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Growth dynamics in a changing environment - long-term observations

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Abstract

Natural influences as well as human activities have changed forest environments. As a result, growth conditions have changed with time. The annual and periodic growth of needles, shoots, tree rings and volume growth vary considerably over time. The variation in ring width and volume increment of Norway spruce correlates with precipitation and air temperature. High air temperature and low precipitation during the vegetation period reduce growth rate and increase tree mortality even in some areas where average precipitation is high and average air temperature is relatively low.

Introduction

Forests have always been exposed to changing environmental conditions. Soil, climate, fauna and flora all change with time. Over long periods man has influenced forest ecosystems through the effects of land use, for example livestock grazing, litter racking, felling and regeneration regimes, species selection, fertilization and amelioration. Man also has affected the chemical composition of air and hence the atmospheric deposition and has possibly altered climatic conditions through the effects of pollution. Site and growth conditions are not constant, but instead change continually over time. Discussions about forest decline and climate change have increased the public sensitivity in respect to global changes. Consequently forest scientists are being asked to analyze the impact of such environmental changes on forest ecosystems. Growth and yield studies are one means of studying possible long-term changes in growth patterns and growth rates and this approach forms the basis of the work to be described.

Data and methods

Periodic measurements of diameter at breast height and total height of trees on long-term permanent plots of the Forest Experiment Station Baden - Württemberg were the base for calculating volume increment. In addition, the annual increment of felled trees was reconstructed. Cross sections were collected at heights of 1,3m and the radial annual increment was measured along 8 radii on each cross section. Annual shoot growth was measured in order to reconstruct the annual height increment. For dating and proofing shoot growth, cross sections were cut out of the stem and the total number of annual rings on the cross section was compared with the number of annual shoots from the top of the tree to the point where the cross sections were taken. Whenever needed, additional cross sections were cut. In addition, annual shoot growth was measured along the main axis of the longest branch on each whorl. The size and number of the needles on the annual shoots of the main axis were measured by an image analysis system.

The average monthly air temperature and total monthly precipitation were used to describe the climatic conditions and their variation over time. Potential evapotranspiration has been calculated according to Thornthwaite and Mather (1955). The basis for this calculation were monthly air temperature and correction factors which include day length.

In the public forest land of southwestern Germany ten year cutting plans (allowable cut) are based on sustained yield expectations. Any cutting other than the planned cut is recorded along with the reason for

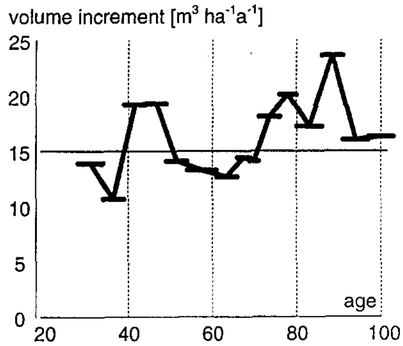

Fig. 1. Periodic annual volume increment of a Norway (*Picea abies*) spruce stand in Upper Swabian plotted over time. The horizontal bars describe the length of the measurement period. (Data source: Forstl. Versuchs- und Forschungsanstalt Baden-Württemberg, unpublished).

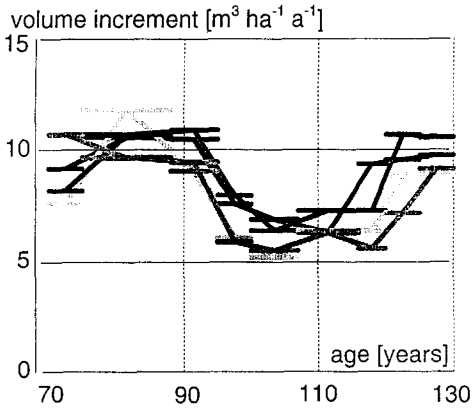

Fig. 2. Volume increment in four differently thinned permanent plots of beech (*Fagus silvatica*) situated in the Swabian Alb. (Data source: Forstl. Versuchs- und Forschungsanstalt Baden-Württemberg, unpublished).

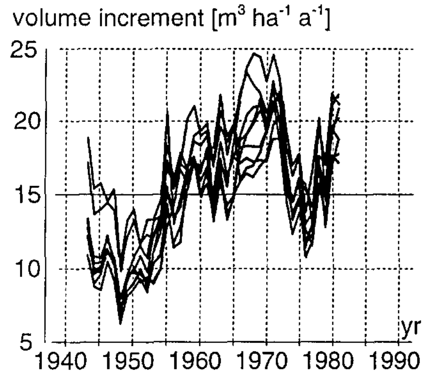

Fig. 3. Annual variation of volume increment of Norway spruces in nine permanent plots in the northern Black Forest.

the unscheduled cut. The annual statistic of the public forest land (Forststatistische Jahrbücher) shows the volume and the season of all cuts. Mortality here is calculated in percentage of allowable cut.

Results

Volume growth of stands

Periodic stem volume increment in long-term permanent Norway spruce plots have been found to vary considerably over time (Fig. 1). Periods of relatively high or low increment may last up to several decades. In addition to these periodic variations, growth in these studies shows an increasing trend with age although a decrease with age was expected. This increasing trend can also be observed in other old research plots (Kenk et al., 1991). Long-term permanent beech plots also show considerable wide growth variations over time. Although four adjacent beech plots of an old thinning experiment (Swabian Alb) shown in Fig. 2 were thinned differently, the volume increment on all plots shows similar periodic patterns. The main features are a depression starting in 1934, at age of 100 years and lasting for 25 years followed by a remarkable growth increase.

In several long-term experimental Norway spruce plots, periodic diameter measurement of all trees were combined with annual ring width measurements of 40 trees per plot to produce values for the annual variation of volume increment per hectare (Fig. 3). Volume increment varies considerably on all nine analyzed plots in the northern Black Forest ranging from less than 10 m^3 ha^{-1} a^{-1} in 1948 to more than 20 m^3 ha^{-1} a^{-1} in 1971. Growth depressions were observed in all plots at the end of the 1940s and in the middle of the 1970s. Besides this short-term variation, growth over the 39 years of observation shows an increasing trend. Possible causes for the growth depression during the 1940s and the high increment at the end of the 1960s will be discussed later.

Radial growth of trees

Annual radial growth is heavily influenced by competition. Trees that have been planted with wide spacing and have not been thinned later show a decreasing trend whereas trees that have been thinned heavily show an increasing radial growth trend even at a rather old

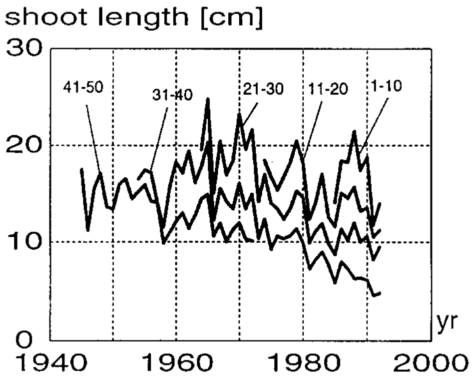

Fig. 4. Shoot length of branches of 60 year old Norway spruce trees stratified according to their heights in the crown. Each curve represents the average of branches on 10 adjacent whorls (whorl 1–10, 11–20, etc., numbering from the top) of 20 trees.

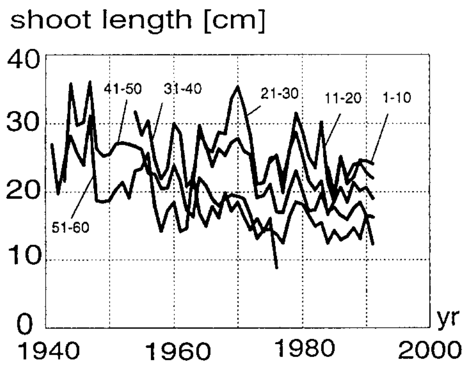

Fig. 5. Shoot length of branches of 110 year old Norway spruce trees stratified according to their heights in the crown (see Fig. 4), average of 9 trees.

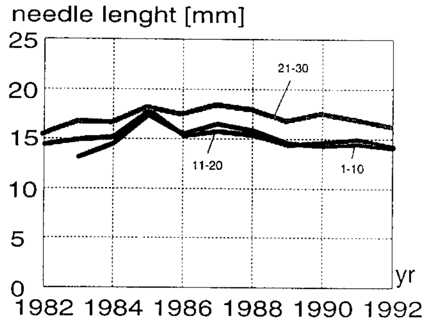

Fig. 6. Average needle length of 6 Norway spruce trees on the shoots along the main axis of the branches. Each curve represents the average of branches on 10 adjacent whorls (whorl 1–10, 11–20, etc., numbering from the top of the tree).

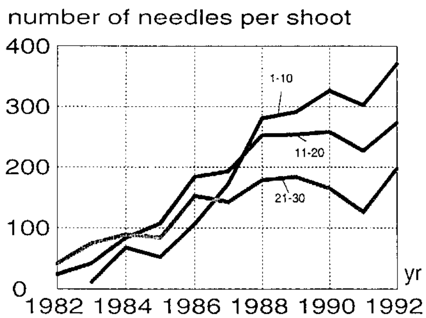

Fig. 7. Average number of needles per shoot on ten adjacent whorls (whorl 1–10, 11–20, 21–30, numbering from the top of the tree) of 6 Norway spruce trees along the main axis of the branches.

age. The annual variation of the radial growth, however, varies synchronously. Periods of relatively low increment and relatively high increment last for several years (Fig. 12).

Shoot length

The annual shoots of the main axis of the longest branch were measured to determine extension growth of branches on each whorl. The branches were stratified in groups of ten whorls according to their height on the tree. Figure 4 shows the average annual shoot growth of 20 dominant Norway spruce trees for each year. The 60 year old trees were growing in an even-aged spruce stand in the southern Black Forest at an elevation of about 1200 m. Fig. 5 shows the annual shoot growth of 9 dominant Norway spruce trees at an age of 110 years in an even-aged spruce stand in the eastern Black Forest at an elevation of about 900 m. As would be expected, in both cases the branches higher up in the crown show a significantly higher annual shoot growth than shoots which grew in the same year at lower parts of the crown. The shoot length decreases with the age of the branches. Despite these differences, however, shoot growth at the various ages and heights varies synchronously.

Needle length and number of needles

For the analysis of needle length, needles from the main axis of the branches of the highest 30 whorls were measured separately for each annual shoot. Average needle length of six 60 year old Norway spruce trees in the southern Black Forest at an elevation of about 1200 m shows little yearly variation (Fig. 6). On the lower branches needles are in general slightly longer.

The number of needles per shoot varies, however, considerably with age and height on the tree. The branches of the most upper ten whorls have the

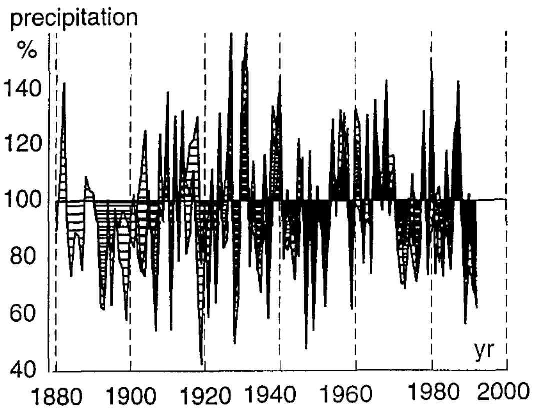

Fig. 8. Precipitation during May to September. Deviation from long-term averages of 5 stations at different locations in the Black Forest plotted over time as shaded area.

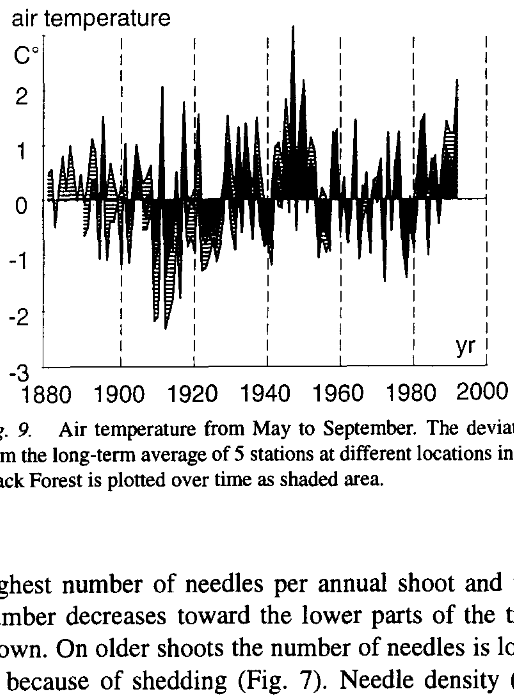

Fig. 9. Air temperature from May to September. The deviation from the long-term average of 5 stations at different locations in the Black Forest is plotted over time as shaded area.

highest number of needles per annual shoot and the number decreases toward the lower parts of the tree crown. On older shoots the number of needles is lower because of shedding (Fig. 7). Needle density (no figure) also decreases with the age of the shoot. Differences between branches at different heights, however, are not as pronounced as differences in the total number of needles because lower branches have fewer needles as well as smaller shoot lengths.

The maximum age of the needles under these site conditions is about 10 years. Besides the decrease of the number of needles along with needle age there is also a variation from year to year. In 1988, 1990 and 1992 the number of needles per shoot is relatively high in all groups whereas in 1991 this number is somewhat lower.

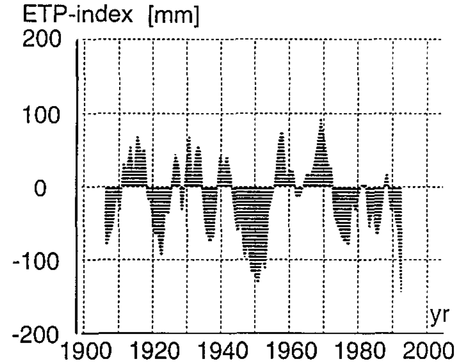

Fig. 10. Drought-index (ETP) - running average of the preceding five years. ETP-Index is used as a drought index. The deviation of the last four vegetation periods and the actual period from the long-term average is plotted as shaded area over each year.

Climate and its impact on growth variation

In the Black Forest precipitation and air temperature vary considerable with elevation and local position. Precipitation is distributed rather equally during the year. At the higher elevation mean annual precipitation reaches up to 2000 mm. Mean annual air temperature at the higher elevation is about 6°C. The annual deviations of precipitation and air temperature from May to September of five stations in the Black Forest (data source: Deutscher Wetterdienst, Frankfurt, unpublished) from the long-term average are shown in the Figures 8 and 9. Annual deviations of precipitation fall in a range of ± 50%. Years of relatively low precipitation tend to group and are followed by sequences of relatively high precipitation (Fig. 8). Periods of low or high air temperature often last up to several years (Fig. 9). The difference between precipitation and potential evapotranspiration (according to Thornthwaite and Mather, 1955) was used to calculate a drought index. Since air temperature and precipitation during the vegetation period have an effect on growth that may last several years, previous five year periods are the base for the drought index shown in Figure 10. This drought index for the Black Forest area displays two periods of the most extreme drought conditions to occur so far in this century, the first at the end of the 1940s and the second at the beginning of the 1990s.

The variation of annual stem volume increment of Norway spruce stands (Fig. 3) is found to correlate highly with variations in the drought index (Fig. 11, $r^2 = 0.65$, $F_{1,37} = 61.43$, $p < 0.001$). Since the observation period here only covers 39 years, the findings have been compared with a longer data series of radial

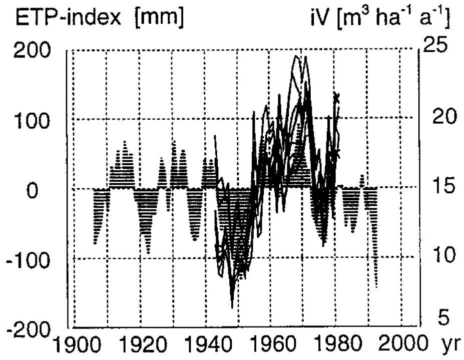

Fig. 11. Correlation between the annual volume increment on nine Norway spruce permanent plots (curves) and the drought index (shaded area).

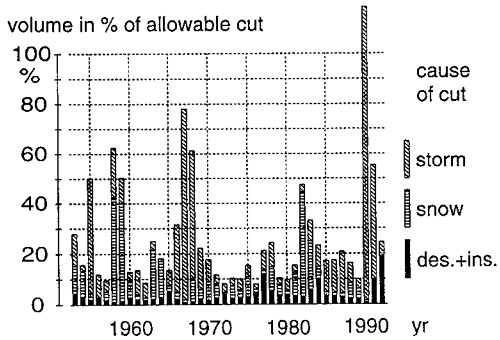

Fig. 13. Annual storm and snow damage as well as the volume of desiccated trees and trees killed by insects expressed as a percentage of the allowable annual cut.

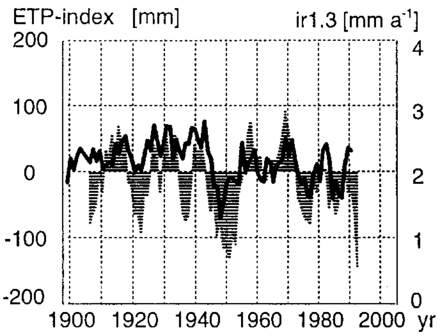

Fig. 12. Correlation between the average annual radial increment of 66 Norway spruce trees at higher elevations in the southern Black Forest (curves) and the drought index (shaded area).

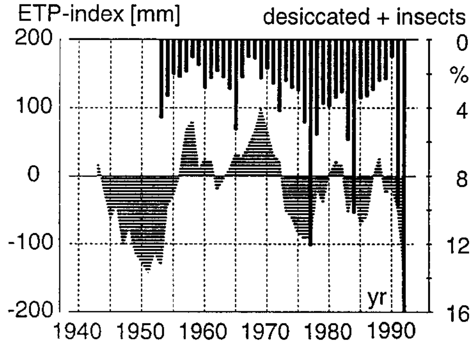

Fig. 14. Volume of desiccated trees and trees killed by insects (dark columns) and drought index (shaded area).

increment of 66 dominant Norway spruces growing at high elevations on different sites in the southern Black Forest. During the period from 1943 to 1981 the radial increment shows a pattern similar to the annual volume increment pattern shown in Figure 11. Furthermore, the correlation between increment and drought is also seen in the preceding decades and again in the years after 1981. During the 90 year period, radial increment is relatively high whenever the water supply is above average during the vegetation periods of the last five years including the actual period. Increment is low whenever water supply is short (Fig. 12). The deep drop of the drought index in recent years indicates a drastic decrease in increment in the near future.

Mortality and climate variation

In the public forest land of the Black Forest, which covers about 250,000 hectares, a record is made of any cutting other than the planned cut and the reason for the unscheduled cut is documented: The reasons being snow, storm and trees that have been desiccated or killed by insects. In Figure 13 the volume of the unscheduled cut is expressed as a percentage of the allowable annual cut which in turn was calculated on the basis of sustained yield expectations. Storm damage as well as snow damage vary on an irregular pattern over time. Storm damage was especially high in 1967 and more particularly in 1990 when more than 100% of the allowable annual cut was blown down. In 1990 trees were blown down on unstable sites and were broken on stable sites due to the heavy storms in late winter of that year. Compared to this damage the volume of desiccated trees and of trees killed by insects has been relatively low in recent years.

The desiccated trees and the trees killed by insects are of special interest to the discussion of forest

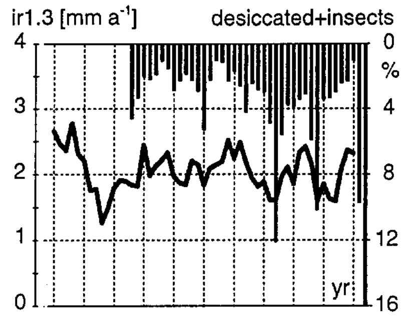

Fig. 15. Average annual radial increment of 66 Norway spruce trees correlates with the annual volume of desiccated trees and trees killed by insects on total public forest land of the Black Forest.

dieback. The annual variation in the volume of these trees correlates with the drought index. Whenever water supply during the last five years is above average, the volume of desiccated trees and trees killed by insects is low. Yet, after periods with a relative poor water supply this volume is high (Fig. 14).

Since radial growth as well as mortality correlate with the drought index, it follows that radial growth correlates with mortality (Fig. 15).

Discussion

Tree and stand growth as well as tree mortality vary considerably over time. The number of needles, shoot length as well as ring width show time specific variations. Variations on radial increment and mortality correlate with climatic factors, especially with temperature and precipitation during the vegetation periods of the preceding years. The close correlation between water supply and growth corresponds with other observations on Norway spruce (Holmsgaard, 1955; Nilsson and Wiklund, 1992). The results are remarkable since total precipitation, especially at higher elevations, in the Black Forest is relatively high while mean air temperature is relatively low. A stimulation of growth by an temporarily increased water supply under rather cold and wet conditions has also been observed in irrigation experiments (Holstener-Jørgensen and Holmsgaard, 1988; Nilsson and Wiklund, 1992). It is expected that the sensitivity of growth to water supply increases with nitrogen input (Spiecker, 1991a).

Conclusion

Growth shows a high variation over time. Periods of relative low and of relative high increment last up to several decades.

Growth variation and mortality correlate with climate variation. Low rainfall during the summer combined with high air temperature reduce growth and increase mortality in the following years even at higher elevations in the Black Forest where the mean temperature is low and mean precipitation is high. These findings show that climate and it's variation have an essential effect on the dynamics of growth and mortality. Forest ecosystems are developing in a dynamic and complex environment. Long-term field experiments are needed in order to analyze the dynamics of nutrient uptake and cycling in forests. Not only treatment variables, but also changing environmental conditions including disturbances have to be taken into account.

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