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Forest Ecosystems in a Changing Environment: Growth Patterns as Indicators for Stability of Norway Spruce within and beyond the Limits of its Natural Range

Waldökosyteme in einer sich verändernden Umwelt: Wachstumsmuster als Indikatoren für die Stabilität von Fichtenwäldern innerhalb und außerhalb ihres natürlichen Verbreitungsgebiets

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Abstract

Norway spruce is one of the most common and economically important tree species in northern and central Europe. Its area has expanded far beyond the limits of its natural range. Changes in climatic conditions such as changes in the frequency and intensity of extreme warm and dry weather may seriously affect Norway spruce growth. We hypothesised that especially sites outside of its natural distributional range might be under risk. In the present paper, we were able to demonstrate that indeed sensitivity of radial growth of Norway spruce to changing weather conditions is significantly increased on sites outside of its natural range.

Zusammenfassung

Die Fichte (*Picea abies* L. Karst.) ist eine der häufigsten und wirtschaftlich bedeutsamsten Baumarten in Nord- und Mitteleuropa. Ihr Verbreitungsgebiet hat sich weit über die Grenzen ihres natürlichen Vorkommens ausgedehnt. In Gebieten außerhalb ihrer natürlichen Verbreitung wird das Fichtenwachstum in einem stärkeren Maße durch Veränderungen der klimatischen Bedingungen sowie Veränderungen hinsichtlich Häufigkeit und Intensität von extrem warmen und trockenen Wetterlagen beeinflußt. Es konnte gezeigt werden, daß die Fichte in Gebieten außerhalb ihrer natürlichen Verbreitung sensitiver auf Witterungsschwankungen reagiert als auf Standorten innerhalb ihres natürlichen Verbreitungsgebiets.

1 Natural and actual range of Norway spruce in Central Europe

In Scandinavia, the Baltic and parts of Russia, natural Norway spruce (*Picea abies* L. Karst.) dominated forest types cover extensive contiguous areas, whereas the largest area in Central Europe in the Alps is discontinuous (Figure 1). The few other natural ranges of Norway spruce are enclaves in lower mountain regions such as in the Black Forest, the Harz, the Bavarian Forest and the Ore Mountains. Those forest types in Central Europe where Norway spruce plays a major role are classified as montane spruce and fir forests (BOHN et al. 2000). In these forests Norway spruce and silver fir (*Abies alba* Mill.) are the dominant tree species, accompanied by European beech (*Fagus sylvatica* L.) and admixed with sycamore (*Acer pseudoplatanus* L.), and other broadleaved tree species.

In many central and northern European countries the area of Norway spruce has expanded far beyond the limits of its natural range (SPIECKER 2000). In Baden-Württemberg for example 44.7 % (626.000 ha; HRADETZKY 1995) of the forest land is covered by Norway spruce. Forest types with naturally high Norway spruce percentages would only cover 16.8 % (105.000 ha) of the land surface in this region (data based on BOHN et al. 2000). This expansion was caused by the increased importance of Norway spruce as a readily established, fast-growing tree species with a wide ecological potential and its high potential to produce valuable timber.

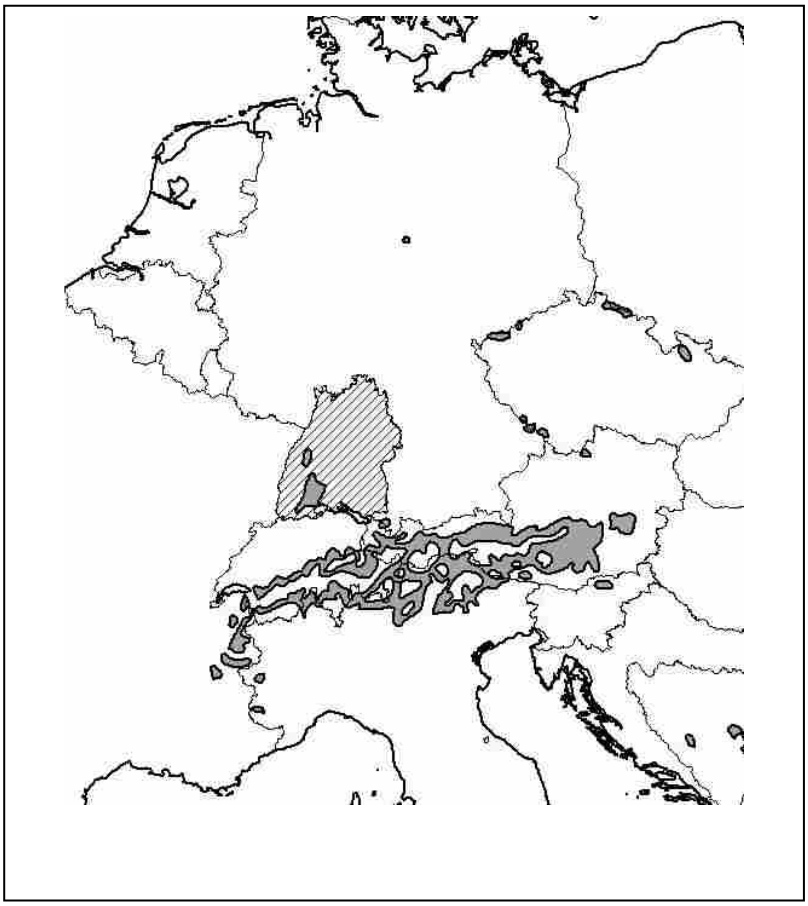


Figure 1: Natural range of Norway spruce (grey background) in Central Europe. Baden-Württemberg with diagonal lines (BfN, 2000)

Some of the major factors limiting its natural range are climatic conditions such as drought periods in summer, frost dryness and late frost (SCHMIDT-VOGT 1991). At the xerothermic limits of its natural range, Norway spruce grows on moist northern slopes and in areas where summer precipitation is relatively high.

2 Growth patterns as indicators for stability of Norway spruce

In Baden-Württemberg, suitable conditions are available to analyse growth of Norway spruce both within and outside its natural range: on the one hand there is a large area with a natural occurrence of Norway spruce in the Black Forest; on the other hand this region, due to its rich topography, is characterized by a wide range of sites with distinctly different climatic, geological and pedological conditions where Norway spruce can be found today. In most parts of northern Baden-Württemberg altitude and precipitation are lower, but the soils are more clay-rich than in the southern parts. The Black Forest is characterized by more or less acidic geological formations and higher precipitation.

Today much information about the natural resources and conditions in Baden-Württemberg is available in form of regionalized variables maintained in geographical databases. This offers the possibility to apply geostatistical methods to analyse spatial patterns and relationships between, e.g., geology, soil, climate and growth patterns of Norway spruce. The retrospective growth data we have used for this study have been derived from stem analyses of Norway spruce sampled on a systematic 4 km x 4 km grid in Baden-Württemberg, comprising altogether more than 3,000 sample trees. Tree-ring and foliar-nutrient analyses as well as a soil inventory on a subset of the grid points have been conducted in 1983 and 1988 by the Forest Research Centre Baden-Württemberg, FVA (EVERS & SCHÖPFER 1988; HILDEBRAND & SCHÖPFER 1993; FVA 1999). The analyses described in the following chapter give an overview on the growth behaviour of Norway spruce in a spatial and temporal perspective. Based on these findings, conclusions are drawn regarding the stability of Norway spruce under changing environmental conditions.

3 Results

3.1 Site classification

According to their site and location, the analysed Norway spruce sample trees were classified into the four most widespread main forest formations in Baden-Württemberg (Table 1). The dominant potential natural vegetation (PNV) in Baden-Württemberg are “beech and mixed beech forests” (PNV-Code 3). Most of the sample trees are classified into this formation. Nearly 200 trees were sampled in the area of natural “spruce and fir forests” (PNV-Code 7). The topographic and bioclimatic conditions in this area are distinctly different from those in the other formations: the average altitude is close to 900 m a.s.l., mean temperature during the growing season (May to September) is significantly lower and mean seasonal precipitation sum is significantly higher.

Table 1: Number of Norway spruce sample trees classified into the four most widespread forest formations of the potential natural vegetation (PNV) and corresponding average altitude, mean seasonal temperature and mean seasonal precipitation sum.

Forest formation (PNV)		**Oak forests**	**Beech forests**	**Oak-Hornbeam forests**	**Spruce and Fir forests**
PNV-Code		1	3	4	7
Sampled spruce trees	N	36	1850	163	194
Average altitude	m	481	607	424	873
Mean seasonal temperature (May-Sept., 1961–1990)	°C	14.4	14.0	14.9	12.3
Mean seasonal precipitation sum (May-Sept., 1961–1990)	mm	390	500	410	580

3.2 Comparison of physical soil and foliar nutrition properties

The box plots in Figures 2 to 6 illustrate the distribution of three important growth-influencing factors among the different PNV formations, according to water-supply, maximum rooting depth, plant available soil water storing capacity and potassium content in needles.

In addition to the soil and foliar nutrition factors, the corresponding box plots for the site index (mean annual volume increment at base age 100 years, $m^3 \cdot ha^{-1} \cdot yr^{-1)}$ and the mean sensitivity of annual radial increment of the Norway spruce sample trees are given. The site index is an indicator for the site productivity of forest stands, in this case according to the yield table of WIEDEMANN (1957).

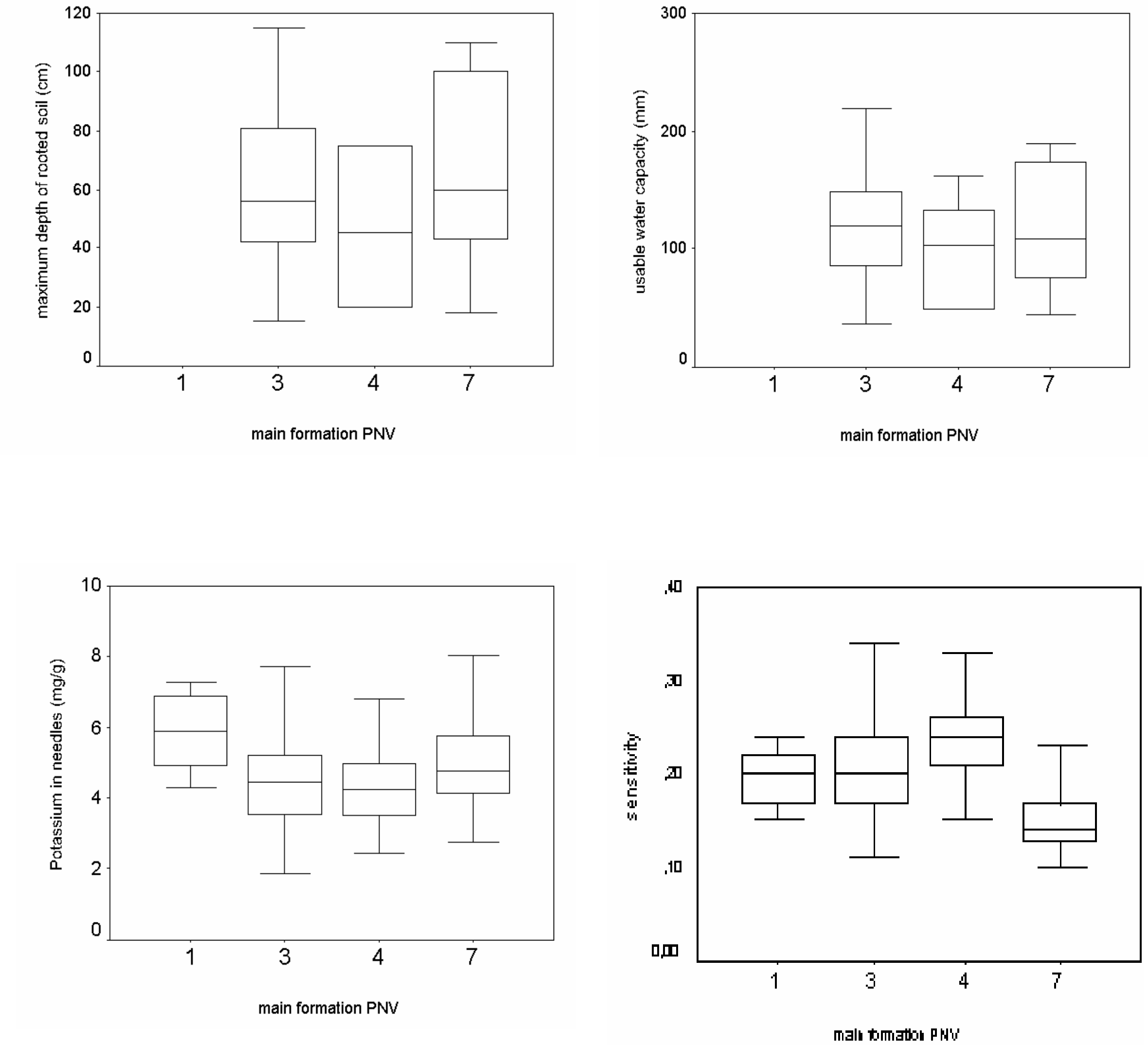
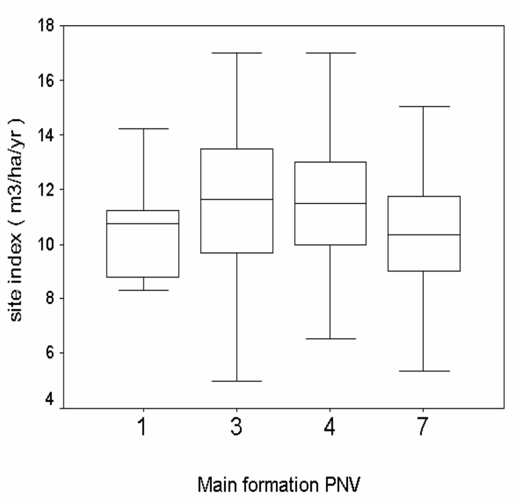


Figure 2-6: Box-Plots with median values (horizontal line), 50-(box) and 75-(whisker) percentiles of maximum rooting depth, plant available soil water storing capacity, potassium concentration in needles and mean sensitivity of annual radial increment as well as site index of spruce trees (mean annual volume increment according to yield table Wiedemann, 1957) classified in different main formations of PNV in Baden-Württemberg.

PNV-Code: 1: oak forests, 3: beech forests, 4: oak-hornbeam forests, 7: spruce and fir forests.



The mean sensitivity is a measure of the mean relative change between subsequent radial increments (SCHWEINGRUBER, 1988).

Differences between the median values were tested by ANOVA (Duncan-Test) and the Kruskal-Wallis-Test in case of inhomogeneous variances. The physical soil factors for the “oak forest” type (PNV-Code 1) were left out in the figures because soil information was not available in all plots and the number of sample trees was too small for a meaningful calculation.

On sites within the natural distributional range of Norway spruce (PNV-Code 7), the soils are further developed and on average the trees tend to root deeper than on “oak-hornbeam forest” sites. However the median values of the maximum rooting depth among the analysed main forest formations were not significantly different.

The depth of the rooting zone is an important determinant for the plant available water storing capacity of the soil. Therefore the corresponding box plots are similar. However it can be observed that the plant available soil water storing capacity at the “oak-hornbeam forest” sites is not as different as the rooting depth. This is attributed to the enhanced clay fraction in these soils. Soils in “spruce and fir forest” sites in Baden-Württemberg often are characterized by a remarkable sand fraction which leads to a reduced water capacity.

Potassium is an important macro nutrient which affects the drought stress susceptibility of conifers (BRÜNING 1959). An important indicator for the level of potassium supply is the potassium concentration of the needles. The box plots show that spruce trees in the area of their natural range have higher foliar potassium contents than spruce in the beech-dominated areas. However the highest contents are found in spruce needles on sites naturally dominated by oak. For this parameter the difference of the median values between PNV-Code 1 and 3 is significant. This finding is remarkable since natural oak and natural spruce forests in Baden-Württemberg often grow on acid soils with low cation content (widespread soil types are podzols or acid brown-earths). But the observation can be explained under the consideration of an antagonism between potassium and calcium (BRÜNING 1959) and therefore on typical lime soils like on the Swabian Alb or the foothill zone of the Alps (mostly PNV-Codes 3 and 4) potassium is taken up by spruce less strongly as on acid soils.

The site index reflects the productivity of the Norway spruce stands on the different site types. The median productivity of the investigated sample trees among all areas lies between 10.2 and 11.7 m^3 of wood per hectare and year. Although Norway spruce experiences some unfavourable conditions in its natural area, such as a shorter growing season as in the other areas, the growth index is not significantly lower than on warmer sites. Obviously higher precipitation compensates this growing factor (see also Table 1).

The mean sensitivity of the annual radial increment is calculated over the period 1922 to 1983. A high value on the average indicates rapid and strong changes of radial increment between subsequent years. The median value of the Norway spruce sample trees in their natural range is significantly lower than in the other classes. The sensitivity in the “oak-hornbeam forest” is highest although the values of the plant available water storing capacity of the soil or the supply with potassium on average were quite similar.

3.3 Comparison of spatial patterns

In order to compare spatial patterns between the variables of interest, continuous maps were calculated using Kriging on the basis of the available point information (MATHERON 1955; 1963). As a meaningful parameter for the behaviour of the diameter growth of trees, the mean sensitivity was chosen. This variable is compared with the spatial pattern of the mean precipitation during the growing season. The spatially interpolated monthly precipitation data have been provided by the German Weather Service (see MÜLLER-WESTERMEIER 1998).

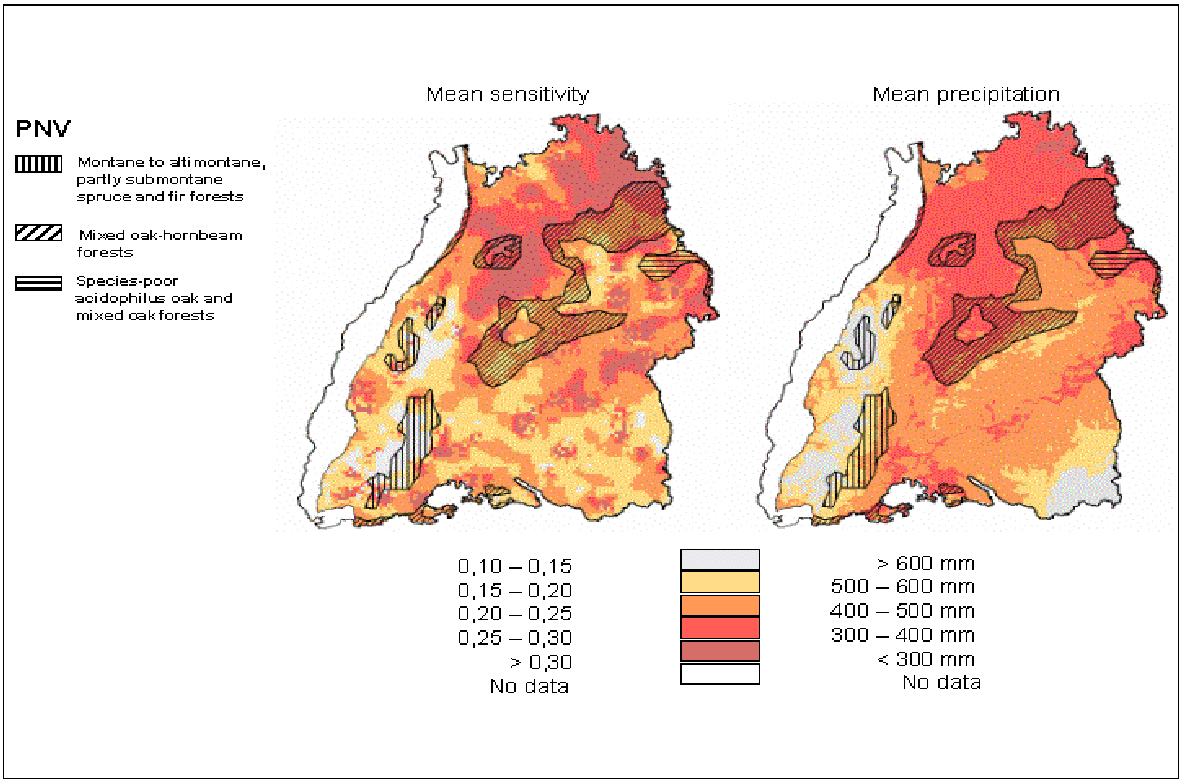
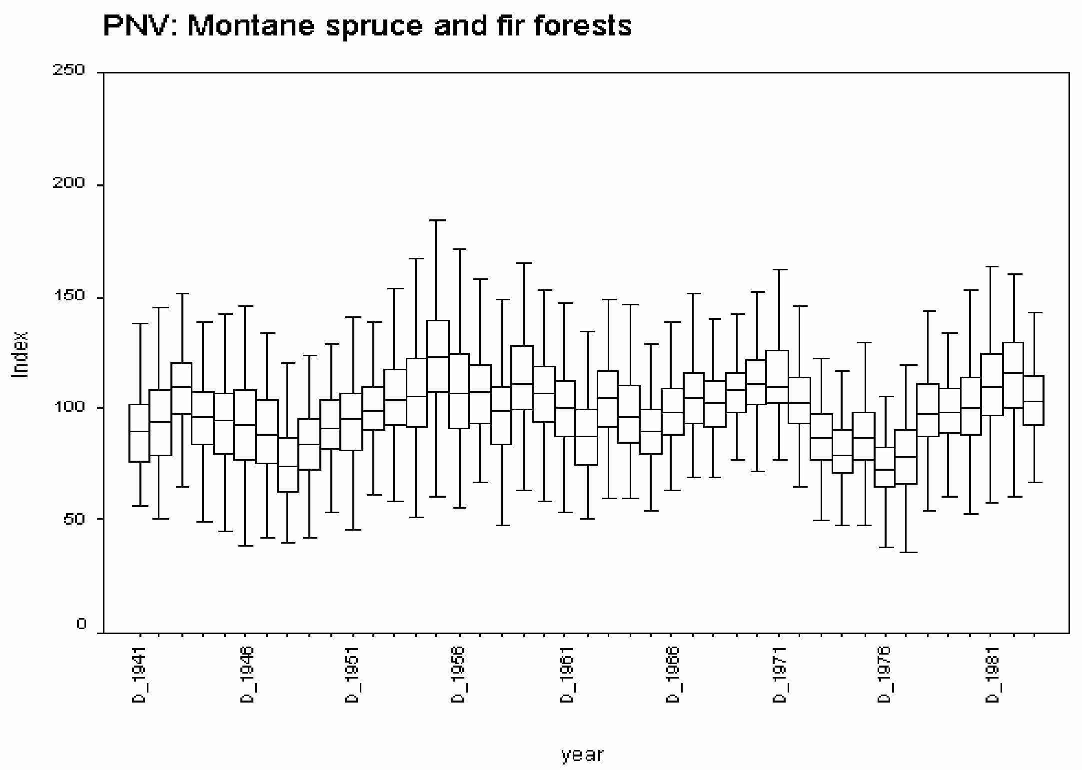


Figure 7: Mean sensitivity of radial increment of Norway spruce (Forest inventory TWI 1983 and 1988), mean growing season precipitation (May-September) (DWD, 1999) and important main formations of PNV (BOHN et al. 2000/2003) in Baden-Württemberg.

When comparing the two maps in Figure 7 close interrelations can be recognized: in the north of Baden-Württemberg (Neckarland) mean sensitivity is highest and precipitation is lowest. In the area of the natural range of Norway spruce seasonal precipitation is high and mean sensitivity is low. Smaller structures with higher sensitivity values can be found embedded in the Black Forest. These are larger river valleys which drain the Black Forest to the river Rhine.

The seasonal precipitation has a decisive effect on the mean sensitivity of Norway spruce, whereas micro- to meso-scale site factors such as hillside, aspect or differences in the soil-type are of secondary importance.



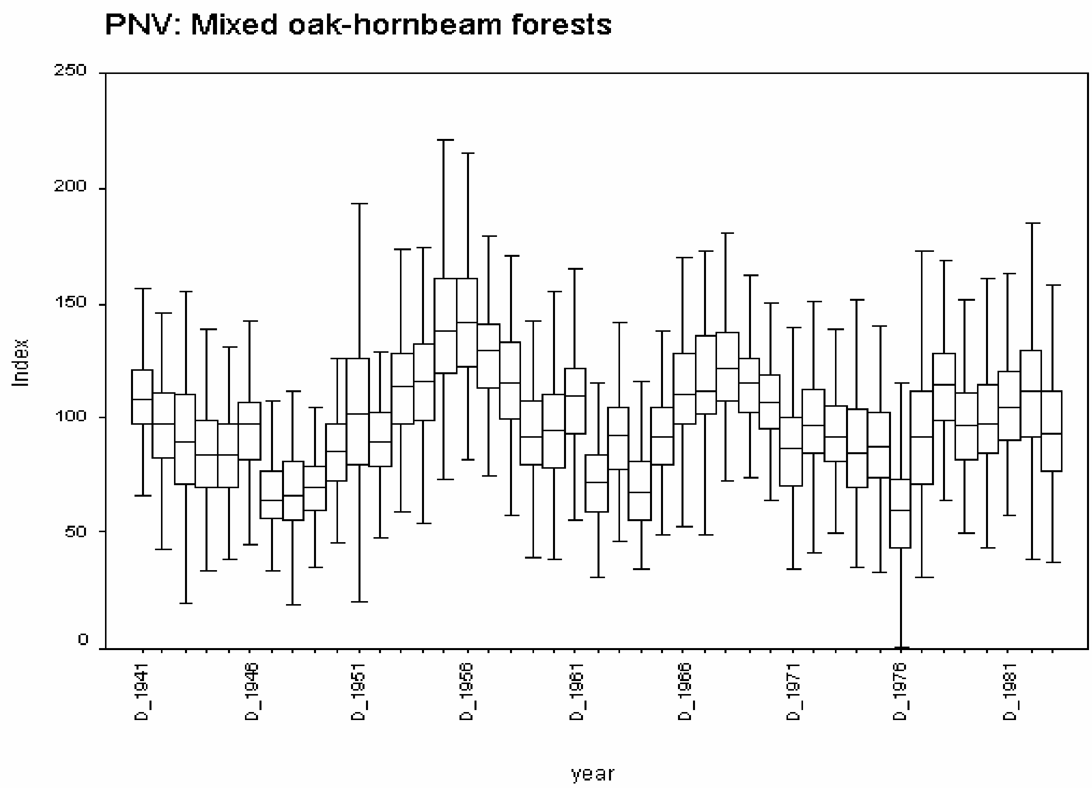
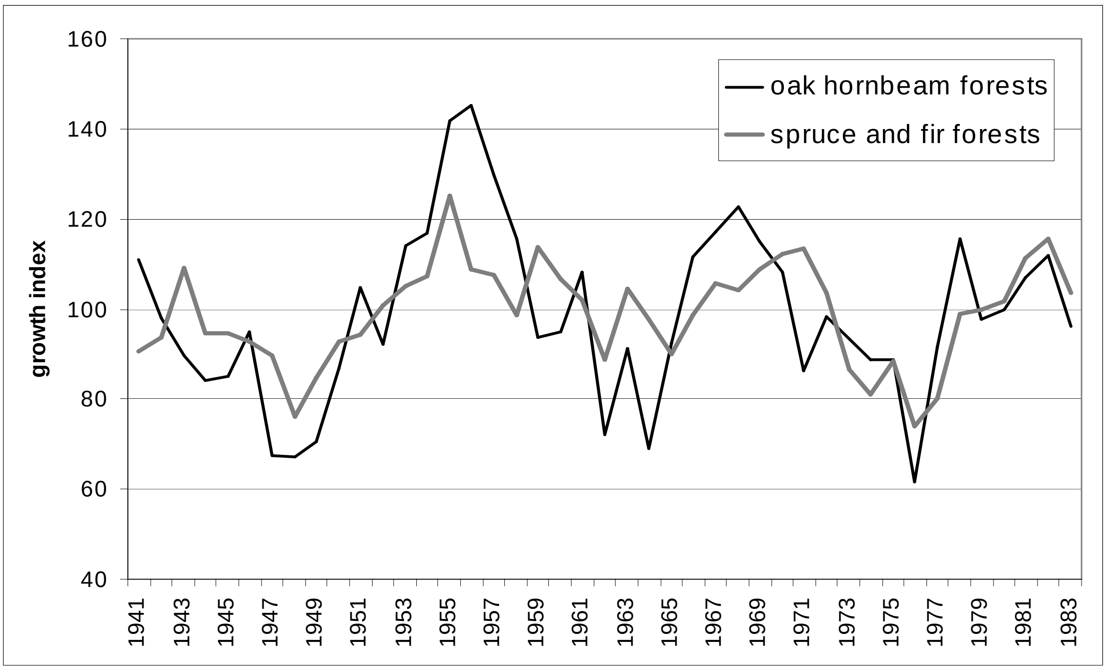


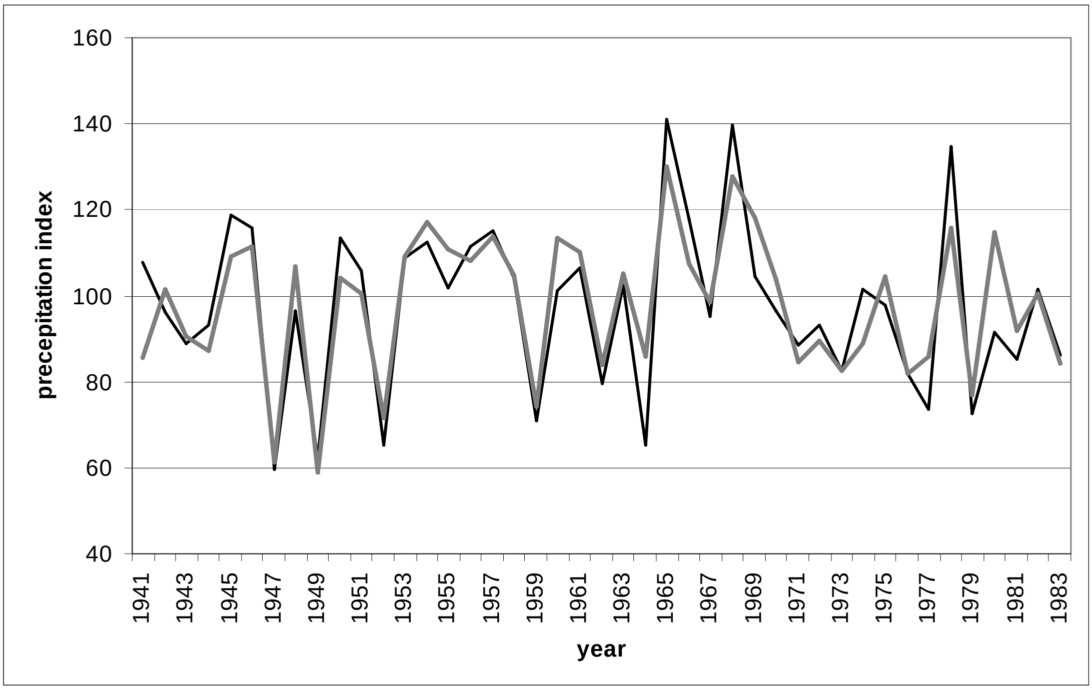
Figure 8/9: Time series of radial increment indices (%) of Norway spruce sample trees growing on sites within their natural distributional range (above) and on sites in the area with natural potential vegetation of mixed oak-hornbeam forests (below) as box-plots with median values, 50 (box) and 75 (whisker) percentiles.

3.4 Comparison of time series

As illustrated in Figure 7, Norway spruce exhibits lower sensitivity on sites within its natural range than on sites outside this range. To examine simultaneously the temporal behaviour of the annual radial increment, time series of radial increment indices are represented (Figure 8 and 9). For the index values, the time series of the annual radial increment are detrended and standardized to a mean of 100 %. The radial increment indices of Norway spruce growing on sites within their natural distributional range are compared with those from trees growing on sites in the main formation of “oak hornbeam forests” where the largest mean sensitivity was observed (Figure 5).

Despite distinct differences in baseline climatic (Table 1) and geological conditions between the sites in these two areas, the radial growth reactions are similar. In both cases local minima can be observed in the years 1948, 1962, and the absolute minimum value in both cases occurs in 1976. Synchronous maxima occur in the years 1955 and 1982. However the degree of variability is different: a large amount of variability can be observed in the areas where spruce grows outside its distributional range on sites naturally dominated by oak-hornbeam forests. The year-to-year behaviour of radial growth is more complacent on sites within its natural range.
In Figures 10 time series of radial growth indices are compared with time series of growing season precipitation. Again we have calculated the values for Norway spruce growing on sites in the main forest formations “montane spruce and fir forests” and “oak-hornbeam forests”.
When comparing the time series of the mean radial increment indices it is evident that spruce growing on sites outside its distributional range shows larger growth variations. The central figure shows the precipitation index, which is the percentage-deviation of the precipitation from the long-term mean (1961-90). The courses of the time series are in both cases similar: extraordinarily dry conditions (e.g. 1947, 1949, 1976) as well as above average moist conditions occurred in both areas in the same years





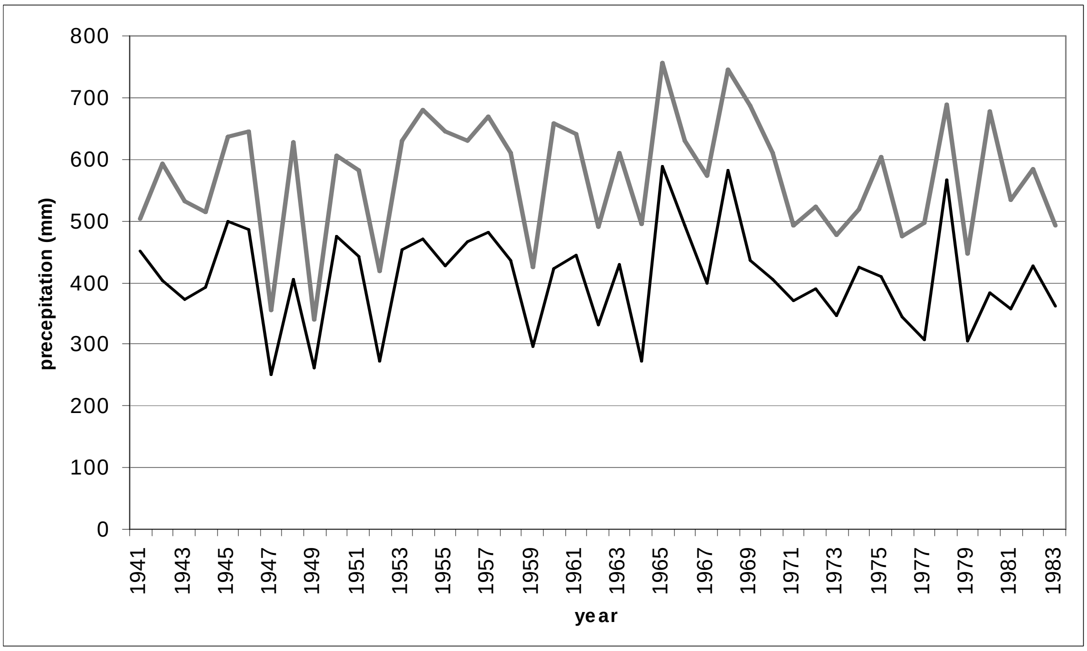


Figure 10: Time series of radial growth indices (%, top), precipitation index (%, centre) and absolute precipitation sum (mm, below) during the growing season (May-September) on Norway spruce sites within their natural distributional range (red thick line) and in the area with a natural potential vegetation of mixed oak-hornbeam forests (black thin line).

with similar amplitudes. When looking on the absolute precipitation values it can be seen that the sites in the areas of oak-hornbeam forests received significantly lower precipitation than in the area naturally dominated by Norway spruce. During drought periods, spruce reaches the critical point of soil moisture depletion earlier and growth decreases more strongly. However, spruce in the oak-hornbeam forests profits from high precipitation during the growing season: during moist summers spruce growth is accelerated more than in the natural spruce areas. This might be due to higher nutrient content in the loamy soils and higher temperature on the oak-hornbeam sites.

4 Conclusions

It could be shown that the mean sensitivity of radial growth of Norway spruce is significantly higher on sites outside its natural distributional range. The growing season precipitation has a decisive effect on radial growth of Norway spruce, whereas micro- to meso-scale site factors such as hillside, aspect or differences in the soil type are of secondary importance.

A continuation of the recent trends in climatic conditions characterized by an increase in winter and July and August temperatures and accompanied by a simultaneous decrease in summer precipitation will lead to higher risk of drought periods. The observed higher sensitivity of radial growth of Norway spruce outside its natural range indicates that on these sites, the inter-annual variability of growing season precipitation, but especially the occurrence of drought periods, has had a strong impact on growth already in the past. It is expected that more frequent drought stress in the future will strongly increase the risk of damage to Norway spruce especially when growing on sites outside its natural range. In addition it can be expected that the associated reduction in tree vitality will lead to an increasing risk of biotic and non-biotic damage factors such as storm and insects and that therefore the stability of these Norway spruce ecosystems is especially endangered.

Acknowledgement

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