SITE AND SPECIES INFLUENCE ON TREE GROWTH RESPONSE TO CLIMATE IN VRANCEA MOUNTAINS

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The actual climate change scenarios predict significant changes of the current growing conditions that will impact Carpathian forest ecosystems productivity. To investigate the potential for differential species and site specific responses, we compared the growth of three of the major coniferous species, Scots pine, Norway spruce and silver fir, growing in mixture in the same stand. We also compare the response of Scots pine growth on two contrasted situations, one on south dry site and the other on plateau. Our experimental sites were chosen to be representative of the mountainous Eastern Carpathian forests where pine occurs naturally.

In order to investigate the consequences climate fluctuations at different temporal scales, we examined both inter-annual growth variations and decadal signals in tree-rings in relation to climate.

Our study reveals a differentiation between species in climate sensitivity. Pine was overall the most sensitive to precipitation, while spruce showed a higher response to temperature at high frequency of both the current and the previous years growing season. Fir was different in that it was the least sensitive of the comparison. However, for both species, decadal signals show precipitation as a common and strong productivity driver of trees on the dry south-facing slopes. Pine on the plateau responded more to the interannual fluctuations in precipitation than on the steep slope site.

Key words: Dendroclimatology; Norway spruce; Silver fir; Scots pine.

INTRODUCTION

Trees have been known for more than fifty years as being very sensitive to fluctuations in climate. Literature abounds of reports relating the strong dependence of growth and productivity on climate. Variation in radial growth rate, studied mostly by the means of radial core, was proved to be linked to either precipitation regime or temperatures in many species, but with noticeable variations between species in the sensitivity. Also, the topographic situation and the edaphic local conditions modulate trees response to climate[16]. The interaction between variations in environmental constraints and trees sensitivity drive the diversity of forest types and structure at landscape level, with clear altitudinal stratification in mountain[18]. With the fast changes in climate reported and thought to be worsening, the vulnerable Mountain forest ecosystems experience deep mutation pressure and the question of their adaptation, the migration of the species and its consequences on the landscape is raised. One of the species that could be particularly concerned is Scots pine.

Scots pine recently experienced severe diebacks in the dry inner-alpine valleys of Switzerland[12, 35]. The extent of the mortality is large enough to raise uncertainties about the survival of these stands because of the[34]. This species is particularly exposed to any changes because the recent increases in mean annual surface temperatures reported in Europe[24] are likely to decrease the water availability while Scots pine is already encountered on dry sites. Scots pine could therefore be threatened in Carpathian Mountains as well. Indeed, similarly to the Alps where pine forests are covering the lower slopes, Scots pine is occurring naturally mostly in the south-facing dry rocky slopes in Carpathian Mountains, sometimes in mixture with fir and spruce[39]. On these sites, the topographic position is worsening the water balance during drought episodes by increasing both its length and its intensity. It is hypothesized that Scots pine growth would respond very strongly to climate fluctuations and that its productivity could decline in response to trends in climate.

Another limitation to pine productivity in the situation of increasing drought frequency is its ability to compete against spruce and fir whenever they grow in mixture. The three species could differ in their sensitivity to climate, due to specific biological demands. A change in the equilibrium triggered by higher water or heat stress could relatively favor, or affect, a given species, therefore modifying the competition between species. More generally, the change in the dominance of a given species leads to dramatic modifications of forest structure, as being largely controlled by the interaction between trees and species composition. Forest productivity, its resistance to wind and snow-damages would be affected. Further, species diversity and landscapes could thus be strongly impacted, with large economic and ecological consequences.

Our study aimed at comparing the sensitivity to climate of the three major species growing in mixture in steep south-facing natural stands in Carpathian Mountains: silver fir, Norway spruce and Scots pine. Also we compare the effect of site on Scots pine's response to climate by choosing a contrasting well watered site located on a plateau, near to the precedent. We put the accent on their specific responses to high summer temperatures and variations in precipitation regime. Their co-occurrence on the south-facing site offers a means of comparing species having exactly the same environmental constraints and to have a point of comparison for understanding pine ecology. The existence of species-specific variations of climate influence on growth was rarely adequately assessed because it supposes to have a very conservative edaphic and dendrometric trial where only the species varies but not their growing conditions. The occurrence in the same stand in the social position is a unique opportunity for such study. Finally, regarding the large-scale decline of Scots pine in Alps, the potential of a depression of productivity in Carpathian Mountains is discussed.

MATERIAL AND METHODS

Sites

Our study is based on a dual comparison. First, two pine stands located on contrasted situations were compared: one in a south-facing steep slope site, typical for this species, another one on a plateau at only a few kilometers away. The difference in the hydrological position between these two sites is purposely maximized. The second comparison aims at estimating which of Scots pine, Norway spruce and Silver fir shows the greatest growth's response to climate. This inter-specific comparison is undergone on the south-facing site exclusively.

This last site was chosen to be representative of the coniferous south-facing sites where Scots pine occurs naturally, mostly in mixture with spruce and fir. The site is located in Vrancea Mountains at 45°36'18 N, 26°41'55 E, the altitude was around 1200 m (Fig. 1). This site that lies at the extremity of the hydrologic gradient is offering limiting conditions for each species: steep slope (45°), shallow soil (circa 20 cm) with a reduced water holding capacity in spite of the clayey soil. The soil is superficial with a high stone charge. The stand was composed by spruce, fir and pine with 50%, 30% and 20% of basal area respectively. The stand was uneven-aged with ages typically ranging between 5 to 200 years. They were no traces of disturbance and it should be underlined that no human activity is known in this stand, mainly because of the inaccessibility.

The plateau site was located at a reduced distance from the south-facing site. This second site is located at 45°36'32 N, 26°41'22 E, the altitude was 900 m. It is characterized by a much deeper soil, no slope and a neutral hydrologic situation. The stand is under management plans and cuttings were observed in field.

Climate

Instrumental meteorological data for this area were available only from 1961 to present, from the Lacauti weather station (45°49' N, 26°23' E). Average temperature along the instrumental period was +1.27°C with a maximum in July (10.14 °C), and annual precipitation 654 mm. In order to extend the instrumental data we realized an interpolation based on the 10'×10' resolution CRU2.1

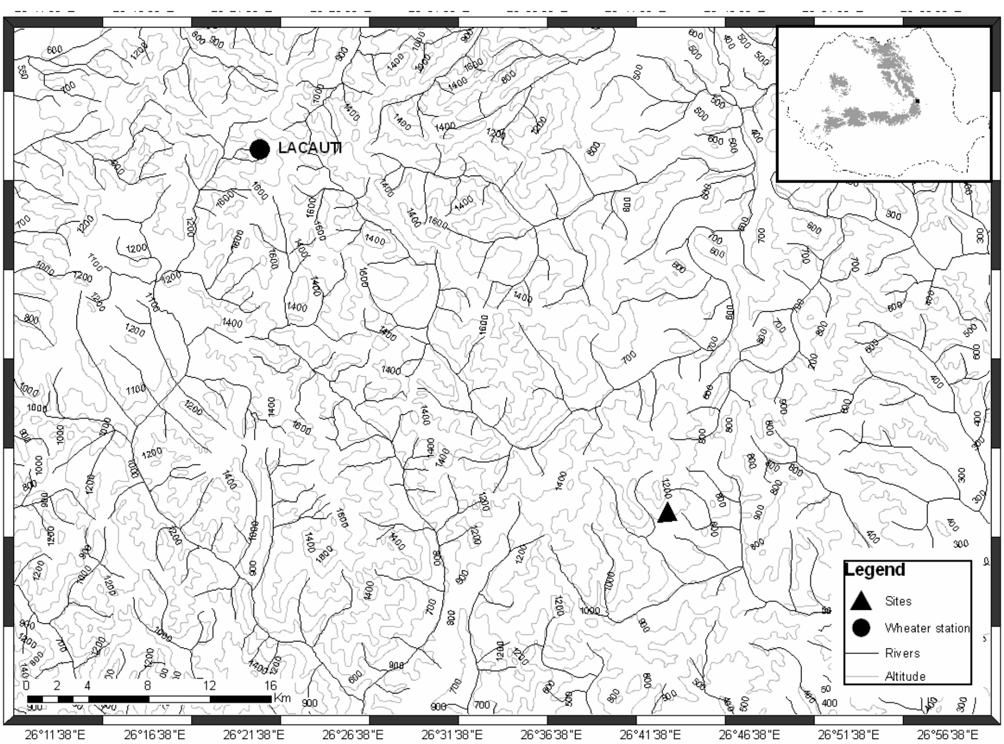

Fig. 1. Map of sampling sites and weather station location.

grid data-basis downloadable at (http://www.cru.uea.ac.uk/~timm/data/index-table.html)[28].

Monthly precipitation, minimum and maximum temperatures were computed over 1901–2003 by inter-calibration between gridded data at the closest contiguous cells and the available instrumental data. The coefficient of determination of the relationship derived between the reconstructed and the measured climate series ranged between 0.90 to 0.95 for monthly temperatures and 0.6 to 0.8 for precipitations.

Tree-ring processing

According to the standard dendrochro-nological procedures[16, 31], 15 to 20 trees of each species or each site were sampled at two opposite directions at breast-height, on the cross-slope sides. Trees sampled were all locally dominant, showing no visible damage. Ring width series were measured using a digital positioning table (Lintab) with associated software (TSAPWin)[37] at a precision of 0.001 mm. Individual series were checked for missing rings and dating errors using the program COFECHA[20] prior to detrending. This fundamental step aims at ensuring that each rings is correctly associated to its corresponding calendar date and constitutes a true quality-process test[17].

Individual ring-width series were transformed into basal area increment (BAI) using a simple geometric model ($BAI_n = \Pi d^2_n - \Pi d^2_{n-1}$) where d_n is the radius of the stem at year n as quadratic mean of diameter obtained by both cores. In plus of offering a better representation of trees productivity[14, 25], BAI series have the advantage of avoiding the end-effect problems otherwise frequently encountered in the detrending. They also achieve better variance homogeneity along the series than ring width series. A stiff spline with a 50% frequency response cutoff in 200 years was fitted to the individual series to remove the low-frequency signal variation caused by ageing (Fig. 2). The BAI indices were calculated as the ratio between observed and fitted values and averaged by species to form the inter-decadal and higher frequency chronologies referred to as standard chronology further. A smoother 10-years spline was further fitted to the individual BAI indices resulting from the first phase. The smooth splines fitted were considered as representing the decadal variations in trees growth[9, 2]. Predicted values were averaged by species to form the decadal BAI chronologies. High-frequency BAI indices were subsequently calculated as the ratio between the indices calculated by the first spline fit and prewhitened using a first- to second-order auto-correlation model.

The average correlation coefficient between individual series and mean chronology as well as the first-order autocorrelation coefficient (AR1), the mean sensitivity (MS) and the signal-to-noise ratio (SNR) were computed as a description of the fundamental chronology quality and potential in climate-growth analysis[16, 42] over the common period of the series 1875–1900, and over the period for which climate information are available: 1901–2003.

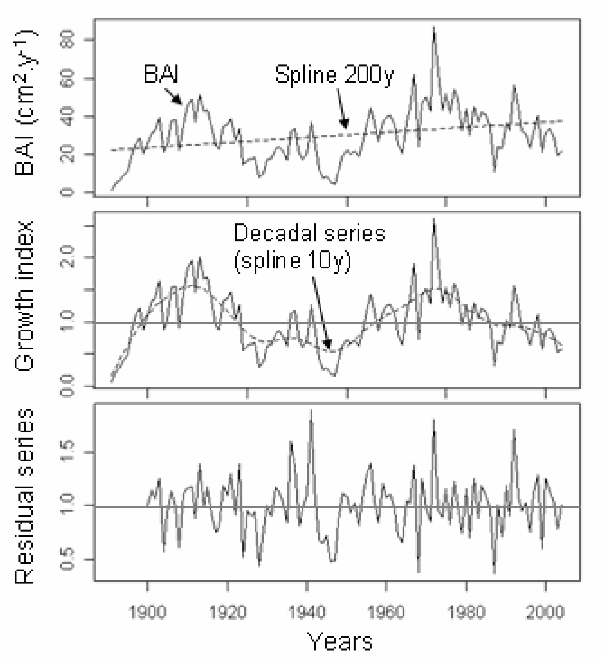

Fig. 2. Different phases of detrending used to generate both decadal and high-frequency series.

The mean sensitivity is defined as:

$$MS = \frac{1}{n-1} \sum_{i=1}^{n} \frac{2(x_{i+1} - x_i)}{x_{i+1} + x_i}$$

where: x represents the ring width of the ith year, n the length of the series.

The signal-to-noise ratio is defined as:

$$SNR = N \cdot r / (1-r)$$

where N is the number of trees, r is the average Pearson correlation between trees. The expressed population signal (EPS) is defined as:

$$EPS = N \cdot r / (N \cdot r + 1 - r)$$

Climate-growth relationship

Relationships between the climatic variables and standardized BAI series were analyzed by computing correlations with monthly climate data. Computations included climate data from the year prior to growth, as carry-over and lagged effects are observed frequently on coniferous species. Additionally to these monthly estimates, yearly and seasonal estimates were computed that represent respectively the annual climate, and the climate prevailing during the growing season. The annual sum is computed from September of previous year to current-year August included, while the seasonal climate from April to August.

The correlations were computed for each climate data (*e.g.*, monthly, seasonal or yearly climate series)[3, 16]. Decadal variations in climate data were extracted using the same methodology than the one used for BAI indexes (10-years fixed spline) in order to analyze the influence of climate on tree growth at this larger time-step.

RESULTS

Comparison of the growth rates and main growth characteristics

Spruce was having the fastest growth amongst the species growing in the slope site, followed by Scots pine and then Silver fir (Table 1). A comparison of BAI time-curse as a function of tree age shows a divergence between species, spruce being the most productive species at all ages (Fig. 3). Fir and pine strongly differ in the dynamic of their production as the optimum is reached at young stages in pine (50 years old already) but decreases fast, while in fir productivity increases continuously and remains at high levels even for old individuals. The effect of site on pine growth is more pronounced. Pine growing on the plateau was 50% faster than on the sloped site, therefore growing even faster than Spruce on this last site.

Table 1

Growth characteristics of the pine, spruce and fir trees sampled. The mean sensitivity (MS) is a measure of the year-to-year variability and SNR is the signal-to-noise ratio. AR1 is the first-order autocorrelation coefficient.

Species	N	MS	SNR	AR1	Mean ring width (1/100 mm) for 0–100 years old
Fir	31	0.250	33.9	0.774	186.96
Spruce	36	0.259	76.2	0.615	223.82
Pine on steep slope	40	0.269	53.1	0.675	179.22
Pine on plateau	44	0.301	58.4	0.518	270.40

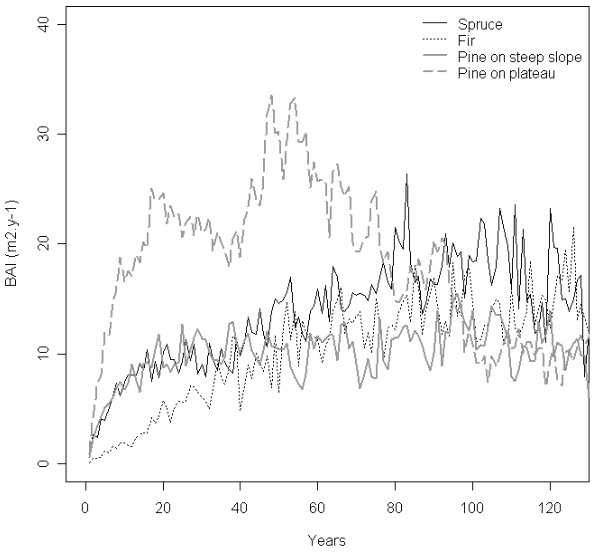

Fig. 3. Comparison of the growth dynamic of three coniferous species growing in the same site in Carpathian Mountains, respective, comparison of pine growth on two contrasted sites.

Fir had the lowest MS and SNR (Table 1) but the auto-correlation was the highest. Spruce had the largest SNR and inter-tree correlation. Pines on plateau show higher MS and SNR than on the steep slope site while the auto-correlation is strongly reduced. MS in plateau is sensibly higher than for other site or species. In spite of these differences, the expressed population signal exceeded 0.97 for all species for the common period, indicating a large potential climate signal for all chronologies regardless of the site.

In the south-facing steep sloped site, the residual chronologies of the three species were significantly correlated to each other but the correlation matrix showed that growth variation in spruce and pine are more similar than spruce and fir or pine and fir (Table 2). The correlations of residual chronologies confirm the differentiation of fir inter-annual variations from pine and spruce ones (Fig. 4) with a minimum correlation of 0.606 between residual series for pine and fir surprisingly low for trees growing in the same stand.

Table 2

Correlation between residual series estimated for the climate period (1901–2000)

Species	Spruce	Pine on steep slope	Pine on plateau
Fir	0.695	0.606	0.608
Spruce	–	0.772	0.666
Pine on steep slope	0.772	–	0.852
Pine on plateau	0.666	0.852	–

Response of growth to climate fluctuation at interannual time step

The overall pattern of climate response of the three species was quite similar (Fig. 5) showing both a positive influence of spring precipitation (April, May), July precipitation, and a significant influence of the climate of the previous year, in August and September, up to June for Spruce.

Temperature had an opposite influence than precipitation, and tended to be less significantly correlated, as also expected considering the topographic situation. Some variations between species were noticeable. Spruce was more sensitive to both temperature and precipitation of the previous year (July to September) than pine or fir, and more correlated (negatively) to summer temperatures of the current year (significant in June, July and August). On the other hand, Fir was strongly and positively correlated to December temperatures. Pine was the most responsive to precipitation with high correlations in April, March and July. A significant and negative influence of temperatures was seen only in September of year prior to growth. Over the round year or the growing-season period (May to August, represented by MJJA in Fig. 5) spruce shows its particularity by presenting no significant correlation while pine clearly was the most responsive species.

If the response of Pine to temperature was not differing amongst sites, on the other hand, it showed a marked difference in its sensitivity to precipitation fluctuations, but not in the sense hypothesized. Indeed, the strongest response was not observed on the steep slope site where drought are supposed to be longer and more intense, and trees growing in the plateau systematically present higher correlations throughout the year.

Decadal variations in growth in relation to climate

Decadal growth chronologies were showing a very high similarity with climate ones and a stronger dependence on the precipitation regime. Correlations with precipitation were ranging from 0.68 to 0.76 for Pine and Spruce respectively (Fig. 6) on the steep slope site. Pine on plateau is clearly less sensitive to variations in precipitation regime at decadal time step as it responds solely to the largest changes (around 1920 and 1975) and its growth is otherwise fairly even although seemingly conserving trends at longer timescales.

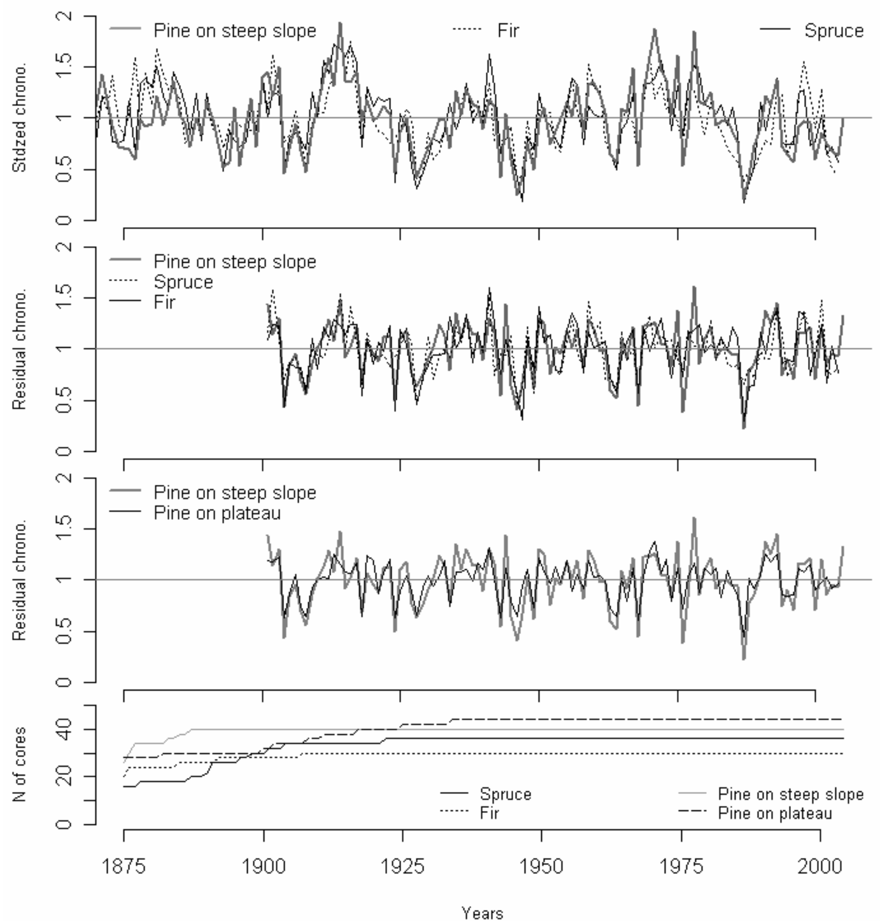

Fig. 4. Comparison of the chronologies resulting from three different species growing in mixture in the same stand: standard chronologies (up) with the corresponding residual chronologies for the period 1900–2004 (middle) and sample depth (bottom).

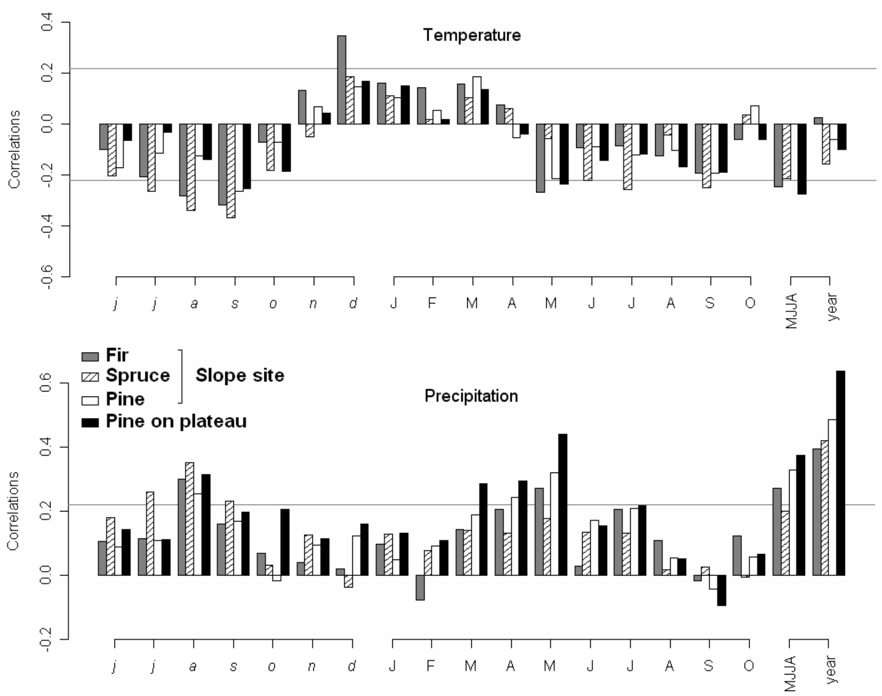

Fig. 5. Comparison of the correlations between monthly or seasonal climate (italic letters for month of previous year) and growth chronologies during the period 1901-2003. Horizontal gray lines represent the limit for p<0.05 (*i.e.*, 95% significance).

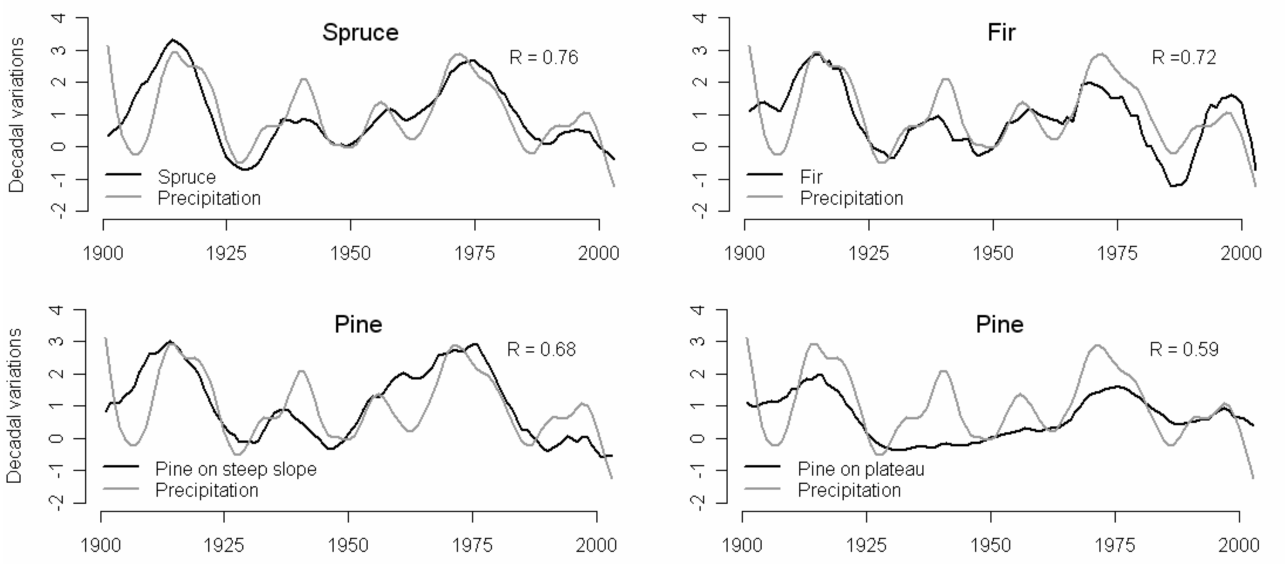

Fig. 7. Decadal variations in growth and yearly climate (precipitation, top, and mean temperature, bottom, each decadal anomalies) over the last century for the three species growing in the same stand. The Pearson coefficient of correlation between the two curves is inserted.

DISCUSSIONS AND CONCLUSIONS

Between-species comparison

All three species showed a remarkable common response to precipitation at decadal time-scale, which can be largely explained by the water-limiting growing conditions imposed by a steep slope and the shallow soil. Species-specific differences in sensitivity to climate fluctuations were expressed at inter-annual frequency. At this frequency, Fir growth proved to be noticeably less influenced by climate than spruce or pine. A reduced sensitivity was expected as the SNR was only half that of other species one, and this apparent lack of response to climate was already reported in previous dendroclimatic studies. Its tree-ring series are said to contain more non-climatic signal than other species[41]. Spruce was the most sensitive to temperatures and had stronger carry-over effects. The fact that pine was the most responsive species of the comparison is unexpected because this species is known as a drought resistant one [13, 29, 34]. A higher productivity could have triggered a higher demand, as a higher transpiration would expose more trees to drought effects, but the fastest growth is actually observed in spruce. These results therefore do not indicate a higher ability of pine to manage limited water resources. In turn, pine may well resist better to extreme droughts, but our study shows that fir and spruce achieve a larger productivity in the site studied and do not reduce their growth in as much as pine does during dry years.

Influence of the site on the impact of climate on growth

It has been known for a long time that site conditions modify trees response to climate, and our results bring a new example to this feature. However, un-conformingly to the hypothesis formulated, pine trees were responding more to precipitation fluctuations on the plateau site with a deep soil than on the steep slope site with a shallow soil. A high dependence of growth was expected on the dry site and is not as obvious in the context of a site with favorable conditions. However, several factors contribute to this apparent contradiction. First, more contrast was present in the rings of the faster growing trees. Trees growing on the dry site are probably more depending on precipitations to achieve their annual growth but are likely to experience constraints much more often, which would tend to make their rings more uniformly narrow. Second, the higher productivity observed on the plateau is the result of a faster growth which implies a higher evaporation rate made possible by a larger water reserve. But the larger reserves and evaporations are balancing out and the result is that trees having more potential available resource are not depending less on the yearly supply. However, the results clearly show that the decadal fluctuations in precipitation do not affect as much the trees growing in a thicker soil. At this time-scale, the larger reserve enables the trees to buffer or adapt to changes in precipitation regime, and this could have strong implications in the case of repeated drought episodes where a severe depression could be observed in each situations but with far less consequences on long-term productivity for trees growing on the plateau.

Species-specific responses to climate

Fir growth proved to be positively correlation to winter temperature, limited to December in our study, but highly significant. This particular sensitivity to winter climate was already reported[10, 11, 26] and seems to be specific to fir. In a spruce-fir mixed stand of Eastern Carpathians ca. 300 km away, [30] reported a positive and significant influence of winter temperatures from December to March on current growth. Fir was a little older than the other species which could have minimized its response to climate as trees response to climate decreases when trees age [7]. Unlike pine, fir is a species very shade-tolerant, spruce can be considered as an intermediate as it withstands temporal shading [22]. Fir trees sampled in our analysis may have experienced a change in their social position as it is usual for this species to grow below the canopy in its young stage. This could explain too the lower growth rate observed at young stages, which could denote that trees were shaded. We detected abrupt variations in the growth rate in two of the 16 individuals studied only, both occurring in 1964, but we cannot rule out a progressive change towards clear dominance for the other trees. The change in the social status might have influenced the response to climate fluctuations as it has been shown that there are interactions between social status and climate sensitivity [33].

Norway spruce showed the largest productivity but the weakest response to precipitation, and its modest response to precipitation is surprising for such a dry site. This shows the impressive capacity of this species to buffer interannual fluctuations of precipitation. Its ability to maintain a shallow vertical fine root distribution pattern even in mixture with other species [4] could enable a more complete capitation of precipitation which is particularly important in the situation of a shallow soil and a high lateral water runoff. A high response to temperature in high-elevation or high latitude sites were reported for spruce trees growing in Germany and Ferroscandinavia [15, 1, 32], where growth is limited by low air temperature. [10] for high elevation sites in Alps and [38] in the Tatra Mountains also showed a positive influence of temperature during the growing season. On the contrary, our study shows a negative influence of temperatures. These correlations were reflecting a greater water-stress induced by a high evapotranspiration demand during hot days. Spruce growing on lower altitude on a plain in Eastern France had shown the strong dependence of radial growth on soil water reserve at intra-annual time-step and pointed out the influence of drought on wood formation [5]. Our study also pointed out a stronger sensitivity of growth to climate of the previous year, which has been documented substantially for spruce [10, 21, 40].

Scots pine is known as a drought-resistant species maintaining a tight control over its transpiration and preventing the development of a widespread embolism [8, 23]. It is also known as a good species for climate-growth analysis and has been used intensively in numerous climate reconstruction studies [6, 19, 27]. For trees growing in Alps in a similar situation to the one we studied, that is, on steep slopes of the inner-alpine Swiss Alp valleys, [29] found a strong response of pine growth to spring precipitation [35, 36] report a significant influence already in March. In our study, trees response was not limited to the spring but persisted throughout the whole growing season, while temperature was not found to be significantly influent at high frequency.

Our study pointed out a stronger sensitivity to interannual precipitation variations and to decadal temperature modulation in pine. Pine sensitivity to climate on the steep slope site was the largest of the comparison, which indicates that this species would be more affected by a change of the climate regime towards dryer conditions than spruce or fir. Therefore, even if climate do not shift towards extremes that pine could not withstand, the disappearance of this species could occur as a result of a stronger reduction of growth in pine than in spruce or fir. Our study thereby confirms the threat on pine in case of more frequent drought in future also in Carpathian Mountains.

Also we showed the great potential of the tree-ring in Carpathian Mountains for dendroclimatic studies. Further investigations will be necessary to extend to other species and ecological conditions.

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