_PM_{JAN} /
$Y_{ij} = \beta_0 + \beta_1 D_Tij + \beta_2 (D_Tij)^2 + \beta_3 D_Pij$	D_TM_{JUL} / D_TM_{VEG}	D_PM_{JUL} / D_PM_{VEG}
$Y_{ij} = \beta_0 + \beta_1 D_Tij + \beta_2 (D_Tij)^2 + \beta_3 (D_Pij)^2$		
$Y_{ij} = \beta_0 + \beta_1 D_Tij + \beta_2 D_Pij + \beta_3 (D_Pij)^2$		
$Y_{ij} = \beta_0 + \beta_1 D_Pij + \beta_2 (D_Tij)^2 + \beta_3 (D_Pij)^2$		
$Y_{ij} = \beta_0 + \beta_1 D_Tij + \beta_2 D_Pij + \beta_3 (D_Tij)^2 + \beta_4 (D_Pij)^2$		

Note. Abbreviations: *Yij* - the mean *H31* or *D31* of the provenance i at site j, *D_Tij* - the difference between the temperature conditions at the location of provenance i and at the trial site j, *D_Pij* - the difference between the precipitation at the location of provenance i and at the trial site j.

populations' means for H31 and D31 were regressed on climate variables of the plantation sites.

To simulate potential impact of climate change on European silver fir populations, we used the obtained growth response function to model the future European silver fir distribution for the climate change scenario RCP4.5 for means of two time periods, namely 2021-2050 and 2071-2100.

Results

Genotype x environment interaction

Significant differences among provenances were found for growth traits at each trial site and across-sites. The analysis of variance across sites is presented in Table 2. The genetic variation among provenances was significant and represented 2-3% of total variance. The differences among regions of provenances were also significant both for H31 and D31.

The influence of site factor was greater than genetic factor and accounted for 78% (for H31) and 45% (for D31) of the total variance. These differences can be associated with climatic characteristics of the trial sites relating to temperature and precipitation or with other ecological factors not considered in this article. Thus, TMA and PMA have varied substantially among trial sites with 2.3°C temperature and 234 mm precipitation differences, respectively (Table 3). Also, the provenance x site interaction was significant, indicating that growth performances of provenances depend on environment of planting site and they could change with changing the site conditions. The highest growth performances occurred at Domnești and Băuțar trials situated in the mountain beech layer. Depending of values of De Martonne aridity index (Marcu 1983) the trial sites could be divided into two categories: wet (Moinești, Domnești and Băuțar trials) and very wet (Săcele and Strâmbu Băiuț trials).

Populations transfer functions

For modelling populations' response to climatic transfer among geographic regions we used growth traits as the response variables and climatic distances (difference in climate value between the origin location of a given provenance and the test site) as independent variables.

The transfer functions were calculated for each growth trait in each trial site. The best models were selected based on higher proportion of variance explained (R^2) and were presented in Table 4 and 5. Thus, the best models have included both temperature and precipita-

Table 2 Analysis of variance and genotype x environment interaction of growth traits at 31 years old

Source of variation	H31			D31		
	DF	s^2	% from total variation	DF	s^2	% from total variation
Region of provenance (R)	9	2.856*	1	9	6.412*	2
Provenance (P)	26	2.368*	2	26	4.209*	3
Site (S)	4	657.790***	78	4	359.901***	45
Repetition	3	21.169	2	3	27.905	3
Interaction P × S	104	1.744*	5	104	4.438*	14
Error	312	1.360	12	312	3.364	33

Note. The level of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 3 Geographic and climatic variables for European silver fir trial sites

Trials	Provenance region	Altitude m	TMA ^{0}C	TM_{JAN} ^{0}C	TM_{JUL} ^{0}C	TM_{VEG} ^{0}C	PMA mm	PM_{JAN} mm	PM_{JUL} mm	PM_{VEG} mm	De Martonne index
Băuțar	D2	650	6.20	-3.57	15.78	12.18	904.40	58.24	103.84	558.28	55.83
Domnești	C2	880	5.90	-3.64	15.73	11.96	853.14	37.65	119.78	577.77	53.66
Moinești	A2	815	5.42	-4.88	15.80	11.99	719.12	25.33	125.30	530.00	46.62
Săcele	B1	1225	3.91	-5.17	13.47	9.76	946.60	41.36	135.91	653.11	68.08
Strâmbu Băiuț	A1	890	5.62	-4.54	15.40	11.86	953.45	61.17	117.11	574.45	61.03

Table 4 The best climatic transfer models developed for total height of European silver fir provenances at 31 years old

Trial	Climatic transfer model	*DF*	R^2	Partial R^2	
				Temperature	Precipitation
Domnești	$17.384 + 0.004D_TMA^2 - 0.012D_PM_{JUL}$	25	0.063	0.001	0.062
Moinești	$17.240 - 0.208D_TMA + 0.001D_PM^2_{JUL}$	25	0.097	0.084	0.068
Băuțar	$17.231 - 0.052D_TMA^2 - 0.0004D_PM^2_{JUL}$	25	0.072	0.023	0.045
Strâmbu Băiuț	$13.175 + 0.015D_TM^2_{JUL} - 0.009D_PM_{JUL}$	25	0.060	0.013	0.046
Săcele	$12.508 - 0.014D_TM^2_{JUL} - 0.0001D_PMA^2$	25	0.153	0.064	0.011

Note. Abbreviations: D_TMA is the differences in annual mean temperature between the location of a given provenance and of the trial site; D_TMJUL is the differences in mean temperature of the warmest month between the location of a given provenance and of the trial site; D_PMA is the differences in annual mean total precipitations between the location of a given provenance and of the trial site; D_PMJUL is the differences in mean precipitations of the warmest month between the location of a given provenance and of the trial site.

tion variables. The climatic variables involved in these models depend on test site, thus at wet sites were D_TMA and D_PM_{JUL}, and at very wet sites were D_TM_{JUL}, D_PM_{JUL} or D_PMA. For H31, all individual transfer models were non-significant, while for D31 were significant only in two trial sites: Săcele and Moinești. Săcele trial is situated at the upper altitudinal limit of European silver fir distribution and at Moinești trial PMA is less than optimum and

Table 5 The best climatic transfer models developed for diameter at 1.30 m of European silver fir provenances at 31 years old

Trial	Climatic transfer model	*DF*	R^2	Partial R^2	
				Temperature	Precipitation
Domnești	$20.980 - 0.004D_TMA^2 - 0.019D_PM_{JUL}$	25	0.063	0.001	0.063
Moinești	$18.253 - 0.515D_TMA + 0.002D_PM^2_{JUL}$	25	0.252	0.191	0.220
Băuțar	$19.692 - 0.066D_TMA^2 - 0.016D_PM_{JUL}$	25	0.120	0.053	0.072
Strâmbu Băiuț	$17.215 + 0.030D_TM^2_{JUL} - 0.001D_PM^2_{JUL}$	25	0.108	0.027	0.104
Săcele	$16.836 - 0.041D_TM^2_{JUL} - 0.0001D_PMA^2$	25	0.251	0.188	0.102

Note. Abbreviations similar to table 4.

the De Martonne aridity index is the lowest. Both sites are situated inside of species distribution, in the mixed forests layer, but in suboptimal climates for species. The values of partial R^2 (Table 5) showed that D_PM_{JUL} at Moinești trial and D_TM_{JUL} at Săcele trial are the most important climate variables to climatic transfer. Figure 2 illustrates the transfer functions for D31 at Săcele trial. Although in most studies, data from multiple test sites were pooled to generate a generalized transfer function, we could not develop a transfer function at species distribution scale since the provenance x site interaction was significant.

Growth response functions

Table 6 summarises the response functions of European silver fir provenances for H31 and D31 over the testing sites. In terms of R^2, the relationships with TMA and PMA of trial site for both traits were very significant. In the case of H31, the climate variables had almost similar influence, explaining 56% and 60% of the total variation (partial R^2), respectively. However, regarding D31, the trial site TMA was the most important predictor, accounted for 33% of the variation.

The transfer of populations to warmer environments (Domnești and Băuțar trials, mountain beech layer) resulted in an increase of the growth – mainly due to a longer growing season. However, the developed growth response models are quadratic functions. TMA and PMA of the planting site constitute the limitative factors and at some point maladaptation will occur. The growth response functions across all sites are presented in Figures 3-4.

The magnitude of variation is directly proportional to plastic capacity of provenances. Ecovalence analyses were performed for that purpose, allowing the identification of provenances with high adaptive capacity and stability to environmental variations. According with Becker & Leon (1988), the genotypes with zero ecovalence value are regard as stable across environments. Based on the ecovalence values and their variances, European silver fir provenances could be separated into four groups: high stability and high growth, high stability and low growth, low stability and high growth, and low stability and low growth. The provenances which have highlighted good growth performances (over the experiment mean for both traits) and high stability (ecovalence near zero) were: 2-Azuga, 4-Avrig, 14-Asău, 47-Moinești, 50-Mălini, 13-Soveja, 53-Botiza, 5-Valea Moților, 9-Polovragi (Fig. 5). The weakest and unstable growth performances had the following provenances: 52-Solca, 17-Gârcina, 11-Gura Teghii, while provenance 20-Rusca Montană (Banat Mountains) has obtained the weakest growth in all planting sites. We did not found any correlations between ecovalence values and the climate variables of the provenances location.

Table 6 Climatic response models developed for total height and diameter at 1.30 m of European silver fir provenances at 31 years old

Trait	Climatic response model	*p*	R^2	Partial R^2	
				Temperature	Precipitation
H31	14.407 + 1.591TMA – 0.0001PMA^2	<0.001	0.791	0.560	0.608
D31	15.164 + 1.290TMA – 0.0001PMA^2	<0.001	0.478	0.329	0.171

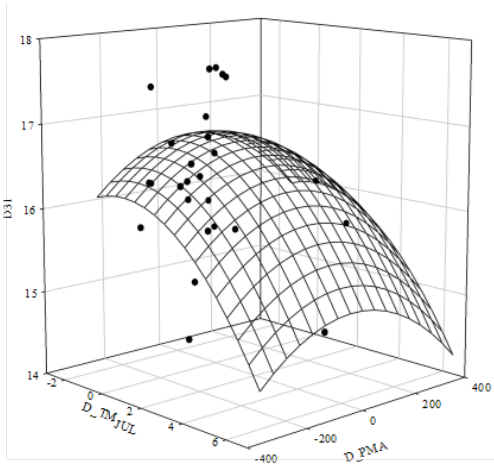

Figure 2
The transfer function for diameter at 1.30 m of European silver fir provenances at Săcele trial. D_TMJUL represent the difference in mean temperature of the warmest month between the location of a given provenance and of the trial site; D_PMA is the differences in annual mean total precipitations between the location of a given provenance and of the trial site.

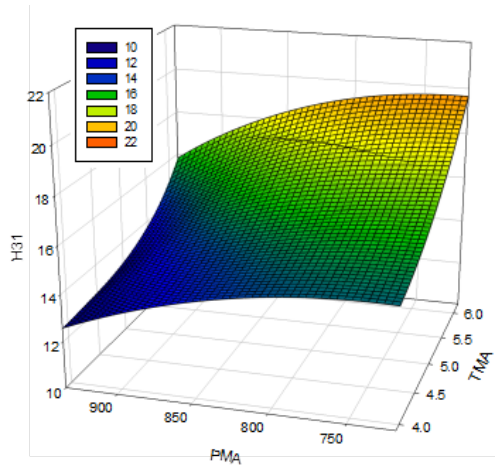

Figure 3
Growth response function of European silver fir provenances for total height. TMA is the annual mean temperature of the trial site; PMA is the annual mean total precipitation at the trial site.

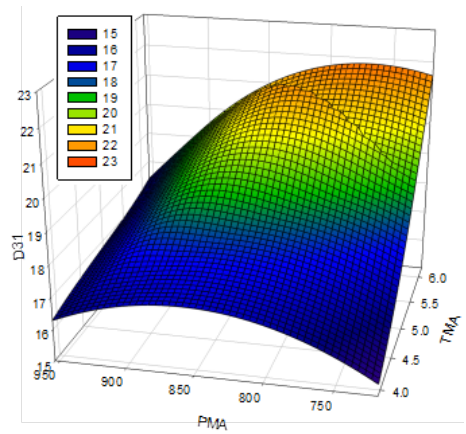

Figure 4 Growth response function of European silver fir provenances for diameter at 1.30 m. TMA is the annual mean temperature of the trial site; PMA is the annual mean total precipitation at the trial site.

Potential impact of climate change projections

The populations' response models (Table 6) were used to predict the potential impacts of climate change on current distribution of European silver fir in Romania. Prediction models were tested using the RCP4.5 scenario and results are summarised in Table 7. Thus, warming will cause some changing in current distribution of European silver fir in Romania. The gained area, until the year 2100 will be

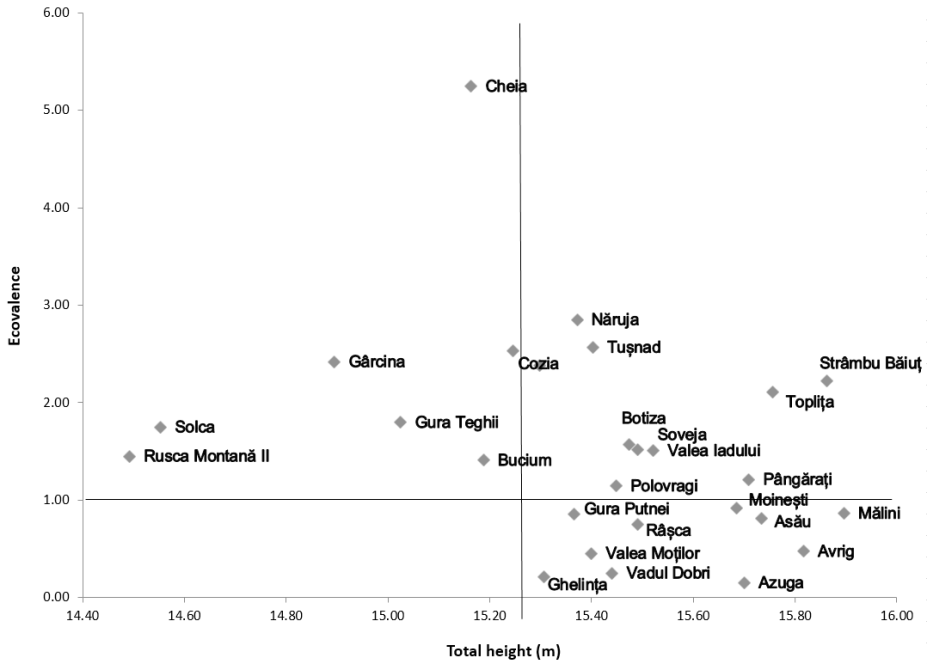

Figure 5 Ecovalence for total height of European silver fir populations at 31 years old

Table 7 Changes in present natural distribution of European silver fir as predicted by the response functions under the RCP4.5 scenario

Period	RCP 4.5 scenario TMA (^{0}C)	Percentage change in present natural distribution		
		Gain area	Lose area	Total remaining area
2021-2050	+1.4 (0.9-2.0)	+4.0	- 4.1	99.9
2051-2100	+1.8 (1.1-2.6)	+4.1	- 6.9	97.1

8.1%, while the lose area will be 11%. Figure 6 shows the changes in species present distribution and which will be the areas where the populations will be maladapted over the next decades.

Discussion

European silver fir is an exigent species in terms of climatic-edaphic conditions (Șofletea & Curtu 2001). In Romania, its optimum climate is in the mixed mountain forests, characterised by annual mean temperature between 4.0°C to 6.5°C and precipitations between 800 to1100 mm (Enescu & Doniță 1988, Doniță et al. 1990).

Long-term climatic changes over Romania are well documented in various recent papers (Birsan et al. 2014, Cheval et al. 2014a, 2014b, Marin et al. 2014), pointing to a significant warming in all seasons except autumn (Dumitrescu et al. 2015, Dobrinescu et al. 2015), an increase in frequency of rain showers (Busuioc et al. 2015, 2016; Manea et al. 2016), decreasing wind speed (Birsan et al. 2013) and snow pack (Birsan & Dumitrescu 2014). In last decades, climatic changes have varied

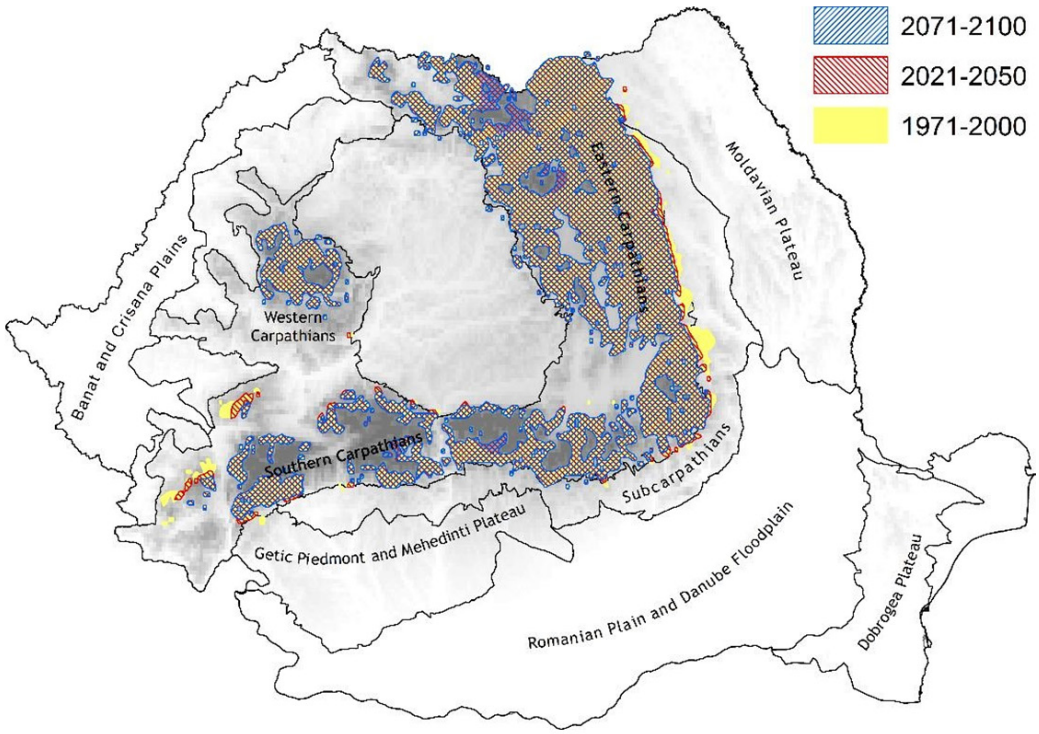

Figure 6 Changes in natural distribution of European silver fir until 2100. In yellow: the present distribution, in striped red: 2021-2050, in striped blue: 2071-2100.

among geographic regions of Romania (Birsan 2015). Thus, the magnitude of climate changes which occurred among European silver fir provenance trials varied during the evaluation period. This regional – specific climate change has determined an increase of the growth in Băuțar and Domnești trials situated in warmer and moister regions where both annual mean temperature and precipitations increased or precipitations decreased insignificantly (Table 3). The site factor had a greater influence on species growth performances than genetic factor, at this age. Results show that the growth was very significantly influenced by the annual mean temperature (TMA) and total mean precipitations (PMA) of the trial sites. These are the driving factors of tree growth that should be associated with the risk in case of the transfer of forest reproductive materials.

Also, there is a large genetic variability among studied provenances in terms of growth traits that suggests a local adaptation to the climate of the origin location of provenances. The developed transfer models have allowed highlighting the climate variables, which have the most important role to the transfer of European silver fir reproductive materials. The climatic variables involved in these models were the differences in TMA, TM_{JUL}, PM_{JUL} and PMA between the origin location of a given provenance and the trial site. These are the major climatic factors controlling genetic differentiation of European silver fir provenances and limiting how far the forest reproductive material could be transferred among provenances regions. The transfer models were generally low, significant models were obtained for D31 and in two sites only (R^2 = 0.251). Results

could be explained by the very high influence of the environmental factor, which accounted 78% (for H31) to 45% (for D31) from total variance, at this age. However, the population transfer functions seem to be significant at those sites situated in climatically marginal environments (higher elevation and the lowest PMA). These results suggest that the provenance origin should be especially considered if the species will be planted outside of its current climate optimum. Lack of significance for the transfer functions in the other sites can be explain by the fact they were in climatic optimum of the species. The results are in accordance with those reported for other species (Carter 1996, Andalo et al. 2005, Rweyongeza et al. 2007). Individual or general transfer functions are generally low and could explain at most 30-55% of total height variation (Wang et al. 2010).

In all planting sites, the best provenances, which have produced the greatest yield, are non-local sources. Generally, in almost all transfer models, the values of the predictors were negative and suggest that the best provenances in terms of total height and diameter at 1.30 m came from origin climate close to site climate (small transfer distances). Except Sacele trial, D_PM_{JUL} is the major factor of variation for D31 (partial R^2, Table 5), while for H31 both D_PM_{JUL} and D_TMA are important factors.

The growth response functions developed are quadratic regression models indicating that growth will decline exponentially as the seed sources will depart from a climatic optima. TMA and PMA of site together explain 79% and 48% of the total phenotypic variation observed in H31 and D31, respectively. Also, the provenance x site interaction was very significant and shows that growth performances are limited by environment conditions of planting site and they could change from site to site. However, the ecovalence values emphasize that there are provenances exhibiting high phenotypic plasticity. Based on the ecovalences calculated for H31, 58% of the provenances belong to the category „high stability and high growth". Results are suported by the recent studies which show that European silver fir is more resilient to climate change than other conifers of temperate forests (Becker 1989, Zang et al. 2014, Gazol & Camarero 2016).

Future projections suggest that the trend toward warmer climatic conditions will continue in the coming decades. Based on growth response functions and RCP4.5 scenario we could project the shifts in species distribution for 2050s and 2100s. Thus, the gained area until the year 2100 will be 8.1% through migration to high elevations, while the lost area will be 11%. Our results confirm that climate changes could increase the European silver fir productivity at higher elevations as a consequence of improving growth conditions. The most vulnerable populations will be those from climatically marginal environments, from low elevations and facing higher temperatures coupled with moisture deficiency, like the edges of the Eastern Carpathians and the Banat Mountains; Figure 6 presents how the European silver fir range will withdraw in the eastern and south-western part of their distribution.

Conclusions

The experiments revealed a large genetic variability within species level. European silver fir populations demonstrated resilience to climate change, which certainly is adaptive and has a genetic basis. However, changes in environmental conditions can affect the phenotype of particular provenances and thus the transfer of forest reproductive material must be done with caution.

The transfer to warmer climate, at lower altitude, in mountain beech layer, resulted in an increase of the provenances growth. But growth is significantly influenced by TMA and PMA of planting site and also by the differences in TMA, TM_{JUL}, PM_{JUL} and PMA between

provenance site and test site. These are the climatic factors which should be associated with risk in case of a transfer of provenances.

The transfer of European silver fir populations to small climatic distances will contribute to enhance growth and could be a key forest management strategy to mitigate negative impacts of climate change in some areas.

The study highlights the importance of the long-term genetic tests and assisted migration in evaluating the adaptive capacity of forest species to climate changes. The risk of maladapted reproductive material can be minimized if we consider genetic differences within species and will identify the best performing and adapted provenances for each provenance region.

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