

The Dynamics and Variability of Radial Growth in Provenance Trials of Norway Spruce (*Picea abies* (L.) Karst.) Within and Beyond the Hot Margins of its Natural Range

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Abstract

Multi-site field trials provide valuable data for the investigation of possible effects of environmental changes on forest tree species. We analyze the descendants of plus trees from 33 Norway spruce seed sources of Romanian Carpathians, at age 30, in four comparative field trials: two established in the natural range of species and two outside of it. The dynamics and variation of radial growth, earlywood and latewood were analyzed. The influence of populations, site conditions and climatic factors were also quantified. The provenances response in the four comparative trials was asymmetric for mean radial growth, but its dynamics was less favourable outside of the natural range. Analysis of variance showed significant differences ($P < 0.001$) between the testing sites, but non-significant ($P < 0.05$) for the populations. Populations \times localities interaction was high ($P < 0.001$) in the first half of the testing period, but decreased over time, becoming not significant at the age of 30. At intra-population level, the average coefficient of variation for radial growth was higher outside the natural range, whereas the proportion of latewood decreased. The temperature in the first half of the growing season negatively influenced ($P < 0.001$) the radial increment, but in the latewood proportion significant effects ($P \leq 0.05$) were recorded only in trials located outside of the natural range. An increased variability of radial growth and a decrease of latewood proportion are expected in Norway spruce stands located at lower altitudes, towards the limits of the natural range. Our results may contribute to the sustainable management of Norway spruce forests within and outside its natural range.

Keywords: adaptive traits, climatic changes, growth-climate correlations, field trials, radial increments, wood characteristics.

Introduction

Norway spruce (*Picea abies* (L.) Karst.) is the keystone species of different types of complex forest ecosystems in the boreal and temperate zones of Europe (Castagneri *et al.*, 2013; Koski *et al.*, 1997; Rybniček *et al.*, 2010). In the last 200 years, intensive spruce plantations were installed not only in its natural range, but also outside of it (Hannerz and Westin, 2005; Spiecker, 2000), which has influenced the distribution of populations and sometimes their adaptability to local environmental conditions (Kahle *et al.*, 2005; Latalowa and van der Knaap, 2006). Negative ecological consequences have occurred especially in areas with extreme climate events (Carrer *et al.*, 2012; Schütz *et al.*, 2006). It considers the existence of asymmetric response of populations to these environmental changes (Mátyás *et al.*, 2010), which can be evaluated by simulations, but also by ecological investigations under different climatic conditions (Andreassen *et al.*, 2006), in or/and outside the natural range.

Norway spruce plantations continue to be established outside the natural range, particularly as a result of actions targeting carbon sequestration (Olofsson *et al.*, 2011; Peichl *et al.*, 2006).

Many studies carried out in natural populations or in field trials aimed at getting insight into the performance of Norway spruce at various altitudes, latitudes or along of gradients. Some of these approaches have evaluated the growth rate and fiber traits or the resistance to biotic or abiotic pests (Battipaglia *et al.*, 2009; Mäkinen *et al.*, 2002; Saren *et al.*, 2004; Sawa *et al.*, 2006; Skråppa, 1994; Steffenrem *et al.*, 2009). Other studies investigated the physiological response at various altitudinal levels or by gradiental analysis (Matyssek *et al.*, 2009; Oleksyn *et al.*, 2002). However, comparative data on performances of Norway spruce in its natural range and outside it is limited, particularly in the Romanian Carpathians.

The sustainable management of genetic resources is an important requirement (Matyssek *et al.*, 2009; White *et al.*, 2007) and includes multiple targets, such as the use of genetically

improved forest reproductive material, adapted to the local environmental conditions. In this context, the comparative evaluation of Norway spruce response in field trials established in and outside its natural range may contribute to the improvement of silvicultural practices. Even more, data is needed for natural populations or crops at the limits of its natural range.

The adaptation of populations to the environmental conditions of the four trials, completed by the recommendation of valuable populations for use in similar environmental conditions in which they performed, was previously presented in Șofletea et al. (2012) and Șofletea and Budeanu (2015). In this paper are analyzed: *i*) the dynamics of radial increments; *ii*) the inter- and intrapopulation variations of radial growths and the testing site influence; *iii*) the influence of climatic factors on annual growths.

Materials and methods

Plant material, experimental design and sampling

Ten plus-trees per stand were selected in 33 seed sources located throughout the natural range of Norway spruce in the Romanian Carpathians (location and geographical coordinates of the populations in Șofletea et al., 2012). The populations Coșna, Dorna Candrenilor, Frasin, Marginea, Moldovița, Stulpicani, Nășăud, Prundul Bârgăului, Rodna, Sânmartin, Toplița, Gurghiu, Sovata and Tarcău are from Eastern Carpathians, where the average annual temperature and precipitation are closer to the values registered for Gurghiu trial (5.7 °C and 810 mm). The populations Comandău, Nehoiu, Nehoiășu, Brașov and Azuga are originated from Curvature Carpathians where the average annual temperature and precipitation are closer to the values registered for Brețcu trial (4.8 °C and 830 mm). The populations Domnești, Orăștie, Bistra, Voineasa and Retezat are originated from Southern Carpathians where the average annual temperature and precipitation are closer to the values registered for Brețcu trial (4.8 °C and 830 mm). The populations Bozovici, Văliug, Beliș, Turda, Beiuș, Dobrești, Sudrișiu, Cămpeni and Gârda are originated from Western Romanian Carpathians where the average annual temperature and precipitation are approximately 6 °C and 800 mm.

The seeds collected from ten trees per stand were mixed up and sowed in a nursery (at 45°18' N, 25°34' E, 745 m a.s.l.), resulting in a total of 33 samples of provenances. Each sample will be considered as a local population. Four field trials were established with two-year-old seedlings: two field trials (Brețcu and Gurghiu) in the natural range of species and other two field trials (Câmpina and Avrig) outside of the natural range, considered beyond the hot margins of natural distribution of Norway spruce in Carpathian area (Table 1). In each field trial the experimental design was incompletely balanced, type 6 x 6, with 3 replications and 49 seedlings per plot planted at 2 by 2 m spacing. Since there are 33 populations, three populations were repeated in each replication to complete the 6 x 6 experimental design.

Data collection and analysis

Core samples were collected at the breast height (1.3 m) from 9 trees of each population (3 per replication, belonging to the mean diameter category of population in each replication, age 30) in dormant season and with an increment borer. The annual radial increments (RI) and the values for latewood (LW) and earlywood (EW) were determined in the laboratory. To measure radial growth, a Rinntech LINTAB 5 tree-ring measurement station was

Table 1. Location and climatic characteristics of field trials

Trial	Location	Average annual temperature (°C)	Average annual precipitation (mm)
In the natural range (INR)			
Brețcu	1100 m a.s.l.	4.8	830
	45°58'16"N 26°24'12"E		
Gurghiu	1000 m a.s.l.	5.7	810
	46°48'13"N 25°03'58"E		
Outside the natural range (ONR)			
Câmpina	570 m a.s.l.	9.3	645
	45°11'11"N 25°48'47"E		
Avrig	615 m a.s.l.	8.3	680
	45°39'36"N 24°26'12"E		

used. TSAP Win software was used for data recording and primary processing. Each ring-width series was checked for crossdating and measurement errors using Cofecha software (Holmes, 1983).

Starting from the last annual ring, annual values for radial increment (RI) and latewood (LW) was registered and also the average values for 5-years intervals (RI/5y, LW/5y and %LW/5y) were determined. Data were also processed to determine intra- and interpopulation coefficients of variation of radial increment (CVRI) and latewood (CVLW) in each comparative trial. A bifactorial ANOVA analysis was conducted in order to highlight the influences of testing site and population x locality interaction, according to the following model:

$$X_{ijk} = m + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijk}$$

where: m = overall average value, α_i = component of i populations (i = 1...a), β_j = component of j localities (j = 1...b), $\alpha\beta_{ij}$ = interaction of i populations with j localities, ε_{ijk} = random error.

The normal distribution was checked with the Kolmogorov - Smirnov test and Levene's test was used to assess variance homogeneity before applying ANOVA. The statistical significance was determined by using Fisher (F) test for 5%, 1% and 0.1% transgression probability.

A matrix of correlation between annual/seasonal values of climatic data of tested sites (Table 6) and annual values of RI and %LW, respectively, was produced and analyzed. To eliminate the influence of age and for obtaining the growth standardized indices the ASTRANwin program was used (Cook and Krusic, 2006). Average climatic data for the last 25 years provided by the Romanian National Meteorological Administration were used. Data were collected from weather stations located closest to the field trials. STATISTICA ver. 10.0 software was used for data processing

Results and discussions

Dynamics of radial increment

The evolution of radial growth as average values calculated every year for all populations, in each of the four testing sites is showed in Fig. 1. Maximum values of radial growths were recorded between (9) 10-11 years after planting, in both categories of field trials (Table 2). The two major testing variants (in the natural range of the species – INR and outside it – ONR, respectively) could not be differentiated with respect to the maximum radial growths: in each of them, the values were higher in one of the testing site (6.901 mm/year in Avrig test – ONR,

and 6.581 mm/year in Brețcu test - INR). However, the two tests indicated a similar pattern and for the average values of radial growths (RI = 4.053 mm/year in Avrig and 4.104 mm/year in Brețcu trial).

Compared to the maximum radial growth (RImax), the mean radial growth (RI) decreased on average by 40.2% ONR (Avrig = 41.3%; Câmpina = 39.1%) and by 36.0% INR (Brețcu = 37.6%; Gurghiu = 34.3%). This indicates the huge growing capacity of spruce in the first third of the testing period. In the last 5 years, the average value of annual radial growth has decreased by 13% in the two ONR tests, compared to the same period in INR tests, but clearly more in Câmpina field trial (16.5%, Table 2). On average, ONR, the percentage ratio between the average radial growth of the last 5 years and their average for 25 years is 5.3% higher. On the other hand, in the two ONR field trials there was a higher decrease of the percentage ratio between maximum annual radial growth and the average in the last five years (on average, 69.6% ONR and 64.4% INR, respectively).

Among the populations originating from the lower limit of the natural range, it was noted the Dobrești provenance (ranked 7 in Avrig test, 3 in Câmpina and Gurghiu), followed by Bozovici population that performed well in Avrig and Gurghiu trials (ranked 8 and 3, respectively), while Marginea population performed well only in the field trials established in ecological optimum of the species (1st in Brețcu and 6th in Gurghiu).

With regard to the periodical radial growths for five year intervals (RI/5y) and their dynamics, up the age of 10, the values were higher in the two field trials located ONR, compared INR trials (Fig. 2). Compared to radial increments registered between 6-10 years, the values decreased 3 times in the last 5 years in ONR field trials, but only 2.5 times in INR field trials. Three marginal populations (Marginea, Dobrești and Bozovici) did not register fluctuations of theirs ranking along the 5 years analyzed periods.

For all 33 populations, there were no significant differences between the two major variants (INR and ONR) in the first part of testing period. After that, the annual radial growth decreased particularly in Câmpina field trial. In both ONR field trials, the radial increment values were lower than those of INR tests especially in the last third of the evaluation period. The climatic conditions were less favourable in both ONR tests: low precipitation and higher temperatures during the growing season. This led to higher values of thermo-pluviometric factor between May and September (Șofletea et al., 2015), a climatic parameter considered very important for Norway spruce at the hot limit of its natural range (Schmidt-Vogt, 1977). As a consequence, the decrease of radial growth in the last decade, outside of the natural range, indicated the occurrence of stress caused by the combination low precipitation-high temperatures, because the consumption has

increased as a result of previously accumulated biomass. Therefore, it is likely that the differences between INR and ONR field trials to increase in the future.

The pattern of the radial growth dynamics is similar both in INR and ONR field trials, explained by a polynomial function of 3rd degree. On the other hand, the dynamics of LW showed a linear pattern, but LW decrease with age was more evident in the INR tests.

Influences of different testing locations were also reported in a study conducted in Slovakia for 30 spruce provenances assessed at a tree age of 26 (Pacalaj et al., 2002), in four field trials distributed between 335 and 950 m altitude, and the smallest values of diameter were registered at the upper limit of the altitudinal transect.

Dynamics of latewood proportion

As shown in Fig. 1 (a, b, c and d), the latewood width decreased with age, particularly in the two INR tests, and also in the Avrig field trial (ONR). Unlike the dynamics of radial increments that vary by a polynomial model, LW decreased linearly, and the coefficient of determination indicated a good response of populations in Avrig, Brețcu and Gurghiu field trials, by age, but much weaker in Câmpina. In this latter case, a 2nd degree polynomial function better explained the relationship between the independent and dependent variable (R² = 0.684). The marginal populations Beiuș and Marginea stand out in terms of the latewood percentage.

Higher values were recorded for %LW/5y in INR trials, but their temporal evolution was different than that in ONR tests (Fig. 3). The largest differences were recorded in the first 15 years after planting (around 16% between 6-10 years old and 11% between 11-15 year old), but decreased to 5-6% up to 25 years. The trend in the last 5 years was a relatively constant 5-6% difference between INR and ONR.

The experimental data indicate the existence of some interdependencies between radial increments and the production of latewood or earlywood. Therefore, the simple correlations between the periodical average values RI/5y and LW/5y (mm) indicated in nearly all testing situations a direct connection between them (Table 3). In the first half of the assessed period, the intensity of these correlations is stronger in the two field trials established in the spruce natural range. The correlations between RI/5y and %LW/5y values (data not shown in table 3) were negative and of low intensity.

Radial increment variability

There was a greater variability of radial growth in both ONR trials (Table 4). Thus, the mean of CVRI was higher by about 7 units in ONR than in INR field trials. In three out of the four

Table 2. The dynamics of radial growth

Trial	RI mm/ year	RImax mm/ year	5-year periodical growth - RI/5y (mm/year) - at the age of:					% decreasing RI/last 5 years reported from:	
			6-10	11-15	16-20	21-25	26-30	RI	RImax
ONR									
Avrig	4.053	6.901	5.897	5.603	4.374	2.599	2.032	49.9	70.5
Câmpina	3.713	6.096	5.980	5.562	3.785	2.660	1.877	49.4	69.2
Mean	3.883	6.499						49.7	69.9
INR									
Brețcu	4.104	6.581	5.520	5.831	4.078	2.925	2.295	44.1	65.1
Gurghiu	3.980	6.056	5.763	5.715	4.311	3.007	2.200	44.7	63.7
Mean	4.042	6.318						44.4	64.4

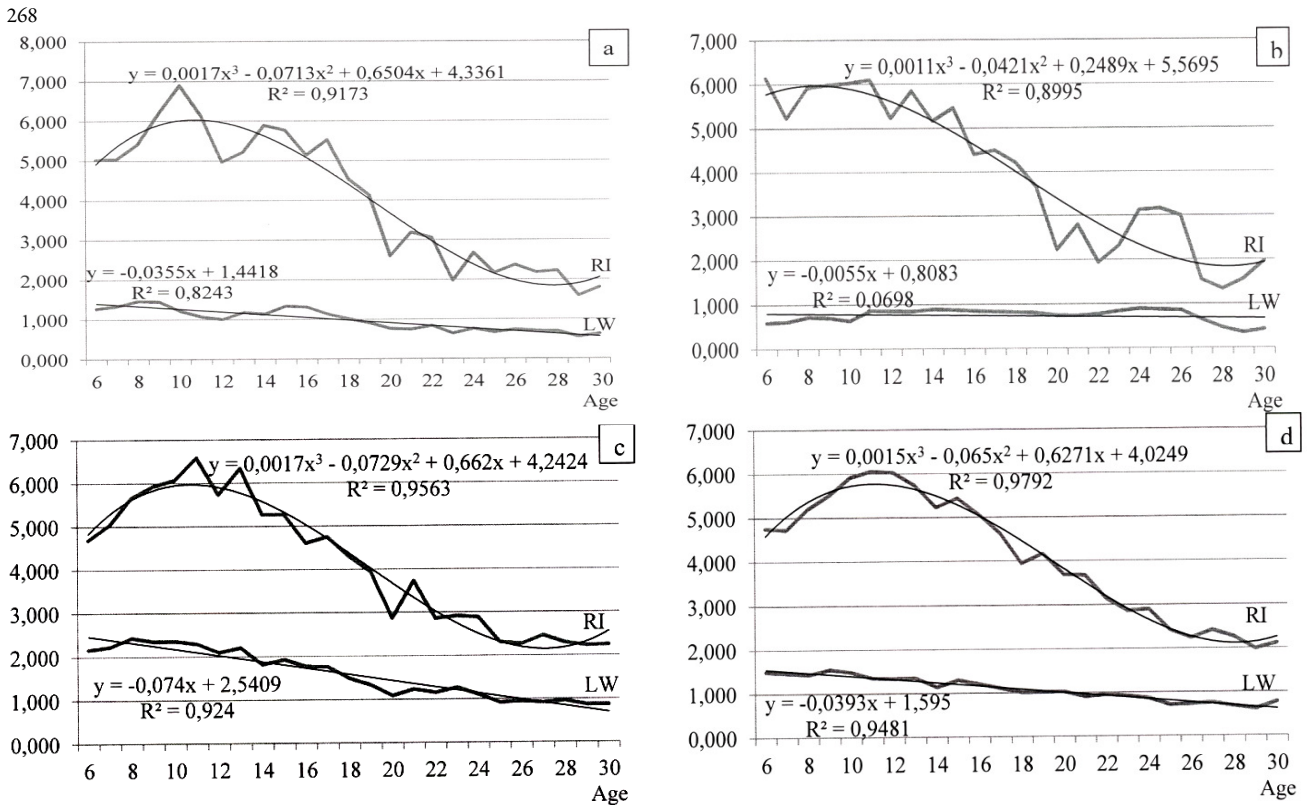


Fig. 1. The dynamics of RI (mm/year) and LW (mm/year) in field trial: a - Avrig; b - Cămpina; c - Brețcu; d - Gurghiu

comparative trials (Brețcu, Gurghiu and Avrig), the average coefficient of variation was slightly higher for EW, compared to CVLW or CVRI. The same situation, but with a much clearer differentiation was recorded in Cămpina test (ONR), where the average coefficient of variation was much higher for EW (64.4%) compared to LW (35.6%).

The experimental data obtained indicated a lower variability for the annual radial increment in the field trials located in the natural range. This suggests a higher level of adaptive homeostasis in the natural distribution area, which allows a better prediction of biomass production under such conditions. Also, the average coefficients of variation showed higher values for EW than for LW, the highest difference (of about 30 percentage units) being observed in the Cămpina field trial, outside the natural distribution area. This, once more, suggests the existence of restrictive environmental conditions in this area. On the other hand, inside the natural range, in Gurghiu field trial, the local provenance, for which radial increment was 9.1% higher than the overall average in this location, showed a reduced variation of annual radial increment (CVRI = 40.0). This value, which is by 10.9% less than the average value of the field trial, suggests a high level of stability of radial increments in the natural and optimal habitat.

Table 3. Correlations matrix between RI/5y and LW/5y

Field trial	Correlation RI/5y-LW/5y in the interval:				
	6-10 years	11-15 years	16-20 years	21-25 years	26-30 years
In the natural range					
Avrig	0.15	0.25	0.08	0.64***	0.70***
Cămpina	-0.20	0.24	0.46**	0.56***	0.36*
Outside the natural range					
Brețcu	0.83***	0.81***	0.73***	0.51**	0.65***
Gurghiu	0.49**	0.46**	0.41*	0.57***	0.74***

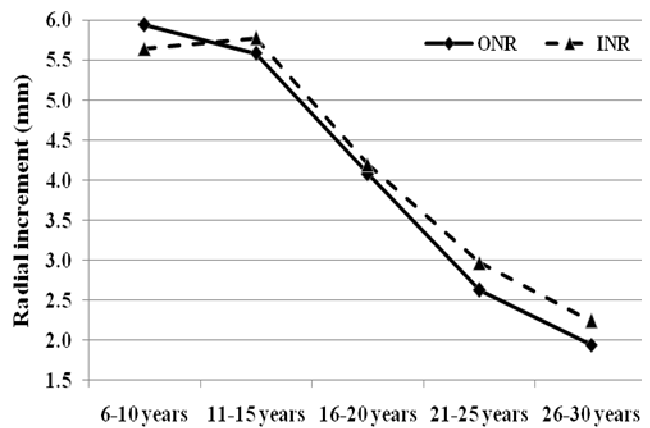


Fig. 2. The dynamics of periodical radial growth (RI/5y) between 6 and 30 years

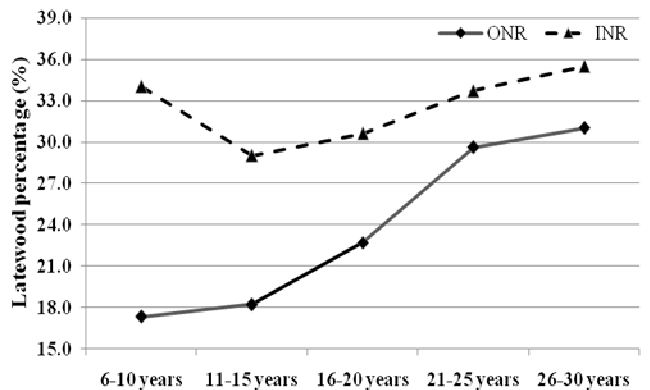


Fig. 3. The dynamics of mean values of latewood proportion (%LW/5y)

Table 4. The coefficient of variation for radial growth (CVRI), earlywood (CVEW) and latewood (CVLW)

Trial	CVRI	CVEW	CVLW
In the natural range			
Brețcu	43.6	48.4	47.3
Gurghiu	44.9	50.4	45.0
Mean	44.2	49.4	46.1
Outside the natural range			
Câmpina	52.7	64.4	35.5
Avrig	49.3	56.8	52.8
Mean	51.0	60.6	44.2

At the same time, a low interpopulational level of variability (CVRI between 8.0% and 9.6%) has been determined in all tests, including the two field trials located outside the natural range. On the other hand, compared to INR, the interpopulational variability in ONR tests was higher for latewood (15% in ONR and 10% in INR trials). Consequently, in ONR field trials the latewood proportion is lower but the interpopulational variability increased. The lower proportion of latewood at low altitude (ONR), which was negatively correlated with wood density (Jyske *et al.*, 2008; Saranpää, 2003), is a risk factor for spruce stand because of increased cavitations frequency (Hacke *et al.*, 2001).

Influences of testing site and climatic conditions

The influence of populations on the mean values of radial increment was not significant ($P > 0.05$). On the other hand, the testing site showed an important influence ($P < 0.001$) on the radial growth, including its dynamics evaluated for 5 years intervals (Table 5).

Our determinations revealed important climatic influences on the radial growth both in INR and ONR tests (Table 6). Thus, there was a great and negative influence ($P < 0.001$) of the average temperature of the growing season on the radial growth, in all four testing sites. However, these influences were significant and more intense in the first half of the growing season ($P < 0.001$), and became non-significant in the second part of the

growing season. At the same time, the radial growth was less influenced by the average precipitation amount of the ongoing or of the previous growing season (non-significant correlations).

Moreover, the populations x localities interaction was highest in the period of maximum radial increment, indicating the possibility of applying juvenile selection to identify the populations with high reaction capacity toward the local environmental conditions.

Norway spruce populations from different areas of its natural and cultivated distribution have been intensively studied with regard to the effects of climatic factors on radial increments and their dynamics (Feliksik and Wilczynski, 2009; Kahle and Spiecker, 1996; Koprowski and Zielski, 2006; Lebourgeois, 2007; Mäkinen *et al.*, 2001; Petráš and Meko, 2011; Rybniček *et al.*, 2010). Thus, in contrasting climatic conditions from southwestern Germany, the annual rings width was strongly correlated with variable climate conditions of the previous year and also of the first half of the growing season in current year; at low altitudes, a negative correlation between rings width and temperature of current summer period was determined (van der Maaten-Theunissen *et al.*, 2013). In southern Norway, at low elevations, the trees growth was restricted by the precipitation from June, while at high altitudes by the temperatures of the same month (Andreassen *et al.*, 2006). Pronounced reactivity of radial growths was recorded along an altitudinal gradient in Norway spruce populations from different parts of its range (Čejková and Kolář, 2009; Mäkinen *et al.*, 2002). Bouriaud *et al.* (2004) highlighted that intra-annual climate variations influence the radial growths and wood density. Our data indicate a negative influences ($P < 0.001$) of the average temperature of the growing season on radial growth, in all field trials ($r = -0.58^{**}$ to -0.65^{***}), but the influences of the average temperature in the first half of the growing season are stronger than in the second part of it. The negative correlations that have been determined in our study with regard to the influence of temperature in the growing season on radial increments are slightly different from those registered in eastern Finland (Miina, 2000) or in the Austrian Alps (Gindl *et al.*, 2000). These differences may be induced by the reaction of Norway spruce to the ecological specificity of the testing sites.

Table 5. ANOVA for mean radial increment (RI) and for 5-year successive intervals (RI/5y)

Source of variation	Mean squares (s^2) for all intervals and for periods of 5 years					
	RI	RI/5y (6-10 years)	RI/5y (11-15 years)	RI/5y (16-20 years)	RI/5y (21-25 years)	RI/5y (26-30 years)
Locality (L)	9.95**	10.1**	4.9***	21.9***	11.7***	11.09***
Population (P)	0.29	2.01	0.90	0.84	0.86*	0.69
Population x locality (P x L)	0.47***	3.98***	1.56***	1.00**	0.78**	0.64
Error	0.29	2.03	0.88	0.72	0.56	0.62

Table 6. Correlations matrix between the radial growth and climatic factors

Climatic factors	RI in trial:				%LW in trial:			
	Avrig	Câmpina	Brețcu	Gurghiu	Avrig	Câmpina	Brețcu	Gurghiu
AAT	-0.44*	-0.39	-0.47*	-0.53**	0.42*	0.27	-0.13	0.34
ATVS	-0.64***	-0.65***	-0.63***	-0.58**	0.64***	0.58**	0.04	0.39
ATFHVS	-0.59**	-0.66***	-0.57**	-0.54**	0.63***	0.68***	0.11	0.44*
ATSHVS	-0.33	-0.25	-0.28	-0.40*	0.26	0.09	-0.08	0.17
ATPY	-0.42*	-0.41*	-0.38	-0.46*	0.40*	0.24	-0.13	0.48*
AAP	-0.24	-0.14	-0.02	-0.18	0.11	0.02	-0.31	-0.01
APVS	-0.11	-0.11	-0.01	-0.15	-0.03	0.06	-0.34	-0.04
APFPVS	0.03	0.06	0.09	-0.12	-0.24	-0.14	-0.32	0.03
APSPVS	-0.23	-0.27	-0.19	-0.11	0.27	0.27	-0.17	-0.11
APPY	-0.29	-0.22	-0.08	-0.17	0.26	0.20	-0.12	0.09

Thus, in the cases analyzed here, it can be assumed that the relatively high temperatures in the first part of the growing season, as in Brețcu and Gurghiu trials, and even higher outside of the natural range, at low altitudes (Avrig and Cămpina trials), had negative effects on the annual ring width. Otherwise, Kahle and Spiecker (1996) identified an inverse correlation between radial growth and potential evapotranspiration from the first part of the growing season, and Petráš and Mecko (2011) reported that the high temperatures in the growing season in general negatively influenced the growth. In Cămpina field trial, where summer temperatures were the highest, the average value of annual radial growth was the lowest, but the CVRI was the highest. At the same time, Mäkinen *et al.* (2001) indicated a negative correlation between radial growth and the summer high temperatures of the previous year. A similar situation was found in low elevation stands, in south-western Germany (van der Maaten-Theunissen *et al.*, 2013). Moreover, the radial growth was to a lesser extent influenced by the average precipitation amount of the growing season of the current or previous year (non-significant correlations). However, in our study the correlations were negative and of greater intensity in relation to the amount of precipitation from the second half of the growing season, especially in the two comparative field trials located outside the natural range of Norway spruce.

Bouriaud *et al.* (2004) found a relative independence of wood density from climatic conditions in the first part of the growing season, and on the other hand, the wood density was positively correlated with the proportion of latewood (Bergquist, 1998; Wimmer and Downes, 2003). However, our results showed that the average temperature in the first half of the growing season significantly and positively influenced ($P < 0.001$) the latewood proportion in the two field trials located outside the natural range ($r = 0.63$ in Avrig trial, $r = 0.68$ in Cămpina trial). In the field trials located in the natural range, the influence of the temperature of the first half of the growing season on latewood proportion was lower. Consequently, the formation of latewood started earlier in ONR than in INR field trials. The effect of precipitation in the growing season on the latewood proportion was non-significant. A negative influence of high intensity was determined by the amount of precipitation in August.

Conclusions

Our study revealed substantial differences in the performance of Norway spruce in experimental field trials located outside and in the natural range. In Norway spruce plantations established outside the natural range we found: a change of radial growth dynamics (reduction of radial growth than in the ecological optimum); a reduction of the latewood proportion, thus affecting the mechanical characteristics and increasing the vulnerability to cavitations (Wolkerstorfer *et al.*, 2010); a greater variability than in the natural range of the width of annual rings, thus reducing the wood homogeneity; a greater amplitude at interpopulational level for CVRIA, at the same site. The temperature in the growing season negatively influenced the radial growth, while the precipitation amount had a small effect. However, the temperature in the first half of the growing season showed a smaller influence on the radial growth in the field trials located in the natural range of the species. This is another argument for the risks of planting Norway spruce outside its natural range in Romania.

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