

Growth and Adaptive Capacity of Douglas Fir Genetic Resources from Western Romania under Climate Change

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Abstract: The most recent climate change scenarios show that Southern and Eastern Europe will be affected by a significant increase in temperature and drought frequency by the end of the 21st century. Romania has already recorded very high temperatures and long periods of drought over recent decades, the most affected regions being the south, west and east of the country. Considering that successful forest management requires suitable species and high-quality reproductive material for reforestation, the aim of this study was to evaluate and compare the growth and drought response of Douglas fir (*Pseudotsuga menziessi* var. *menziesii*) and Norway spruce (*Picea abies*) in two stands installed at the end of the 19th century in western Romania. The growth traits, wood characteristics and drought parameters (resistance, recovery, resilience and relative resilience) of Douglas fir and Norway spruce trees have been analyzed and compared. The climate–growth relationship was determined using growth response functions over the period 1938–2017. Additionally, to simulate the potential impact of climate change on Douglas fir in this region, the RCP4.5 scenario was used over two periods: 2041–2070 and 2071–2100. The results reveal that Douglas fir has an exceptional growth capacity, overcoming the Norway spruce since the early ages in both site conditions. The highest growth performances were seen in the low-productivity site. From analyzing the responses to drought events, considerable differences were found between species. The results highlight the high resistance and relative resilience to extreme droughts of Douglas fir compared to Norway spruce. However, autumn–winter temperatures play an important role in the adaptation of Douglas fir to site conditions in Romania. The use of appropriate provenances of Douglas fir in mixed stands with native broadleaved species may be an option for climatically exposed sites, thus increasing the value of these stands.

Keywords: *Pseudotsuga menziessi*; climatic suitability; standardized precipitation evapotranspiration index; generalized linear mixed models; ring width index; forest genetic resources; climate scenarios; Southeastern Europe

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1. Introduction

The Douglas fir (*Pseudotsuga menziessi*) is one of the most important forest tree species in North America. Since the middle of the 19th century, it has been successfully introduced into many regions with a temperate climate in both hemispheres [1]. In Europe, Douglas fir was introduced in 1827 and currently covers the largest area outside its natural range, being present in 35 countries [2]. In Romania, the first Douglas fir plantations were established in 1887 in eastern Romania (Moldavia) and one year later, in 1888, in the western part of the country (Banat) [3,4]. Although it is one of the most important non-

native tree species, it covers only 0.40% of the total forest area in Europe (approximately 823,534 ha) [2] and 0.12% (7300 ha) in Romania (NFI 2016).

Douglas fir has a wide distribution area in North America, where it is represented by two geographically distinct varieties: coastal (*P. menziessi* var. *menziessii* (Mirbel) Franco) and interior (*P. menziessi* var. *glauca* (Beissn.) Franco). The coastal variety of Douglas fir is the most widespread in Europe because it was more suitable to climate conditions than the interior variety. The coastal variety ranges along the North American Pacific coast (California, Oregon, Washington, and British Columbia) from the sea level to about 1500 m and is adapted to an oceanic climate characterized by mild, wet winters and cool, relatively dry summers, and long frost-free growing seasons. Compared to the climatic conditions in Europe, most of the precipitation occurs in winter, with the annual precipitation rates ranging from 760 to 3000 mm [1,5].

Results from long-term provenance trials in the natural range indicate high adaptive genetic variation among Douglas fir populations and clinal variation patterns in growth, phenology, and cold hardiness [6–9]. Douglas fir can be referred to as an “adaptive specialist” because its populations are closely adapted to their ecological niches [10,11]. The coastal Douglas fir populations reach an increased height, diameter, and volume compared with the interior variety, and they are more tolerant to needle diseases but less tolerant to fall frost, winter cold, and drought. Winter temperatures and frost date are the major factors involved in the adaptation of the coastal Douglas fir, whereas summer drought is of less importance [12]. Furthermore, there is a large variability for wood characteristics within the natural range of the species. The wood of the northern populations is considered more valuable (denser and stronger) than that of the southern ones [13,14].

Since the 20th century, a large number of Douglas fir provenance trials have been established at the national and European levels, indicating a substantial level of interest for the species. Thus, after the Second World War, it became a major tree species used in reforestation in Western Europe. In most European countries, it showed higher productivity compared with the native conifers and good resistance against fungal pathogens and low numbers of pests and diseases [15,16].

Subsequently, the results of International Union of Forest Research Organizations (IUFRO) experiments on Douglas fir provenances in Europe show its sensitivity to winter drought and frosts and the importance of the geographic origin of forest reproductive material [17,18]. Thus, the interior populations (particularly in British Columbia) are the most resistant to early and winter frosts but susceptible to late frosts [19,20]. Coastal populations, with late flushing, are the most resistant to late frost but rather sensitive to early and winter frosts [15]. Further, Breidenstein [21], in a synthesis of the results from 108 Douglas fir provenance tests established by IUFRO (1967) in 15 European countries, has shown that low-elevation coastal and Cascade provenances from Washington State underwent the most rapid growth over most sites and broad adaptability, although mortality was high on several colder sites [22]. Some northern Oregon provenances from west of the Cascades as well as a few southwestern British Columbia sources also had high productivity across much of Europe. Only in continental climates (e.g., in Sweden, Finland, and the Czech Republic), the interior variety outperforms the coastal one. The highest mortality rates were found for the southern coastal Oregon provenances on the coldest sites and the interior of British Columbia provenances on the mildest sites. The success in reforestation work is mostly dependent on the genetic selection of the appropriate forest reproductive material for planting sites.

In Romania, Douglas fir breeding activities started in the 1970s and focused on assessing the genetic variability in provenance trials [23], establishing first-generation seed orchards [24], and preserving valuable stands as genetic resources [25]. Unfortunately, the breeding program was abandoned in the last two decades, and recommendations on the use of appropriate provenances in Romania still need scientific validation. There is also a lack of knowledge regarding the growth potential of Douglas fir in Romania, relationships

between growth and climatic variables, the selection of suitable seed sources, and species response to drought and rapid climate change.

Climate change scenarios show that Southern and Eastern Europe will be affected by a significant increase in temperature and drought frequency by the end of the 21st century [26]. Over recent decades, Romania has experienced record temperatures [27], decreasing wind speed [28,29] and snow depth [30] changes in the frequency of hydrometeors [31], as well as drought periods, which were associated with global climate change [32–35] or changes in atmospheric circulation [36–39]. Climate change will certainly have detrimental effects on forest ecosystems in these regions [40–43]. Norway spruce, one of the most planted conifer species outside the natural distribution area, showed a high sensitivity to decreases in water availability and weak adaptive capacity at lower elevations [44,45]. However, recent studies showed that Douglas fir might be an alternative species because some provenances are well adapted to drought and warmer conditions [46–48]. Therefore, interest in using Douglas fir at lower altitudes or in response to climate change has increased in Europe in recent years.

The aim of this study was to evaluate the growth response and adaptive capacity of Douglas fir genetic resources from western Romania in the context of climate change. These populations were established at the end of the 19th century and are mixed stands with Douglas fir, Norway spruce, and broadleaved species. They are among the oldest Douglas fir plantations in Romania and were designated as forest genetic resources for Douglas fir to be included in the National Catalog of Forest Genetic Resources [49]. Based on the assumption that global warming will reduce the growth and adaptive capacity of Norway spruce at lower elevations in Southeastern Europe, the objectives were to (1) comparatively assess the growth and adaptive capacity of Douglas fir and Norway spruce, (2) evaluate the Douglas fir response to drought, (3) determine climate–growth relationships, (4) evaluate the Douglas fir suitability to future climate conditions, and (5) provide recommendations for the use of Douglas fir.

Considering that sustainable forest management requires productive species and high-quality reproductive material for reforestation, the need to identify valuable seed sources has emerged. Furthermore, knowing the provenance of seed sources or plant material is particularly important for the success of reforestation in response to climate change. This study aimed to provide further information and offer solutions for the sustainable management of forest ecosystems and forest adaptation strategies to climate change.

2. Materials and Methods

2.1. Study Sites

This study was conducted in two of the most valuable forest genetic resources (FGR) of Douglas fir located in the Ana Lugojana Forest District (Banat region). These stands are 105 and 130 years old, respectively, and are mixed stands with Douglas fir, Norway spruce, and broadleaved species. The two stands are located in highly contrasting site conditions: FGR 1 in high-productivity site conditions for European beech at an altitude of 880 m (45°35'N, 22°15' E), whereas FGR 2 is in low-productivity site conditions at an altitude of 460 m (45°35' N, 22°25' E). The characteristics of the two stands are presented in Table 1.

Table 1. The sites and stands characteristics of the Douglas fir forest genetic resources.

Stand Characteristics	FGR 1	FGR 2
Species composition	80% Douglas fir; 20% Norway spruce	30% European beech; 50% Douglas fir; 10% Norway spruce; 10% other species
Age	105	130

Class of production	I	I
Soil	Eutricambosoil mollic	Eutricambosoil lithic
Site conditions	High productivity	Low productivity
Vegetation layer	European beech layer	European beech layer
Altitude	880 m	450 m
Climatic province (by Köppen–Geiger)	Cfb-warm and temperate climate with slight Medi- terranean influences	Cfb-warm and temperate cli- mate with slight Mediterra- nean influences

2.2. Field Measurements and Analyses

In each stand, 20 dominant or (co-)dominant trees per species of 105 and 130 years old, respectively, were measured for total height and diameter at 1.30 m (DBH) and cored at breast height using 5 mm increment borers (Haglof, Sweden). Cores were prepared using standard dendrochronological methods [50]. Then, each core sample was scanned at 1200 dpi, using an Epson Expression 10,000 XL, and the wood characteristics were measured using the Ligno Vision software package to the nearest 0.001 mm. The assessed characteristics were: ring width (RW), earlywood width (EW), latewood width (LW), and latewood percentage (LWP), as an indication of wood quality.

For each study site, a master series was constructed and cross-dated using COFECHA [51] to avoid dating errors due to missing or false rings, which could be present in an increment radial core. Only dendrochronological series that presented intercorrelation values >0.328 ($p < 0.01$) were included in final tree ring data. All tree-ring time series were standardized to a mean value of one to obtain a dimensionless ring-width index (RWI), thus preserving a large portion of low-frequency variability due to the influence of climatic events [52,53]. The negative exponential regression in the R package (dplR) [54] was applied for each raw measurement series because it is deterministic, meaning that it follows a model of tree growth. The final data set consisted of data from 38 Douglas fir trees and 32 Norway spruce trees. The analyzed period was 1938–2017 for each tree-ring series.

2.3. Climate Data

Climatic data series for the study sites were extracted from the CRU TS (Climatic Research Unit gridded Time Series) dataset v.4.04, over the period 1901–2017. CRU TS is a widely used dataset made by interpolating the monthly climate anomalies from weather station measurements at a spatial resolution of $0.5^\circ \times 0.5^\circ$, covering all continents except Antarctica [55].

High-resolution gridded climate data over Romania (1961–2020) were derived from daily precipitation and temperature grids over the period 1961–2020. The dataset consists of a spatial resolution of $1 \text{ km} \times 1 \text{ km}$ and was made using state-of-the-art interpolation techniques for an improved reproduction of the spatial climatic variability (e.g., [56,57]).

Climate projections were derived from the RoCliB dataset [58,59], which includes air temperature and precipitation data from 10 general circulation models dynamically downscaled by several regional climate models and bias corrected (adjusted) over Romania for the 1971–2100 period. We used the 10-model ensemble data for the scenarios RCP 4.5 and RCP 8.5 for the periods 2041–2070 and 1971–2100.

The following climatic variables of FGR location were calculated: mean annual temperature (MAT); mean temperature of the growing season (April to September) (MT_{VEG}); mean temperatures for January (MT_{JAN}) and July (MT_{JUL}) (i.e., the coldest and warmest months, respectively); mean temperature from October to December of the previous year ($MT_{\text{OCT-DEC}}$); mean temperature from October of the previous year to March of the current year ($MT_{\text{OCT-MAR}}$); mean temperature from January to March of the current year ($MT_{\text{JAN-MAR}}$); sum annual precipitation (SAP); sum precipitation during the growing season

(SP_{VEG}); sum precipitation of the coldest (SP_{JAN}) and warmest (SP_{JUL}) months; sum precipitation from October to December of the previous year (SP_{OCT-DEC}); sum precipitation from January to March of the current year (SP_{JAN-MAR}); and sum precipitation from October of the previous year to March of the current year (SP_{OCT-MAR}).

According to the Köppen and Geiger climate classification [60], the site's climate is warm and temperate (Cfb), with slight Mediterranean influences being representative of vegetation conditions in the west of the country. The climate is characterized by mild winters and a richer rainfall regime. Comparative climatic data for Douglas fir populations from western Romania and for the natural distribution range are presented in Table 2.

Table 2. Comparative climatic data for Douglas fir forest genetic resources from western Romania and at the natural distribution range in Pacific Northwest.

Site	MAT (°C)	MTJAN (°C)	MTJAN- MAR (°C)	MTVEG (°C)	SAP (mm)	MPJAN (mm)	SPJAN- MAR (mm)	SPVEG (mm)	Frost-Free Days
Western Romania	8.97	−2.56	0.01	15.62	754	43	183	477	248
Pacific Northwest	3.5 to 14.4	−2.0 to 3.0	−1.5 to 5	7.4 to 23	760–3000	15 to 524	43 to 1233	90 to 750	195–260

TMA—the mean annual temperature; TMJAN—the mean temperature of the coldest month (January); TMJAN-MAR—the mean temperature from January to March of the current year; MTVEG—the mean temperature of the growing season; SAP—the sum annual precipitation; SPJAN—the sum precipitation of the coldest month (January); SPVEG—the sum precipitation during the growing season.

2.4. Determination of Drought Events and Drought Response Parameters

As an indicator for meteorological droughts, we calculated the Standardized Precipitation Evapotranspiration Index (SPEI) [61], which is based on precipitation and the potential evapotranspiration (PET) over the period 1901–2019. The PET was calculated according to the Thornthwaite equation [62]. Given that an extreme drought event must last for a minimum of 2 to 3 months, we calculated the SPEI at a time scale of 3 months (SPEI-3), with the R package “SPEI” [63]. This approach allowed us to detect both seasonal and annual variations of drought events during the analyzed period. The drought years were classified as follows: SPEI ≤ −2 extreme drought year; SPEI between −1.99 and −1.50: severe drought year; SPEI between −1.49 and −1.0: moderate drought year; SPEI between −1.0 and +1.0: normal precipitation year.

The species response to drought events was evaluated using four drought parameters [64]: resistance (Res), recovery (Rec), resilience (Rsl), and relative resilience (rRsl). Resistance (Res) was calculated as the ratio between ring width during drought (Dr) and before the drought event (preDr)— $\text{Res} = \text{Dr}/\text{preDr}$ —and indicates how much the radial growth decreased during drought (Res = 1 means high tolerance; Res < 1 means low tolerance).

Recovery (Rec) was calculated as the ratio between the ring width after the drought event (postDr) and during drought (Rc = postDr/Dr) and indicates the revitalization capacity after a drought period.

Resilience (Rsl) represents the ratio of the ring width after drought (postDr) and pre-drought (preDr)— $\text{Rsl} = \text{postDr}/\text{preDr}$ —and describes the species capacity to reach pre-drought increment after a drought event (Rsl = 1 means full restoration; Rsl < 1 means long-term growth reductions). Relative resilience (rRsl) was calculated by $\text{rRsl} = (\text{postDr}-\text{Dr})/\text{preDr}$. Pre- and post-drought ring widths were calculated as average values for a three-year period before or after the drought year.

2.5. Data Analysis

Analysis of variance were performed using the Generalized Linear Mixed Models (GLM) procedure (SPSS v19). The total amount of variation was divided into tree species, years, FGR (sites), and the species site interaction. Apart from the FGR, which was considered fixed, all effects were considered random. The assumptions of the model were checked by a Shapiro and Wilk test for normality and by Levene's test for homogeneity.

ANOVA was performed as described in the following mixed model:

$$Y_{ijk} = \mu + S_i + R_j + Y_l + BF_{ij} + e_{ijkl}$$

where: X_{ijk} = performance of k th tree in i th species in j th RGF; μ = overall mean; S_i = effect of i th species; R_j = effect of j th RGF; Y_l = effect of l st year; SY_{il} = interaction of i th species and l st year; e_{ijkl} = random error associated with $ijkl$ th trees.

The relationships between climatic variables of the plantation sites and ring-width indices and latewood percentage of Douglas fir and Norway spruce were evaluated through response function analysis. The quadratic models based on both temperature and precipitation as predictor variables were applied in the SPSS program (stepwise selection method), considering them more suitable [64–66]. We used seven temperature and seven precipitation variables, and the best models were chosen based on the R^2 coefficient. Response functions analysis was performed for the period 1938–2017 using the formula of Wang:

$$Y_{ij} = \beta_0 + \beta_1 T_{nj} + \beta_2 P_{nj} + \beta_3 T_{nj}^2 + \beta_4 P_{nj}^2 + e_j$$

where Y_{ij} is the observation of the population i at the site j ; β_s are the intercept and regression coefficients; T_{nj} and P_{nj} are the temperature and precipitation variables, respectively, at the site j ; and e_j is the residual.

To assess the potential distribution area of Douglas fir in Romania, the species climate envelope was developed based on climate predictors that reflect species ecological requirements [67]. The predictors included the yearly (annual) precipitation amount, the sum of precipitation of the coldest month and the mean annual temperature for the period 1961–2020. The same ecological indicators were also used for modelling the species suitability to future environmental conditions in Romania under the RCP 4.5 and RCP 8.5 scenarios by 2100—for the intervals 2041–2070 and 2071–2100.

3. Results

3.1. Variation in Growth and Wood Characteristics

The analysis of variance for each FGR and trait are presented in Table 3. There were significant differences for all traits ($p < 0.001$) within and between species for each site (FGR) and among sites as well. There was also a highly significant year effect for traits and species \times year interaction in both study sites.

Table 3. Analysis of variance of growth and wood traits for the studied FGRs.

		Variance (s ²)					
Source of Variation		DF	Total Height (m)	Diam. 1.30 m (cm)	Volume/ Tree (m ³)	Ring Width (mm)	Latewood %
FGR 1	Douglas fir (DU)	18	5.917 ***	102.894 ***	9.030 ***	34.859 ***	2104.688 ***
	Norway spruce (NS)	15	9.772 ***	29.857 ***	0.622 ***	13.413 ***	2489.699 ***
	Species (S)	1	1282.276 ***	12613.321 ***	694.107 ***	841.898 ***	5330.840 ***
	Year (Y)	79	-	-	-	1.322 ***	388.354 ***
	Interaction S x Y	79	-	-	-	0.618 ***	297.571 ***
	Error	2640	7.669	69.695	5.208	0.080	164.581
FGR 2	Douglas fir (DU)	18	14.618 ***	238.937 ***	24.728 ***	27.718 ***	1592.266 ***
	Norway spruce (NS)	15	7.947 ***	52.250 ***	1.007 ***	13.223***	2137.951 ***

FGR 1 and FGR 2	Species (S)	1	1686.527 ***	15754.121 ***	1260.260 ***	451.099	228.388 ***
	Year (Y)	79	-	-	-	2.371 ***	375.961 ***
	Interaction S x Y	79	-	-	-	0.543 ***	387.809 ***
	Error	2560	12.160	181.358	19.589	0.098	182.471
	Douglas fir (DU)	1	4.995	974.623 *	127.097 *	383.776 ***	55.155 ***
	Norway spruce (NS)	1	12.005	220.500 *	1.620	121.424 ***	30.932 ***
	Species (S)	1	2953.924 ***	28115.320 ***	1898.461 ***	121.424 ***	149.833
	Year (Y) for DU	79	-	-	-	1.144 ***	335.557
	Interaction DU x Y	79	-	-	-	0.721 ***	311.100
	Year (Y) for NS	79	-	-	-	2.429 ***	408.470 ***
	Interaction NS x Y	79	-	-	-	0.495 ***	384.963 ***
	Year (Y)	79	-	-	-	2.911 ***	424.742 ***
	Interaction S x Y	79	-	-	-	0.742 ***	320.916 ***
	Error	5360	9.839	138.784	13.842	0.092	208.275

The level of significance is represented as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

In the case of Douglas fir, the total height ranged from 45.70 m to 54.70 m in FGR 1 and 41.80 m to 57.60 m in FGR 2. DBH ranged from 70.38 cm to 100.34 cm in FGR 1 and 54.78 cm to 129.62 cm in FGR 2. The average of volume/tree was 11.9 m³ in FGR 1 and 15.6 m³ in FGR 2. The best growth performances were obtained by both conifer species in FGR 2, located on low-productivity site conditions for European beech. Overall, Douglas fir exceeded the Norway spruce for all growth characteristics, with percentages on average between 24 and 27% for total height, 56% for DBH, and between 75 and 77% for volume per tree (Figure 1).

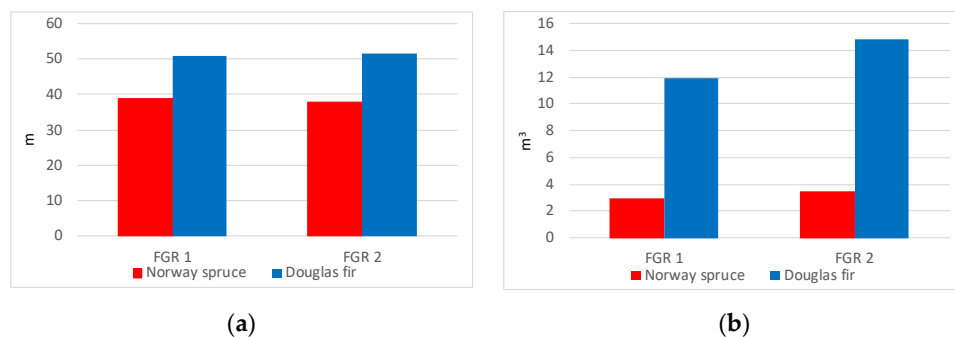


Figure 1. Total height (a) and volume/tree (b) of Douglas fir (DU) and Norway spruce (NS) in forest genetics resources (FGR) located in western Romania.

The ring width and latewood percentage varied significantly across species, site, and year. The ring width for Douglas fir ranged from 0.14 mm to 8.21 mm along all years and sites, whereas for Norway spruce, it ranged from 0.11 mm to 6.20 mm. Averaged by site and species, the average ring width for Douglas fir ranged from 2.74 mm in FGR 1 to 2.02 mm in FGR 2 and from 1.64 mm in FGR 1 to 1.20 mm in FGR 2 for Norway spruce. The overall average values per species were 2.39 mm for Douglas fir and 1.42 mm for Norway spruce.

The average latewood percentage ranged from 6 to 96% for Douglas fir and from 7 to 43% for Norway spruce. The overall average values per species were 53% for Douglas fir and 43% for Norway spruce. The average ring widths and latewood percentage were about 41% and 19% higher, respectively, for Douglas fir than those of Norway spruce for the period of 1938–2017. In both study sites, ring width decreased with increasing age, but growing patterns differed between species (Figures 2 and 3). Thus, at the same age, 105

and 130 years, respectively, the ring width of Norway spruce was 50% lower in FGR 1 and 31% in FGR 2 compared with Douglas fir.

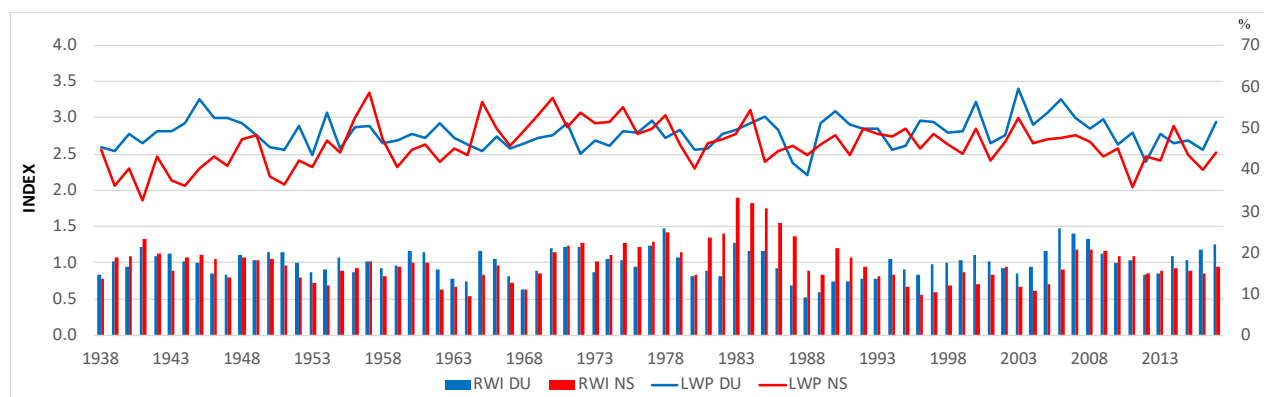


Figure 2. Variation of the ring width index (RWI) and latewood percentage (LWP) of Douglas fir (DU) and Norway spruce (NS) in FGR 1.

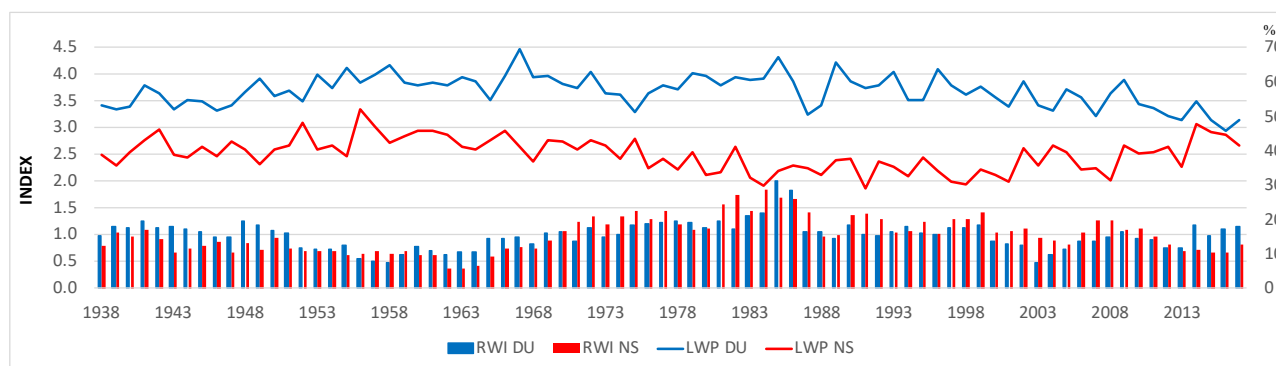


Figure 3. Variation of the ring width index (RWI) and latewood percentage (LWP) of Douglas fir (DU) and Norway spruce (NS) in FGR 2.

3.2. Climate Variation and Identification of Drought Years

The two FGRs are located very close to each other and, therefore, a single climate database was used. The gridded climate data analysis revealed considerable changes in climate conditions of the FGR sites over the analyzed period (Figure 4). MAT varied between 6.8 °C in 1940 and 10.9 °C in 2014. SAP ranged from 467 mm in 2000 to 1055 mm in 2010, whereas SP_{VEG} varied from 284 mm in 2000 to 686 mm in 2010. The most significant changes occurred over the last two decades; MAT increased by 0.9 °C, TM_{VEG} by 1.0 °C, and TM_{JAN-MAR} by 1.1 °C. Surprisingly, in the last 20 years, the precipitation amount did not decrease; in fact, there was a slight increase—SAP by 30 mm, SP_{VEG} by 17 mm, and SP_{OCT-MAR} by 14 mm—whereas MP_{JAN} remained constant.

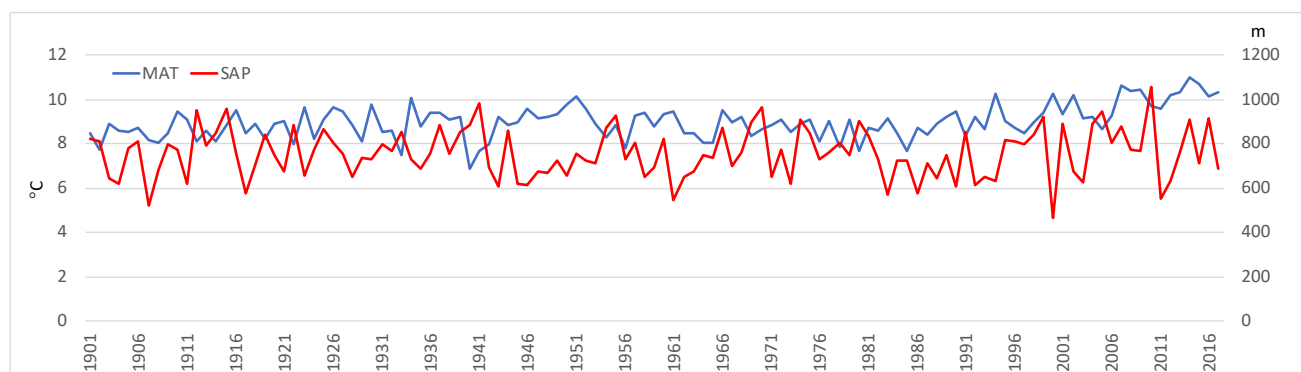


Figure 4. Variation of the mean annual temperature (MAT) and sum annual precipitation (SAP) in 1901–2017 period.

Based on SPEI values, we identified the years of severe and extreme drought for the period 1901–2017. Figure 5 presents the frequency of drought events in these sites. There were six extreme drought years (1958, 1968, 1986, 2000, 2003, and 2012) in this period, whereas the years of severe drought were a total of 32. Most of the drought events (13 out of 38 extreme and severe drought years) occurred in the period 2000–2017. Further, during this period, the highest number of consecutive years of drought was recorded (2006–2009 and 2011–2015). Other such drought periods were 1961–1963 and 1972–1975.

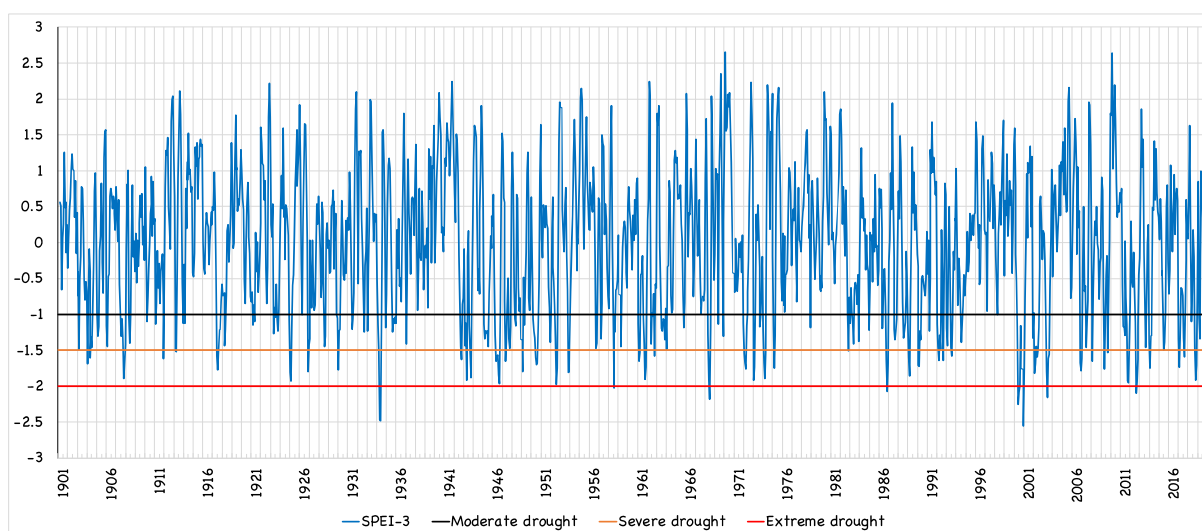


Figure 5. Variation of standardized precipitation evapotranspiration index (SPEI) across the analyzed period.

The most significant drought event occurred in 2000, when two negative peaks were observed. The 2000 drought had the highest intensity and longest duration over the last century. In that year, eight months of drought were observed, of which six extreme droughts included the growing season and fall, until the end of December. The same intensity of drought was observed in 1934 only.

Furthermore, the years characterized by a long duration of drought but lower intensity were 2003 (five months of drought, of which four were of extreme/severe drought), 2011 (seven months of drought, of which three were of extreme/severe drought), and 2012 (five months of drought, of which three were of extreme/severe drought).

3.3. Species Response to Drought

The analysis of variance revealed significant differences between species for all drought parameters in FGR 2, located on a low-productivity site (Table 4). The drought reaction parameters of the two species differed significantly depending on the extreme drought years in both FGRs. Significant differences between study sites regarding the species drought reaction were found for Norway spruce only. Within-species differences were non-significant for both species and FGR. The variation of drought parameters for all extreme drought years on species and FGR is presented in Figure 6.

Table 4. Analysis of variance of Douglas fir and Norway spruce drought parameters for years of extreme drought.

Trial	Source of Variation	DF	Variance (s ²)			
			Resistance	Recovery	Resilience	Relative Resilience
FGR 1	Douglas fir (DU)	18	0.064	0.252	0.106	0.152
	Norway spruce (NS)	15	0.084	0.083	0.360	0.131
	Between species	1	0.027	0.056	0.001	0.035
	Extreme drought year for DU	5	0.658 ***	3.130 ***	1.289 ***	1.706 ***
	Extreme drought year for NS	5	0.120	1.652 ***	1.414 **	1.208 ***
FGR 2	Douglas fir (DU)	18	0.045	0.241	0.082	0.132
	Norway spruce (NS)	15	0.090	0.116	0.118	0.089
	Between species	1	0.595 **	1.454 *	0.147	0.156
	Extreme drought year for DU	5	0.638 ***	3.303 ***	0.865 ***	1.947 ***
	Extreme drought year for NS	5	0.305 **	1.109 ***	1.977 ***	1.187 ***
FGR 1 and FGR 2	Douglas fir (DU)	1	0.076	0.029	0.442	0.143
	Norway spruce (NS)	1	0.423 *	1.221 **	0.067	0.835 *
	Between Species	1	0.183	1.055 *	0.072	0.025
	Between sites for DU	1	0.076	0.029	0.442	0.143
	Between sites for NS	1	0.423 *	1.221 **	0.067	0.835 *
	Extreme drought year for DU	5	0.420 ***	5.353 ***	1.589 ***	3.282 ***
	Extreme drought year for NS	5	0.164 *	2.669 ***	2.688 ***	2.278 ***

The level of significance is represented as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

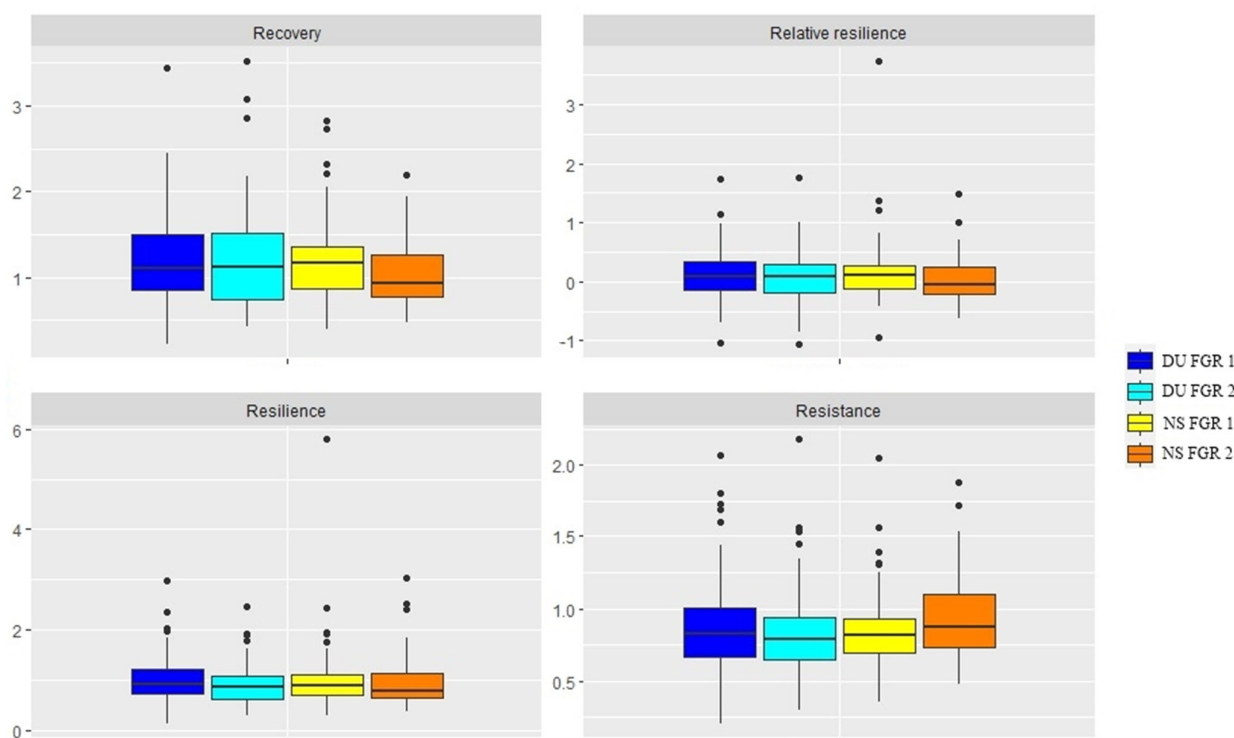


Figure 6. Variation of drought parameters for Douglas fir (DU) and Norway spruce (NS) in forest genetic resources (FGR 1 and FGR 2).

In FGR 2, differences in species reaction were obtained for all extreme drought years, except the year 2000 (Table 5). In FGR 1, only the extreme droughts during 2000 and 2003 produced a significant interspecific variation for recovery, resilience, and relative resilience.

Table 5. Differences between Douglas fir and Norway spruce for the drought parameters during the years of extreme drought.

FGR	Drought Parameters	Variance (s^2)					
		1958	1968	1986	2000	2003	2012
FGR 1	Resistance	0.036	0.198 *	0.042	0.284	0.044	0.014
	Recovery	0.020	0.120	0.008	1.373 *	0.840 *	0.510
	Resilience	0.026	0.389	0.024	1.105	1.355*	0.224
	Rel. resilience	0.001	0.034	0.002	2.504 *	0.893 *	0.122
FGR 2	Resistance	0.552 *	0.284	0.107	0.001	0.972 ***	0.004
	Recovery	1.791*	0.782 **	0.112 *	0.238	3.773 **	1.903 ***
	Resilience	0.041	2.609 **	0.017	0.224	0.005	1.326 **
	Rel. resilience	0.893 *	1.159 **	0.209 *	0.204	0.845 **	1.183 **

The level of significance is represented as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

In FGR 1, Douglas fir exceeded Norway spruce regarding resistance capacity during extreme drought in 2000 and resistance, recovery, resilience, and relative resilience during extreme droughts in 2003 and 2012. In FGR 2, Douglas fir displayed a higher recovery during the extreme drought in 2003 and higher resistance, recovery, resilience, and relative resilience during the extreme drought in 2012. It should be noted that we used a three-year period before and after the extreme event to calculate drought parameters. For the

year 2000, the analyzed period after the drought included the years 2002 (with moderate drought) and 2003 (with extreme drought).

Norway spruce was slightly better than Douglas fir in terms of recovery and resilience capacity during the extreme event in 2000 in both sites, and resistance and resilience in FGR 2 during the summer drought in 2003. Norway spruce also showed a higher capacity of adapting to the spring drought in 1968 and autumn drought in 1986 than Douglas fir.

Establishing the ranking of drought parameters in both study sites for all years of extreme drought, Norway spruce showed a higher resilience to extreme drought events, whereas Douglas fir showed higher resistance and relative resilience. Both tree species recorded similar recovery capacities (Figure 7). Correlations among growth traits and drought parameters demonstrated that Douglas fir had the highest resistance to drought and the widest growth rings (Table 6).

Table 6. Phenotypic correlations between wood characters and drought parameters of Douglas fir (DU) and Norway spruce (NS).

Species	Trait	RW	LW	EW
DU	Resistance	0.594*	0.769 **	0.524
	Recovery	−0.888 ***	−0.692 *	−0.643 *
	Resilience	−0.476	−0.105	−0.224
	Rel. resilience	−0.811 **	−0.594 *	−0.580*
NS	Resistance	−0.046	−0.269	0.151
	Recovery	−0.790 **	−0.173	−0.476
	Resilience	−0.776 **	−0.363	−0.462
	Rel. resilience	−0.797 **	−0.159	−0.483

RW—ring width; LW—late wood width; EW—early wood width; The level of significance is represented as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

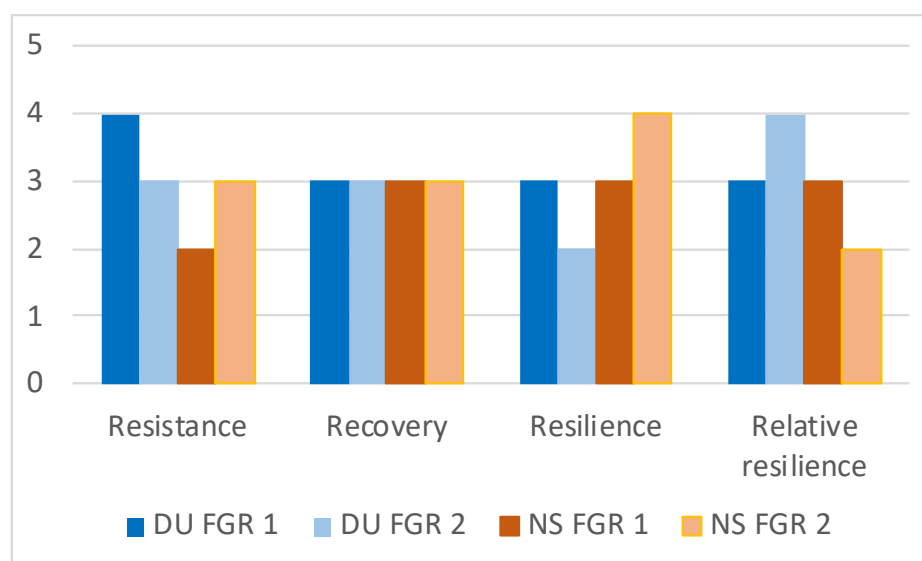


Figure 7. The ranking of drought parameters for Douglas fir (DU) and Norway spruce (NS) in forest genetic resources (FGR 1 and FGR 2).

3.4. Growth Response Functions

The climate–growth response relationships varied between conifer species and study sites (Table 7). The main climate variables linked to tree radial growth of Douglas fir located on the high-productivity site (FGR 1) were $MT_{OCT-MAR}$ and SP_{VEG} , whereas for FGR 2 on the low-productivity site, these variables were MT_{JUL} , $MT_{OCT-MAR}$, and $SP_{OCT-MAR}$. The main climatic drivers explaining radial growth of Norway spruce were MT_{JUL} and $SP_{OCT-MAR}$ in the first study site and MT_{VEG} and $SP_{JAN-MAR}$ in the second study site.

Table 7. Climatic response models for radial growth (RW) and latewood percentage (LWP) of Douglas fir and Norway spruce.

Species	FGR	Growth Response Model	Signf.	R ²
Douglas fir	FGR 1	$RW = 0.864 + 0.008 MT_{OCT-MAR} + 0.001 SP_{VEG}$	*	0.12
Douglas fir	FGR 2	$RW = 1.686 - 0.002 MT_{JUL}^2 + 0.005 MT_{OCT-MAR}^2 + 0.001 SP_{OCT-MAR}$	*	0.10
Norway spruce	FGR 1	$RW = 1.527 - 0.001 MT_{JUL}^2 - 0.0001 SP_{OCT-MAR}^2$	*	0.06
Norway spruce	FGR 2	$RW = 2.813 - 0.003 MT_{VEG}^2 - 0.001 SP_{JAN-MAR}^2$	*	0.10
Douglas fir	FGR 2	$LWP = 74.941 - 0.044 TM_{JUL}^2 - 0.001 SP_{OCT-MAR}^2$	***	0.23
Norway spruce	FGR 1	$LWP = 56.419 - 0.038 MT_{VEG}^2 - 0.014 SP_{OCT-MAR}^2$	*	0.07

MT_{JUL} —the mean temperature for July; MT_{VEG} —the mean temperature of the growing season; $MT_{OCT-MAR}$ —the mean temperature from October of the previous year to March of the current year; $SP_{OCT-MAR}$ —the sum precipitation from October of the previous year to March of the current year; $SP_{JAN-MAR}$ —the sum precipitation from January to March of the current year. The level of significance is represented as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Douglas fir appears to be less sensitive to precipitation than to temperature. The autumn and winter temperatures were positively correlated with Douglas fir growth, but the July temperatures negatively influenced both species. A negative relationship between radial growth and MT_{VEG} for Norway spruce was also found. Increasing precipitation in the growing season and in the autumn–winter interval positively influenced Douglas fir radial growth, but this influence was negative on Norway spruce.

The growth–climate relationships were weak. R^2 ranged between 0.10 and 0.12 for Douglas fir and between 0.06 and 0.10 for Norway spruce, which suggest that only a small portion of the radial growth variation can be explained by climatic factors.

Similarly, a modest response was found for latewood percentage. Thus, significant correlations between climate and LWP of Douglas fir were found in FGR 2, whereas for Norway spruce in FGR 1, MT_{JUL} , MT_{VEG} , and $SP_{OCT-MAR}$ negatively influenced the LWP.

3.5. Potential Impact of Climate Change Projections

The regions suitable for growing Douglas fir in Romania based on climate data over 1961–2020 are shown in Figure 8. For climatic envelope modeling, we used climatic variables, considering them to be the most important in the context of adaptation to climate change and because it is well known that Douglas fir grows on different soil types that are moderately acidic.

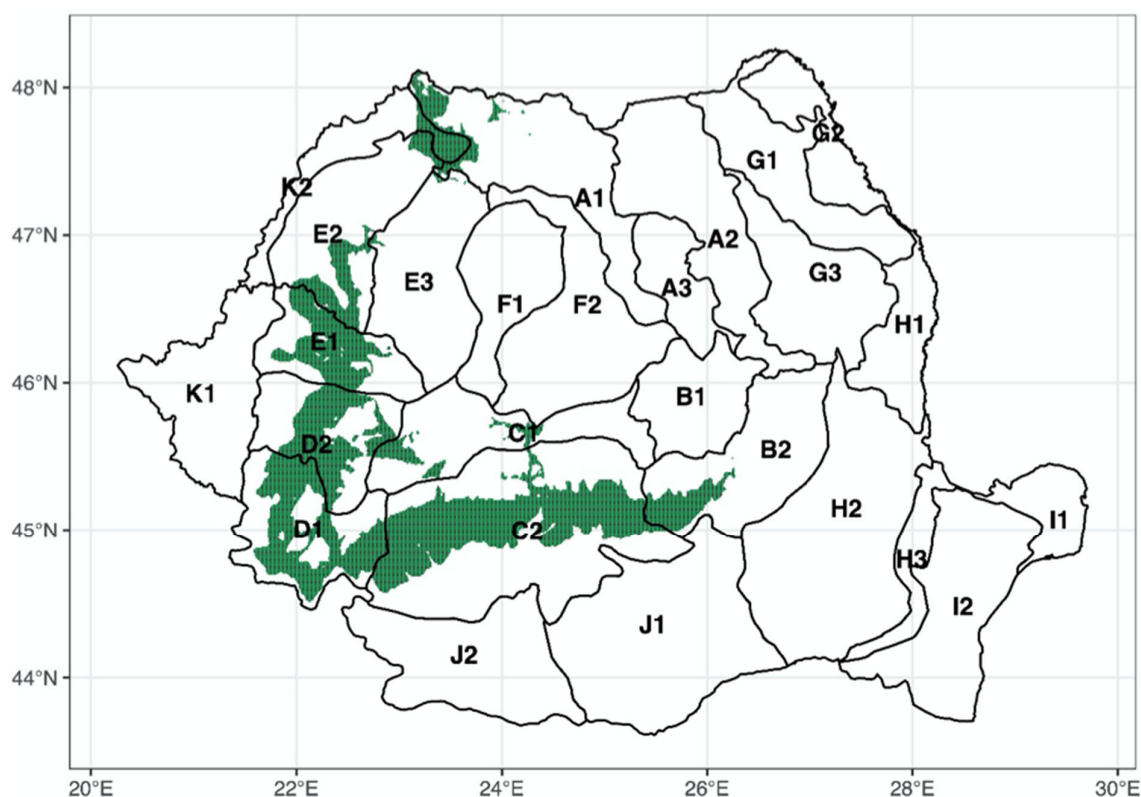


Figure 8. Suitability areas for the Douglas fir in Romania according to the high-resolution climatological data over 1961–2020. The polygons denote the regions of provenance (as in [49]): A1: Eastern Carpathians, western cline; A2: Eastern Carpathians, eastern cline; A3: Giurgeu–Ciuc depression; B1: Brasov depression; B2: Curvature Carpathians, outer cline; C1: Southern Carpathians, northern cline; C2: Southern Carpathians, southern cline; D1: Mehedinti/Cerna/Semenic Mountains; D2: Tarcu/Poiana Rusca Mountains; E1: Zarand/Metaliferi Mountains; E2: Western Apuseni Mountains; E3: Eastern Apuseni Mountains; F1: Transylvania Plain; F2: Transylvania Plateau; G1: Suceva/Siret/Iasi Hills; G2: Jijia Plain; G3: Barlad Plateau; H1: Covur Plateau; H2: Siret and Baragan Plains; H3: Danube water holes; I1: Danube Delta; I2: Dobrogea Plateau; J1: Bucharest Plain; J2: Oltenia Plain; K1: Timis and Arad Plain; K2: Cris/Carei/Somes Plain.

The projection suitability maps under RCP4.5 and the RCP8.5 scenarios over the periods 2041–2070 and 2071–2100 are presented in Figure 9. The maps show that the species suitability will increase along altitudes and in other Carpathians regions with moderate climates. Our results suggest that this species may be cultivated on a larger scale than has been considered so far.

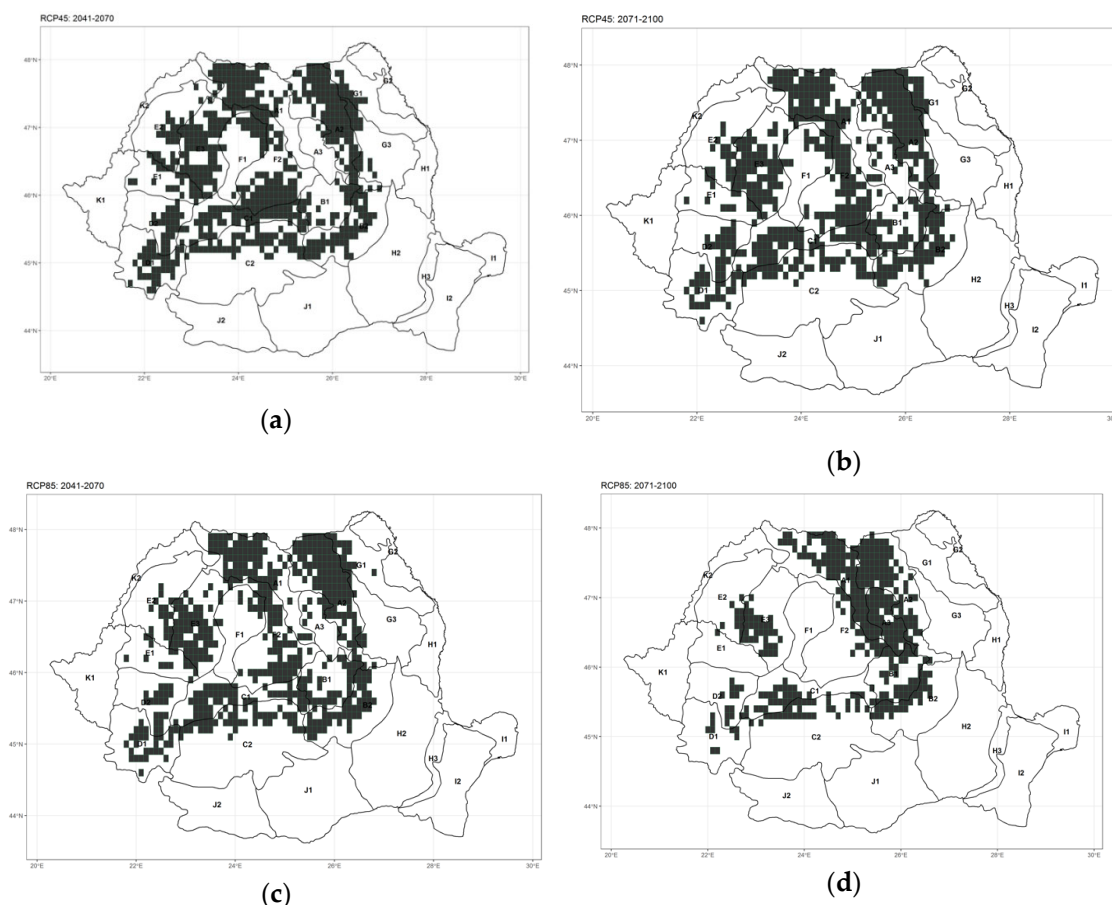


Figure 9. Projected suitability areas for the Douglas fir in Romania under the RCP4.5 (a,b) and RCP8.5 (c,d) scenarios, over the periods 2041–2070 (a,c) and 2071–2100 (b,d). The polygons denote various regions of provenance (as defined by [49]). A1: Eastern Carpathians, western cline; A2: Eastern Carpathians, eastern cline; A3: Giurgeu–Ciuc depression; B1: Brasov depression; B2: Curvature Carpathians, outer cline; C1: Southern Carpathians, northern cline; C2: Southern Carpathians, southern cline; D1: Mehedinti/Cerna/Semenic Mountains; D2: Tarcu/Poiana Rusca Mountains; E1: Zarand/Metaliferi Mountains; E2: Western Apuseni Mountains; E3: Eastern Apuseni Mountains; F1: Transylvania Plain; F2: Transylvania Plateau; G1: Suceva/Siret/Iasi Hills; G2: Jijia Plain; G3: Barlad Plateau; H1: Covur Plateau; H2: Siret and Baragan Plains; H3: Danube water holes; I1: Danube Delta; I2: Dobrogea Plateau; J1: Bucharest Plain; J2: Oltenia Plain; K1: Timis and Arad Plain; K2: Cris/Carei/Somes Plain.

4. Discussion

In this study, we analyzed the growth and adaptive capacity to climate change of Douglas fir compared to Norway spruce in two forest genetic resources, which are among the few oldest plantations with Douglas fir in Romania.

Substantial differences in growth traits and wood characteristics of the two stands were found. Douglas fir exceeded Norway spruce for all studied characteristics in both locations, but the best growth performances were obtained on the low-productivity site. The average volume per tree, ring width, and latewood percentage were approximately 76%, 41%, and 19%, respectively, higher for Douglas fir than for Norway spruce.

The analysis of climate data showed significant changes in climate conditions in the last century in western Romania, indicating that the growing conditions for forest tree species have changed. Significant variations occurred in the last two decades, when the mean annual temperature increased by 0.9 °C, mean temperature in January by 1.3 °C,

and mean temperature during the growing period by 1.0 °C. It is surprising that the precipitation amount did not decrease; in fact, a slight increase was observed.

The growth response functions revealed that the climatic variables of the study sites were a major driver of the growth performance of the two conifer species, but the climate variables depend on species. There was a significant negative response to the temperature in July and a positive influence of previous autumn–winter temperature for Douglas fir. Provenance studies show that winter air temperatures are of the utmost importance for populations' adaptation, limiting Douglas fir growth in Europe [15,21]. Our study confirms that autumn–winter temperatures are the most important factor in determining the tree-ring width in Douglas fir. Furthermore, increasing precipitation during the growing season or in the previous autumn–winter period had a positive effect on trees' radial growth but negatively influenced latewood percentage. These growth–climate relationships are similar to those observed in a number of regional studies in North America [68–70].

For Norway spruce growing outside its natural range in the study locations, the July temperatures and temperatures during the growing season were the limiting factors in determining tree growth. The observed significant negative influence of SPOCT-MAR and SPIAN-MAR point to Norway spruce being less sensitive to precipitation during the period of vegetative rest compared to Douglas fir. The latewood percentage was sensitive to increasing the July and growing season temperatures and autumn–winter precipitation for both species.

The growth–climate relationships were, in general, weak. According to Fritts [52], the strength of the climate–growth relationship depends on how strongly growth is limited by the climate of the study site. At Ana Lugojana Forest District, the mean values of SAP for the 1901–2017 period was 754 mm, and MAT was 8.97 °C, which indicates that Norway spruce is placed in a climatic suboptimum and that decreased precipitation and increased temperatures can have negative effects on its growth and survival. The coastal Douglas fir is a variety adapted to highly different site conditions; in western Oregon and Washington, it occurs from sea level to over 1700 m. Its adaptation is a consequence of trade-offs between selection for traits to avoid exposure to frost and traits that confer high vigor in mild environments [71].

The climate of Ana Lugojana Forest District is at the lower limit of its climatic optimum concerning SAP, winter temperature, and frost-free days. This may explain the exceptional growth performance of Douglas fir in the two study sites from western Romania. The difference between the climate within the native distribution range and western Romania consists of the precipitation distribution over the year. Although precipitation is nearly evenly distributed over the year in Romania, precipitation at the place of origin has a pronounced maximum in winter and a minimum in summer [1].

Considerable differences in response to drought events were found between the two tree species. The species reaction depended on the timing and duration of the drought event. Generally, Douglas fir had higher resistance, recovery, resilience, and relative resilience to the summer droughts from 2000, 2003, and 2012 than Norway spruce, which showed a higher tolerance to spring drought in 1968 and autumn drought in 1986 than Douglas fir. Regarding the ranking of drought parameters for both sites and all extreme drought years, Norway spruce displayed a higher resilience to extreme droughts, whereas Douglas fir showed a higher resistance and relative resilience. Both species recorded a similar recovery capacity.

Norway spruce is particularly vulnerable to drought [72–75]. In contrast, Douglas fir is more drought resistant than Norway spruce [2,47,48]. Rising temperatures and decreasing precipitation in the near future may increase mortality risk for Norway spruce and other native coniferous species, particularly at low elevation sites [44,76–78]. Douglas fir is a fast-growing tree and can be a potential species for biomass production. In Europe, Douglas fir produces high-quality timber, which generally equals or exceeds the value of indigenous softwoods species. Thus, the Douglas fir dry wood density is on average 0.45

t/m³ [2], while of Norway spruce is on average 0.40 t/m³ (wood-database.com/Norway spruce). One of the reasons for this potential is that under the global warming scenario, the likelihood of cold damage to low-elevation sources will decrease with time. Recent studies have shown that planting Douglas fir with broadleaf species had a positive effect on the survival of this species [2,78]. In this context, the selection of suitable Douglas fir forest reproductive material is essential because it affects the growth, frost sensitivity, and tolerance to diseases [15,22,71,79].

Our results based on growth response functions and climate models by 2100 suggest that Douglas fir has a high growth potential in many Carpathians regions, not only in the west of Romania as has been considered so far. Our results confirm that climate change can increase Douglas fir productivity at higher elevations as a consequence of improving growth conditions. Further, the developed models used for the assessment of Douglas fir suitability under future climate in Romania showed good survivability.

5. Conclusions

Selecting suitable tree species and provenances adapted to ongoing climate change is of great significance in forest management. The cultivation of Douglas fir, a non-native tree species, has often been associated with higher risk and uncertainty. The developed models used for the assessment of Douglas fir suitability under the predicted future climate in Romania showed good survivability in many Carpathian regions. Douglas fir has an exceptional growth capacity, overcoming the Norway spruce in both high- and low-productivity sites, currently as well as in the past. Considerable differences were found in drought tolerance as well, with our results demonstrating the high resistance and relative resilience to extreme droughts of Douglas fir compared to Norway spruce. However, autumn–winter temperatures play an important role in the adaptation of Douglas fir to site conditions in Romania.

The use of appropriate provenances of Douglas fir in mixed stands with native broad-leaved species may be an option for climatically exposed sites, thus increasing the value of these stands. Therefore, the conservation of the most valuable genetic resources of Douglas fir should have priority because these stands can be potential seed sources for ecosystem restoration. This study reveals the importance of improving our knowledge about the growth, ecology, and adaptive capacity of this non-native species in the context of climate change.

Author Contributions: Conceptualization: G.M., A.-L.C., and M.-V.B.; methodology: G.M. and A.-L.C., E.C., and M.-V.B.; field measurements and dendrochronological analyzes: A.-M.A.; climate data analysis and processing: I.-A.N. and M.-V.B.; maps: I.-A.N. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The RoCliB climate data is publicly available.

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