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Growth variations of Common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe—a dendroecological study

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Abstract

With increased growth potential on the one hand, but on the other hand a high percentage of trees exhibiting visible damages and the apparent regional decline in Common beech (*Fagus sylvatica* L.) stands in Europe, new questions arise about the sensitivity and resistance of this tree species to current environmental changes. In order to obtain more relevant information about this, 36 beech stands under different climatic and environmental conditions throughout Europe were selected and investigated by dendroecological methods. The variation of tree ring widths of Common beech was found to be a very sensitive indicator, reflecting clearly the signals of environmental influences. A high statistical quality of tree ring chronologies demonstrates a high suitability for dendroecological analysis. The investigation of long-term growth variations results in site-dependent and especially elevation-dependent growth trends.

Since 1950, at lower altitude sites in Central Europe mainly increased growth trends are obvious. At higher altitude sites, however, almost all sites show a slightly decreased growth potential during the last decades. It seems that at higher altitudes in Central Europe, environmental changes in the recent past with negative effects on cambial activity are the predominant growth influences. This is also reflected in short-term growth disturbances and growth depressions after 1975 in tree ring series of beech trees growing on higher altitude sites. The investigation of climate–growth relations by different dendroecological methods results in distinct altitude-dependent growth-limiting factors. The comparison of chronologies demonstrates a high resistance of beech at sites where water supply is the main growth controlling factor. Strong disturbances and depressions in radial increment, however, were found at higher altitude sites in Central Europe especially at the end of the 1970s. Comparisons with reactions in preceding years demonstrate an increased sensitivity or an affected ‘ecological fitness’. Site factors modify the intensity of damage symptoms, but cannot be regarded as primary causes. Recent environmental changes may be responsible for the reduced ‘ecological fitness’ of Common beech in higher altitude sites. The spatial and temporal distribution of the detected growth disturbances leads to the assumption that increased tropospheric ozone concentrations are involved in the process of a changed sensitivity and resistance.

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1. Introduction

The Common beech (*Fagus sylvatica* L.) is a dominant tree species in European forests. In Central

Europe, beech is the most abundant broad-leaved forest tree and, because of height, physiological tolerance and competitiveness, it would be the dominant tree species at most of the sites (Ellenberg, 1996). After a long period, during which foresters preferred Norway spruce (*Picea abies* (L.) Karst.), *F. sylvatica* is now enjoying a renaissance. Its economic importance for forestry and the timber industry has been recognized, and there has been an increase of forest area planted with beech during recent years (Dertz, 1996; Bagnaresi and Giannini, 1999).

Forest inventories and growth trend studies frequently reveal an increased productivity of European forests concerning aboveground biomass since the middle of the last century (Spiecker et al., 1996; Pretzsch, 1999). In permanent beech plots in southern Germany strong positive deviations from expected growth according to yield tables since the 1940s or 1950s were reported (Pretzsch, 1999). As possible reasons, land use history, forest management, natural disturbances, climatic influences and atmospheric deposition—especially of nitrogen—are discussed. The results of crown condition surveys show no uniform correlations between defoliation and radial growth. Even highly defoliated beech trees have not been affected, and in some cases even show increased basal area increments (Bauch et al., 1986; Pretzsch, 1996). The evaluation of inventory data between 1980 and 1992 in Bavarian forests by Felbermeier (1994) revealed an increased average height growth of *F. sylvatica* and a high tolerance of this tree species to drought. For Bavarian forests beech achieves its best height growth in the warmest regions.

But in addition to increasing growth trends, new decline phenomena were also observed. In different regions of Central Europe, strong crown damages and abrupt die back accompanied by growth depressions in the 1970s and 1980s, especially at higher altitude sites, were reported (Schütt and Summerer, 1983; Eckstein et al., 1984; Zech et al., 1991; Dittmar et al., 1997). The intensity of these symptoms could not be valid explained by natural influences like extreme weather events or parasite attack.

Multivariate statistical analyses of growth and environmental data from 57 permanent observation plots with Common beech in Switzerland showed a

positive correlation between growth and nitrogen deposition, but a negative one with tropospheric ozone (Braun et al., 1999). For the calculations diameter increment between 1991 and 1995 was considered. The detected growth reductions in mature beech trees exceed changes found with beech seedlings. Hence, ambient tropospheric ozone concentrations had to be considered as important environmental change and serious risk for the vitality and growth of beech forests.

The continuous survey of crown condition in Europe indicates a slight decrease of undamaged (defoliation 0–10%) and a slight increase of damaged (defoliation >25%) beech trees since the beginning of the 1990s (UN/ECE and EC, 2000). Actually, Common beech is one of the most affected tree species in Europe, with a percentage of only 34.1% undamaged, and 21.9% damaged trees showing defoliation and discolouration. Year-to-year fluctuations of crown condition are often explained by the year-to-year variation of water supply and fructification, and so deteriorations were read as the effect of drought and/or seed production. But despite above-average precipitation during the last vegetation periods, crown condition of beech did not improve. Repeated observations of early leaf discolouration and early leaf fall in beech trees in the humid Alpine region (Flückiger and Braun, 1994; Waldzustandsbericht, 1998, 1999; Skelly et al., 1999; Innes et al., 2000) also indicate that factors other than water stress due to reduced precipitation must be considered.

Knowledge limits our understanding of how these current changes affect the potential sensitivity of Common beech and their resistance against environmental changes in the recent past. The major objective of our study was the gathering of more information about site- and regional-specific sensitivities and potential changes in the vitality of Common beech in Europe during the last decades. To achieve this, mainly dendroecological methods were applied. These allow temporal comparisons, and, if several stands are investigated in the same way, regional comparisons of vitality parameters. For better identification of climatic determined effects and the impact of short-term weather fluctuations, beside stands in Central Europe, border regions of the European habitat of *F. sylvatica* were also included.

2. Materials and methods

2.1. Plot selection and sampling

In order to cover a wide range of different environmental conditions 36 forest stands in the central and border regions of the European habitat of Common beech (*F. sylvatica*) were selected and sampled between 1995 and 1997 (Fig. 1, Table 1). Most of the plots were established in Central Europe (numbers 1–19 in Fig. 1), where beech is one of the most important forest trees and its decline phenomena widespread.

In Northern Europe three plots were investigated in and near Söderåsen, a forest region in Skåne (southern Sweden, plots 25–27 in Fig. 1). The most southern sites are located in Foresta Umbra at the Gargano peninsula (plots 21 and 22 in Fig. 1). *F. sylvatica* is the

dominant tree species in this National Park located on a karst plateau at 400–800 m a.s.l. In Northern Italy an additional site was sampled at Cansiglio Plateau in the southern Alps (1350 m a.s.l., plot 20 in Fig. 1). In the western Pyrenees (Spain) two sites are located in the northern part of the province Navarra, a region very rich in beech forests (plots 23 and 24 in Fig. 1). In the eastern part of Europe several stands were investigated in Slovakia and Romania at different elevations (plots 29–36 in Fig. 1). Field work in the Carpathian mountains included sampling in a region with primeval beech forests (Nera National Park, Semenic Mountains). For stand selection, the following criteria were considered as far as possible: closed mature beech stands with comparable density, no heavy forestry operation in the recent past, availability of information about stand history and of climatic or other relevant data. In some cases samples could be taken in plots where

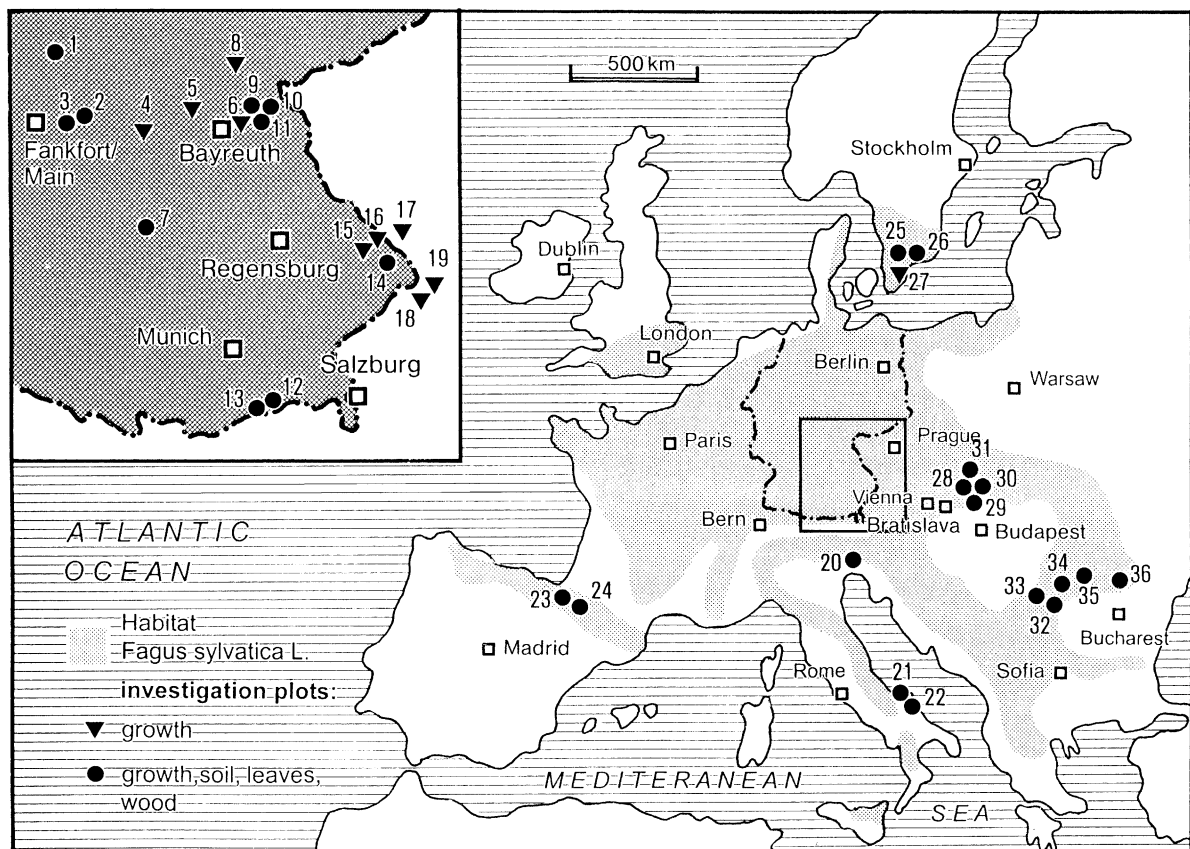


Fig. 1. Location of Common beech (*F. sylvatica* L.) stands under study.

Table 1
Description of the Common beech (*F. sylvatica* L.) stands under study

Plot no.	Site and location	Latitude/longitude	Altitude (m a.s.l.)	Sampled trees	Mean stand age
1	Schotten/Sauberg (Vogelsberg/Germany)	50°29'N, 09°07'E	330	11	~140
2	Mittelsinn/Schubertswald I (Spessart/Germany)	50°12'N, 09°33'E	460	20	145
3	Mittelsinn/Schubertswald II (Spessart/Germany)	50°12'N, 09°33'E	470	20	140
4	Ebrach/Steinkreuz (Steigerwald/Germany)	49°52'N, 10°27'E	450	10	~130
5	Scheßlitz/Brandholz (Fränkische Alb/Germany)	49°54'N, 11°04'E	550	8	~150
6	Bayreuth/Ermitage (NO-Bavaria/Germany)	49°56'N, 11°37'E	440	11	~130
7	Dinkelsbühl/Kreuzschlag (Germany)	49°08'N, 10°38'E	480	11	~140
8	Kronach/Güldenstein	50°16'N, 11°32'E	530	20	120
9	Schneeberg/East slope (Fichtelgebirge/Germany)	50°03'N, 11°52'E	840	10	~130
10	Schneeberg/Schacht (Fichtelgebirge/Germany)	50°04'N, 11°50'E	850	11	~160
11	Schneeberg/Farrenleite (Fichtelgebirge/Germany)	50°02'N, 11°51'E	950	11	~140
12	Bayrischzell/Seeberg I (Northern Alps/Germany)	47°39'N, 12°00'E	1030	10	165
13	Bayrischzell/Seeberg II (Northern Alps/Germany)	47°39'N, 12°00'E	1200	12	175
14	Neureichenau/Jägerkopf (Bayer. Wald/Germany)	48°51'N, 13°44'E	1005	20	125
15	Nationalpark Bayer. Wald/Forellenbach (Germany)	48°57'N, 13°24'E	830	16	115
16	Nationalpark Bayer. Wald/Böhmweg (Germany)	48°56'N, 13°29'E	1200	16	250
17	Nationalpark Sumava/Bubin (Czech Republic)	48°59'N, 13°49'E	1100	8	~250
18	Mühlviertel/Dürrwiese (Austria)	48°43'N, 13°51'E	850	8	110
19	Mühlviertel/Buchwaldl (Austria)	48°44'N, 13°51'E	1100	8	130
20	Foresta del Cansiglio (North Italy)	46°02'N, 12°25'E	1350	5	120
21	Foresta Umbra/Gargano I (Italy)	41°48'N, 15°59'E	790	10	~130
22	Foresta Umbra/Gargano II (Italy)	41°49'N, 16°01'E	580	10	~200
23	Navarra/Ansobi (Spain)	42°55'N, 01°40'W	950	10	~175
24	Navarra/Lindux (Spain)	43°00'N, 01°40'W	1170	10	~175
25	Skåne/Söderåsen I (Southern Sweden)	55°59'N, 13°09'E	160	10	~120
26	Skåne/Söderåsen II (Southern Sweden)	56°02'N, 13°14'E	150	10	~150
27	Skåne/Skär (Southern Sweden)	55°54'N, 13°20'E	100	5	~120
28	Ziar n.H./Štiavnicé mountains (Slovakia)	48°33'N, 18°54'E	600	10	~120
29	Vtáčnik (Slovakia)	48°38'N, 18°39'E	1240	10	~200
30	Černatin/Kysucké Beskydy (Slovakia)	49°19'N, 18°54'E	750	10	~170
31	Hrochot'/Veporske mountains (Slovakia)	48°39'N, 19°17'E	580	10	~160
32	Nera National Park/Semenic Mountains (Romania)	45°10'N, 22°06'E	1400	11	>250
33	Anina/Banat mountains (Romania)	45°05'N, 21°47'E	760	10	~100
34	Nature Reserve Retesat (Romania)	45°22'N, 22°47'E	850	10	~140
35	Baile Basna/Transsilvania (Romania)	46°09'N, 24°17'E	460	11	~100
36	Cheia/Eastern Carpathian Mountains (Romania)	45°25'N, 25°58'E	890	11	~200

other kinds of investigations have previously been carried out (e.g. plot 20; Piutti and Cescatti, 1997).

At most of the stands, wood cores for dendrochronology analysis were taken as well as soil and leaf samples. Sampling procedures and the evaluation of leaf and soil analysis are described in detail in Dittmar (1999). Wood cores were taken from 5 to 20 dominant trees (tree class 2 according to Kraft, 1884) at breast height (1.3 m) with a SUUNTO-driller (5 mm core diameter, Teflon-covered). At each tree two cores were drilled in two opposite wind directions, in

0.79 and 3.94 rad to the widest stem diameter, respectively. For transport and drying purposes, cores were put into specially constructed groove boards.

2.2. Measurement and evaluation of tree ring data

For the tree ring width measurement, the device of Aniol in connection with the software programme CATRAS was used (Aniol, 1983, 1987). After measuring radial series, the two series of each tree were cross-dated on a light table to find missing rings and to

avoid measurement errors. Afterwards series were cross-dated reciprocally and dated after the synchronization of each series with the averaged stand curve was proved again. In addition synchronization and dating was tested statistically with the programme COFECHA (Holmes, 1983). For the calculation of climate–growth relations, a statistical treatment of the series is necessary to remove long-term growth variations, signal after effects (serial correlation) and to amplify the common signal (Cook, 1985; Holmes et al., 1986; Cook and Kairiukstis, 1992). For this study, a two-step detrending as recommended by Holmes et al. (1986) was chosen. Detrending was carried out with the programme ARSTAN (Holmes et al., 1986), which additionally allows the statistical description of tree ring data sets by different parameters (e.g. mean sensitivity, signal-to-noise ratio) and the calculation of various chronologies. Tree ring data of each stand were so summarized to one site chronology.

For the response function (Fritts, 1976) and the single-factor analyses (Dittmar and Elling, 1999), the residual version of each site chronology was used. This residual chronology is obtained after double-detrending, auto-regressive modelling and calculation of the single series average using a bi-weight robust mean (Holmes et al., 1986). Pointer and event years for single-year evaluation (Schweingruber et al., 1991) were selected according to Dittmar and Elling (1999). Response function and growth modelling analyses were carried out using the programme PRECON (Version 5.14, Fritts, unpublished), correlation and time series analyses with the programmes STATISTICA (StatSoft, 1998) and DENS (Nogler, unpublished). Response functions are the result of multiple regression analyses between monthly meteorological parameters and tree ring data. The mathematical and statistical background of the response function method is described by Fritts (1976) and Cook and Kairiukstis (1992), respectively. Response functions were calculated for temperature and precipitation separately to avoid the influence of inter-correlations and to increase the number of degrees of freedom (Backhaus et al., 1996). Fourteen predictors were used (monthly data of 6 months of the previous year, July–September, and of 8 months of the year of tree ring formation, January–August). For the growth modelling the two sets of predictors were coupled to 28 in all. For the climate–growth analyses, data from an earlier

investigation in the North Bohemia Mountains (Dittmar et al., 1997) were included.

To compare long-term growth trends between the different stands, firstly all single radial series (raw data) of a stand, were summarized by arithmetic mean to obtain one average time series for each stand (stand mean curve). To visual long-term growth variations, a smoothing curve was calculated by fitting a cubic spline function on this stand mean curve with a flexibility of 132 years (50% cut-off wavelength at 132 years; Holmes et al., 1986).

2.3. Meteorological data

For the calculation of climate–growth relations meteorological data from more than 100 stations with different length and parameter sets was obtained from national or scientific organizations. Names, locations and parameter sets of the meteorological stations are listed in detail in Dittmar (1999). The data series were tested for homogeneity, single missing data were estimated by nearby stations, and in most cases summarized to regional records, which—if no meteorological station is located directly in the forest site—are more suitable for climate–growth evaluations, than data from a single station (Blasing et al., 1981; Yeh et al., 2000). For this regional records several square kilometres were aggregated to one region. According to their availability, the parameters temperature, precipitation, sunshine duration and relative humidity were integrated in the dendroecological investigations. For continuous time series analyses data in monthly resolution were used. For single-year analyses additionally daily data were considered.

3. Results and discussion

3.1. Radial growth of beech as ecological variable

For dendroecological calculations tree ring data sets have to meet important requirements. According to Parker and Hensch (1971) chronologies are of high quality if they have the following features: (1) high average cross-correlation for ring series derived from trees within the site, (2) high mean sensitivity (relative year-to-year variability), (3) high percentage of common variance of the components

Table 2
Statistics of tree ring data of all sites and site groups^a

Sites: site group	Mean sensitivity (%)	First-order serial correlation	Signal-to-noise ratio	Variance in the first eigenvector (%)	Gleichläufigkeit ^b (%)	Mean correlation between trees (y-variance)
Central Europe: high altitude sites (14)	31 (22–48)	0.67 (0.53–0.81)	14.9 (4.5–28.7)	60 (49–68)	72.1 (67.4–80.2)	0.56 (0.45–0.65)
Central Europe: low altitude sites (10)	27 (20–39)	0.67 (0.52–0.79)	15.1 (6.7–26.4)	58 (47–74)	72.7 (69.1–80.2)	0.54 (0.43–0.71)
Southern Europe: Gargano (Italy)	36	0.62	18.2	68	75.3	0.64
Northern Europe: Skåne (Sweden)	30	0.64	7.9	58	74.1	0.53
Western Europe: Pyrenees (Spain)	27	0.79	9.8	55	69.4	0.51
Eastern Europe: Carpathian Mts., Transilvania (Romania)	33 (28–46)	0.61 (0.51–0.77)	9.8 (7.8–13.8)	54 (47–61)	69.6 (65.9–74.7)	0.49 (0.41–0.58)

^a Values: mean and for site groups, mean with range of values (minimum–maximum) in parentheses.

^b According to Eckstein and Bauch (1969).

represented in the standardized stand chronology and (4) low first-order serial correlation. To prove the quality of tree-ring data of all selected plots, different statistical parameters were determined. Results are summarized in Table 2.

In connection with the statistical tests of tree ring data, differences and similarities in growth variations between all sites were identified by principal components analyses, calculation of ‘Gleichläufigkeit’ (according to Eckstein and Bauch, 1969) and cross-correlation. The principal components analysis of all chronologies show a high percentage of similarity in growth variation between sites at lower altitudes (330–600 m a.s.l.) on the one hand and between sites at higher altitudes (740–1350 m a.s.l.) on the other hand in Central Europe (Germany, Czech Republic, Slovakia, North Italy). Hence, the Central European sites were separated into two groups containing 14 plots at higher and 10 plots at lower altitudes, respectively (Dittmar, 1999).

The values in Table 2 give evidence for a high statistical quality of most site chronologies obtained. In comparison to other tree species, tree ring series of Common beech have high values of mean sensitivity, low serial correlation and a strong common signal. The latter is expressed by high values of the signal-to-noise ratio, of the variance in the first ‘Eigenvector’, of the ‘Gleichläufigkeit’ (year-to-year agreement between the interval trends of time series) and of the mean correlation between trees (y-variance). From this data, it can be concluded that the tree ring width of beech is a very sensitive parameter reflecting clearly the signal of exogenous influences. This is in accordance with earlier investigations,

which demonstrated also a high suitability of beech tree rings for dendroecological analyses (Müller-Stoll, 1951; Fürst, 1963; Krause, 1992; Z’Graggen, 1992).

Comparing the tree ring statistics of the two site groups in Central Europe, it is conspicuous that there are only small differences between trees growing on high altitude sites with those growing on low altitude sites concerning the signal strength and the intensity of common signals (Table 2). So, the strong differences which we found in tree ring records between high and low altitude sites cannot be valid explained by a more or less pronounced sensitivity. They must be the result of very different responses to environmental factors. As climate is one of the main exogenous influences, great differences in climate–growth relations are suspected for these two site groups. This was confirmed by the climate–growth calculations described below.

3.2. Long-term growth variations

A great number of yield and growth studies in the last years provided evidence of increased site productivity and growth trends in European forest ecosystems (Spiecker et al., 1996; Pretzsch, 1999). According to Spiecker et al. (1996), Common beech growth trends have also increased generally since the 1950s on many sites in Europe. Land use history, forest management, natural disturbances, climate, nitrogen deposition and increased CO₂ content of the atmosphere are discussed as potential causes.

The examination of the long-term variations in tree ring widths of all studied plots cannot confirm evidence of generally improved growth conditions during

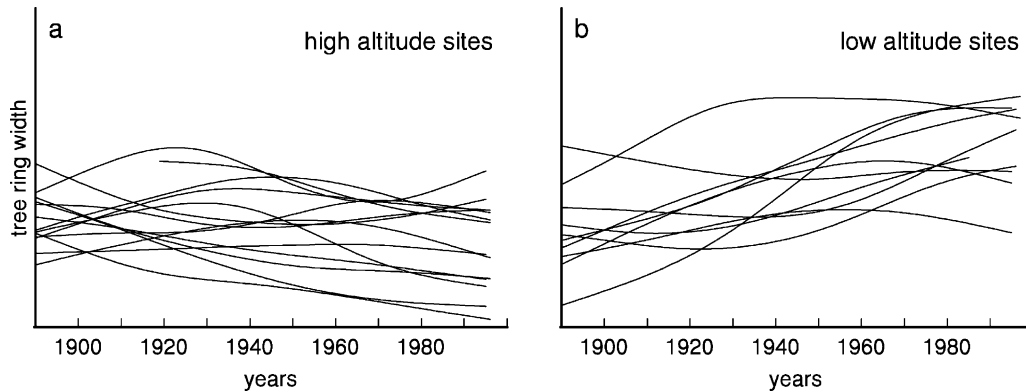


Fig. 2. Growth trends of beech stands in Central Europe, separately plotted for two site groups: (a) low (330–600 m a.s.l.) and (b) high (750–1350 m a.s.l.) altitude sites.

the last decades. In Fig. 2, radial growth trends are plotted for the two Central Europe site groups. At lower altitudes most beech stands have increasing tree ring widths since the beginning of the last century. For only three sites, a small decrease in the last decades is visible (plots 2, 3 and 6). At higher altitude sites, however, a general negative trend of radial growth after about 1950 is conspicuous, with the three exceptions at plots 15, 20 and 30, respectively. Plots 15 and 30 are the lowest plots (750 and 830 m a.s.l., respectively) of the high altitudes and plot 20 is a relatively young (about 120 years old), intensively managed beech forest with last thinning around 1980 (Piutti and Cescatti, 1997). Growth trends of the beech trees studied in the border regions of the European area also show stand-specific differences. Results are described and discussed in Dittmar (1999).

For dominant and co-dominant trees, which were selected for this study as sample trees, increasing radial growth in the last decades is not unusual. These trees are the most competitive individuals inside the stand with a high potential for increasing crown radius and root space. Even old beech trees can use this potential, if light conditions in the crown space improve and stand space enlargement is possible (Burschel and Huss, 1987). Therefore, the average higher age classes of the sampled trees in higher altitude sites are not a sufficient explanation for the occurrence of slightly decreasing radial increments since the middle of the last century. Also younger stands in higher elevation sites (e.g. plots 9, 14, 18 and 19) show decreasing trends. We assume that environmental changes in

Central Europe during the last decades are responsible for a reduction in growth potential and vitality of Common beech at higher altitudes. The same evidence was found in short-term growth variations: at most of these sites strong increment losses were found between 1975 and 1995, which, because of their intensity and duration, could not be compared with growth reductions in earlier periods (Fig. 3). The repeated disturbances in tree ring formation since the late 1970s could not be sufficiently explained by the impact of climate or short-term weather events (see below).

3.3. Climate–growth relationships

To describe the relation between climate and radial growth, we applied different dendroecological methods, continuous and discontinuous data series analyses. In Fig. 4, the results of response function analyses of most of the studied beech sites are summarized. The main obstacle for the interpretation of tree ring variations and for the calculation of climate–growth relations is the unavailability of meteorological data. This is the reason why for a few of the stands, especially in Eastern Europe, response functions could not be determined or the calculation interval only covers the last decades. For the stands in Central Europe, the interval had to be set from 1952 to 1995, in order to make the climate–growth relations comparable among the sites, although for several plots meteorological data records over a longer period were available. To compare response functions it is important to work within the same time interval, because

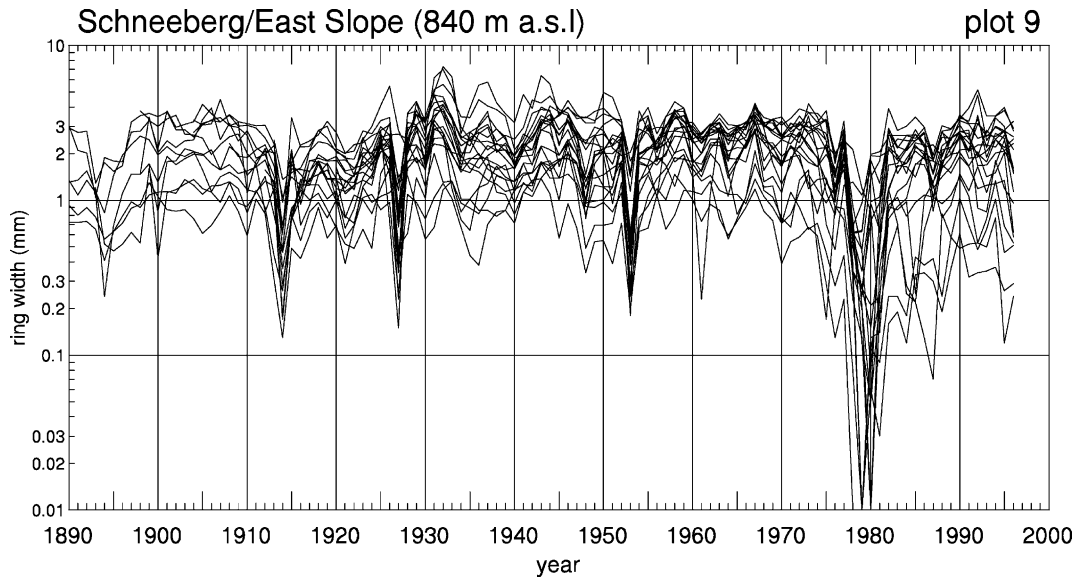


Fig. 3. Radial growth of 10 beech trees (two radii per tree) in the Fichtelgebirge (Germany): growth depressions after 1977 with six missing rings on five radii between 1978 and 1980.

climate–growth relations are not constant with time and the regression model—e.g. seen in the variance explained by predictors—are very sensitive with the number of years included (Cook and Kairiukstis, 1992).

The results show very distinct differences in climate–growth relations between low and high altitude sites in Central Europe. In low altitude sites, during the vegetation period—especially in June and July—low temperatures and high precipitation support the formation of wide tree rings. The occurrence of these weather conditions during the previous season is similarly effective. For the high altitude sites almost the opposite connections are obvious: high temperatures and low precipitation during the summer months favour radial growth. At several sites in high and intermediate altitudes different effects of weather conditions in the previous summer and autumn on tree ring widths were found. These observations could be explained by climatic influences on carbon storage: Unfavourable weather conditions during the previous summer (cold and wet) and favourable weather conditions during early autumn (warm, sunny and dry) improve the filling of carbon storage pools, which can promote radial growth at the beginning of the following season (Fritts and Wu, 1986; Eschrich, 1995). The

strong altitude-dependent climate–growth relations for beech in Central Europe could be confirmed by the application of other methods (Dittmar and Elling, 1999). Dittmar and Elling (1999) also show that the supply of sunshine during the vegetation period is an important minimum factor for beech growth in higher altitude sites. This is in accordance with results in the ‘Solling’ project (Schulze, 1970; Ellenberg et al., 1986) and can explain the negative influence of high precipitation during summer months in higher altitude sites expressed by negative regression coefficients: On these sites soils are well watered in most of the years, but radiation—reduced by wet and cloudy weather conditions—becomes an important growth-limiting factor.

As suspected, in Foresta Umbra (Gargano, South Italy) precipitation has a strong influence on tree ring widths. But it is remarkable that temperature shows a positive impact until May at both investigated sites (plots 21 and 22). It seems that at the very beginning of the vegetation period enough water is stored in the soil. So, high temperatures favour growth at first. Later in the season high temperatures accelerate water deficiency and the influence becomes negative, expressed in negative regression coefficients between temperature and tree ring widths. Additionally, single-year analyses

sites site groups	m a.s.l (plot No.)	temperature										R ² (%)	precipitation										R ² (%)	intervall of calculation							
		previous year					year of tree ring formation						previous year					year of tree ring formation													
		J	A	S	O	N	D	J	F	M	A		M	J	J	A	J	A	S	O	N	D			J	F	M	A	M	J	J
Central Europe: high altitude sites ^{a)}	830 to 1240	↓	↓	↑	↑	↓	↑	↑	↑	↑	↓	↑	↑	↑	↑	44 (27-66)	↑	↑	↓	↑	↓	↑	↓	↓	↓	↑	↓	↓	↓	32 (17-51)	1952-1995
Central Europe: low altitude sites ^{a)}	330 to 600	↓	↓	↓	↑	↑	↑	↑	↑	↓	↓	↓	↓	↓	45 (21-67)	↑	↑	↑	↑	↑	↑	↓	↑	↑	↑	↑	↑	↑	43 (28-69)		
Southern Europe: Gargano	790 (21) 580 (22)	↑	↑	↑	↓	↑	↓	↓	↑	↑	↑	↑	↓	↓	29 36	↑	↑	↑	↑	↑	↓	↓	↓	↓	↑	↑	↑	↑	32 34	1930-1994	
Northern Europe: Skåne	160 (25) 150 (26) 100 (27)	↓	↓	↑	↑	↓	↓	↓	↑	↓	↑	↑	↓	↓	28 13 18	↑	↓	↓	↓	↑	↓	↓	↑	↑	↓	↑	↑	↑	19 15 24	1921-1995	
Western Europe: Pyrenees	950 (23) 1170 (24)	↓	↓	↑	↑	↑	↑	↑	↓	↓	↑	↑	↓	↑	41 45	↑	↑	↑	↓	↓	↑	↓	↑	↑	↑	↓	↑	↓	29 28	1946-1995	
Eastern Europe: Carpathian Mts. Transsilvania	1400 (32) 890 (36) 460 (35)	↓	↑	↑	↑	↓	↓	↓	↑	↓	↑	↑	↓	↓	26 19 32	↓	↑	↑	↑	↓	↓	↓	↑	↓	↑	↓	↑	↑	19 29 31	1957-1996 1947-1995 1910-1994	

<p>↑ positive regression coefficients</p> <p>↓ negative regression coefficients</p> <p>■ significant with P<0.05</p>	<p>a for site groups: direction of average regression coefficients signed as arrows, number of significant regressions coefficients given below</p> <p>R² variance explained by climate (for site groups: mean and range of values [minimum - maximum] in parentheses are given)</p>
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Fig. 4. Climate–growth relationships of all sites and site groups calculated by response function analyses. Directions of the regression coefficients in the response functions are signed as arrows.

revealed that beech trees at Foresta Umbra have a high resistance to drought in radial growth: even in very dry years—up to 3 summer months without precipitation—no extreme growth reduction or missing rings were detected.

In southern Sweden, the climate is favourable during the vegetation period and balanced in most of the years (plots 25–27). No climatic parameter can be extracted as the primary-limiting factor. Therefore the statistical relations between climate and growth carried out by continuous time series analysis are rather low, only a small dependence on precipitation is recognizable. Negative pointer years are often formed in years with precipitation deficits.

The two stands at higher altitudes in the western Pyrenees (Navarra/Spain) demonstrate a kind of transition between temperature- and precipitation-dependent radial growth. During the vegetation period beech trees at the lower altitude site (plot 23, 950 m a.s.l.) only show significant relations in June: negative between temperature and tree ring widths and positive between precipitation and tree ring widths, respectively. Although precipitation per year is high (more than 2000 mm on average), rainfall strongly decreases during the summer months, so that growth reduction due to insufficient water supply may occur (Dittmar, 1999). At the site 200 m above (plot 24, 1170 m a.s.l.), radial increment seems more temperature controlled. Stronger positive influences of temperature and negative influences of precipitation were found. But both the stands also show significant regression coefficients in different months of the previous year and previous winter. Probably these relations indirectly inform about the occurrence of frost and/or weather influences on storage metabolism and frost resistance (Dittmar, 1999).

The unavailability of long and continuous meteorological data records made the calculation of climate–growth relations for the Romanian beech plots very difficult. This is probably the main reason why for the sites at higher altitudes of the Carpathian mountains (plots 32 and 34) no months with significant regression coefficients were found by the response function method. At the low altitude plot north of the chain of the Carpathian mountains (plot 35) precipitation limited radial growth is clearly obvious.

During the dendroecological evaluation of growth data of different beech stands in Europe, apart from

strong elevation-dependent climate–growth relations, a high potential and stability of tree ring formation on such sites were found, where water supply is the primary-limiting factor. Drought and/or water stress in connection with fructification can cause small tree rings in single years, but cambial activity recovers completely in the years following if beech trees are not damaged by other impacts. These observations were confirmed by different kinds of dendroecological analyses and by the findings of other investigations (Flury, 1926; Felbermeier, 1994; Bonn, 1998). Therefore we assume that Common beech is much more resistant to water stress, than is often suspected.

On the contrary, beech cambial activity seems to be very sensitive to late frosts at the beginning of the vegetation period and to cool, wet and cloudy weather conditions during it. Only on sites where the latter influences often affect radial growth, did we find the repeated appearance of missing rings, especially during the strong depressions in the recent past (see below). This kind of site-dependent sensitivity of Common beech had to be considered for assessments of forest vitality and for evaluations of the annual crown condition surveys.

3.4. Growth disturbances and non-climatic growth variations

The establishment of growth history by tree ring widths repeatedly revealed strong growth disturbances in chronologies of beech trees growing at higher altitudes in Central Europe. In Fig. 3, one example is plotted. Tree ring series on these sites often show several depressions in radial growth between 1975 and 1995, which, because of their intensity and duration, are not comparable with signatures in earlier times. Increment losses are frequently accompanied by missing rings and a distinctly increased sensitivity of radial growth (Dittmar, 1999). Similar findings are reported by Eckstein et al. (1984) and Dittmar et al. (1997) in connection with beech decline in the Vogelsberg (Central Germany) and in North Bohemian mountains, respectively.

To test whether these disturbances are caused by climate or other influences, the tree ring time series were evaluated by growth modelling and single-year analyses. To separate climate from non-climate signals in tree rings, different dendroecological methods

were developed and applied (Fritts and Swetnam, 1989; Innes and Cook, 1989). In this study, an approach was used which allows the comparison between growth expected by climate and measured growth for a selected time interval (Kienast, 1985; Eckstein et al., 1984; Greve et al., 1986; Cook, 1987; Verlage and Breckle, 1989). Methods and data selection for this approach are described in detail in Dittmar (1999).

Because of the detected disturbances after 1975 climate and tree ring data before 1970 were chosen to establish climate–growth relations. These relations were used to predict radial growth variations after 1970. By these means—a good model quality provided—it is possible to detect non-climatic growth influences by the comparison of modelled (extrapolated) with measured growth after 1970. For establishment of climate–growth relations, the response function method by Fritts (1976) was applied in a

constant time span of 40 years (1912–1951). The separately calculated relations with different and suitable sets of climatic data for each stand were used to predict radial increment after 1951. Between 1952 and 1970, the model was tested on quality and time stability. As far as data are available after 1970 (mostly until 1995), growth was modelled (extrapolated), and differences between measured and estimated growth were statistically tested according to Verlage and Breckle (1989). Growth modelling, model test and extrapolation were carried out in the same way for all beech stands in Central Europe (17 plots at high and 12 plots at low elevations). Data from earlier investigations in the North Bohemian mountains (Dittmar et al., 1997) were included. To detect signals of effective growth disturbing factors beyond the region, the results were summarized separately for the two site groups in Central Europe and plotted in Fig. 5.

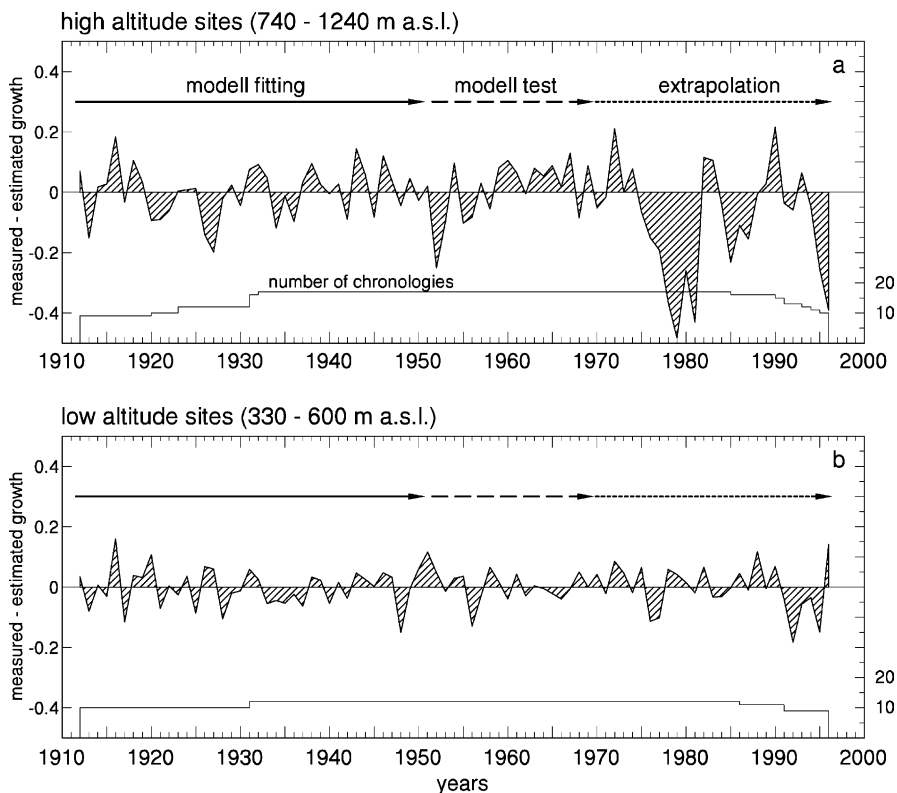


Fig. 5. Differences between estimated and measured growth of 17 high and 12 low elevations sites in Central Europe. Response functions until 1950 were used to model growth after 1951. Between 1951 and 1970 model quality and stability was tested. During the extrapolation period (1971–1995) negative deviations between estimated and measured growth indicate non-climatic growth disturbances.

The model calculations for higher altitude sites show three periods with distinct differences between measured and estimated growth after 1970. In most cases these were significant. In the years between 1975 and 1982, 1984 and 1988 and after 1994, measured growth remains markedly below the growth predicted by the model (Fig. 5a). Hence, the growth depressions at higher altitude sites of Central Europe during these years cannot be explained by the model. This method does not take into account very short-term weather influences like late frosts or the impact of seed production on wood increment. These had to be proved by single-year analyses (see below). But in respect of the latter restriction, the chosen method can be designated as suitable to separate climatic from non-climatic growth variations. This is confirmed by the results for the lower altitude sites (Fig. 5b). Also during the model test period for both site groups, the differences between measured and modelled growth are generally low. The model shows an obvious overestimation rather than an underestimation of radial increment for higher altitudes between 1951 and 1970 (Fig. 5a).

At higher altitudes remarkable negative deviations before 1970 between measured and estimated tree ring widths are only obvious in the years 1926/1927 and 1952/1953. Single-year analyses were applied to prove the impact of short-term influences using climatic data with high time resolution. Additionally the relation between increment loss and seed production was tested by this method. Growth reductions during the years 1926/1927 and 1952/1953 could be explained by short-term and extreme weather impacts: late frost and/or exceptional wet, cool and cloudy vegetation periods (Dittmar, 1999). Short-term and unfavourable weather influences are also important for the understanding of increment losses in the years 1976–1981, 1985–1987 and after 1994. They can explain the synchronization of growth depressions, but not their intensity, duration and the retarded recovery of cambial activity. Reactions in tree ring growth to more or less moderate weather events after 1970 are much heftier and more persistent than to distinctly stronger weather impacts in the years before 1970, as detailed single-year analyses under consideration of earlier periods show (Dittmar, 1999). After the most severe and well-documented late frost during the investigation period in May 1953 (see Elling et al., 1987), for example, most beech trees at higher altitudes show a significant decrease in tree ring

widths, but—although weather conditions were unfavourable—a complete recovery in the following year (see also the example in Fig. 3).

Site conditions (soil, nutritional status) were evaluated at most of the plots and brought in relation to crown condition parameters (see Dittmar, 1999). Site conditions are partially correlated with different intensities of crown transparency, but they cannot explain the presence or absence of strong increment losses and declining phenomena detected in tree rings. Latter symptoms were also found in trees growing under favourable soil conditions and with sufficient nutritional status. Relations between crown damage and growth depressions were only visible in one respect: increment losses in the recent past are always connected with high transparency and damage symptoms of the crown. Diametrically opposed, however, an equivalent relation could not be confirmed.

Growth disturbances under different site conditions in connection with crown damage symptoms (after Roloff, 1986; see Dittmar, 1999), we found mainly in higher altitudes in Central Europe. Hence, we assume the impact of changed environmental conditions with new growth relevant factors in the last decades, which obviously are site-independent, but altitude-dependent effective. The temporal and spatial pattern of the damage phenomena argue against pathogens as primary factors, but they cannot be excluded as additional, secondary stressors (Flückiger and Braun, 1994).

Differences between measured and modelled growth in the early 1990s at lower altitude sites are probably caused by consecutive vegetation periods with insufficient water supply and repeated rich fructifications (Dittmar, 1999; Paar et al., 2000). This kind of additive stress may explain the deviations in the years 1992 and 1995.

4. Conclusion

In order to obtain more information about the sensitivity, vitality and resistance of Common beech (*F. sylvatica*), 36 stands under different climatic and environmental conditions were selected throughout Europe. As parameters for sensitivity, vitality and resistance in the past and present tree ring widths were chosen and evaluated by dendroecological methods. The variation in tree ring widths was found to be a very sensitive

indicator clearly reflecting the signal of exogenous influences. In most of the chronologies, this can be confirmed by a high average sensitivity (year-to-year variation of radial growth) and a strong common signal in the tree ring series of one stand. It can be concluded that the Common beech is very suitable for dendroecological analysis.

The examination of long-term variations in tree ring widths demonstrates site- and altitude-dependent radial growth trends. Most of the stands at lower altitude sites in Central Europe show an increasing growth potential during the last decades. Because of the selection of dominant and co-dominant individuals for sample trees, this finding is not surprising and can be primarily explained by competition effects within the stand. In contrast, slightly decreasing growth trends during the last decades were found at almost all sites at higher altitudes of Central Europe. They reflect reduced growth potential and strong disturbances in tree ring formation between 1975 and 1995. Several environmental changes in the recent past—atmospheric input of nitrogen, increased atmospheric CO₂ content, higher temperatures and an extended vegetation period (Pearson and Steward, 1993; Schönwiese et al., 1993; Myneni et al., 1997; Fabian and Menzel, 1998; Pretzsch, 1999)—should improve growth conditions especially at higher altitudes in Central Europe. Our data, however, cannot confirm a general increasing growth trend. Precisely on these sites environmental influences with negative impacts on cambial activity seem to predominate in the last decades. This underlines the necessity of a site-dependent differentiation for the assessment of growth trends in Europe (Pretzsch, 1999).

The climate–growth relations, established by different dendroecological methods, demonstrate distinct evaluation-dependent growth-limiting factors. At lower altitude sites in Central Europe drought, and sometimes water stress in connection with fructification, reduce radial growth for 1, rarely for 2 years. But even after years with pronounced precipitation deficiency, damage symptoms in the form of strong increment losses over several years could not be detected. In contrast, these phenomena were repeatedly found in tree ring series of Common beech growing at higher altitudes in Central Europe between 1975 and 1995, where these findings were not drought-related but affected by just the opposite

weather conditions. On these sites and in most of those years warmth and radiation is growth limiting, and late frosts as well as cool, wet and cloudy weather conditions during the vegetation period are responsible for small tree rings. Much stronger reactions to these influences and growth disturbances in the recent past (1975–1995) indicate an increased sensitivity or reduced “ecological fitness” (Matyssek, 1998) of Common beech. It seems that beech trees growing at higher altitude sites in Central Europe during the last decades are more sensitive than previously against late frost and unfavourable weather conditions (cold, wet and cloudy) during the vegetation period. To assess the extent and importance of the detected growth disturbances, the special selection of sample trees in these investigation must be considered. For dendroecological analyses, it is necessary to work with dominant and co-dominant individuals in order to avoid competition effects as much as possible. This, however, surely leads to a significant underestimation of growth disturbances and damages with look at the whole stand.

The crown condition variability of the investigated beech trees can be widely explained by different site conditions (Dittmar, 1999). But no relation could be found between site conditions and the presence or absence of the strong increment losses and declining phenomena detected in tree rings after 1975. The spatial and temporal pattern of these growth disturbances leads to the assumption that changed environmental conditions and new growth relevant factors are involved. They are obviously site-independent, but strongly altitude-dependent effective.

Several investigations involving different tree species and pollutants show that deciduous trees like beech and oak are much more resistant to SO₂-dominated emissions than coniferous trees. But they are more sensitive to photo-oxidants like ozone (Smidt et al., 1991; Braun and Flückiger, 1995; Landolt et al., 1996; Guderian and Wienhaus, 1997). Especially concerning photosynthesis beech is considered as O₃-sensitive tree species (Smidt et al., 1991). Increasing concentrations of tropospheric ozone have been reported especially for southern Germany, the Alpine region and southern Europe (Ashmore et al., 1985; Smidt et al., 1991; Grennfelt, 1996; Stockwell et al., 1997; Bussotti and Ferretti, 1998). The repeated observation of adverse effects at ambient ozone concentrations leads to the

substantial evidence that this pollutant does impose major stress on forest trees in Europe (Skärby et al., 1998). Impacts of ozone on metabolism and carbon storage are reported by Seufert and Arndt (1989), Braun and Flückiger (1995), Guderian and Wienhaus (1997) and Matyssek (1998). Influences like this could be involved in changes of radial growth of beech in higher altitude sites in Europe. They could explain, why in the recent past trees have become more sensitive to natural environmental influences like late frosts and unfavourable weather conditions during the vegetation period. Considering the site-specific climate–growth relations described above, especially trees at higher altitudes are most at risk. Tropospheric ozone concentrations increase with altitude and because of humid climate conditions O₃-uptake is not effectively limited by water deficiency (Dobson et al., 1990; Showman, 1991; van den Driesche and Langebartels, 1994; Wieser and Havranek, 1995; Emberson et al., 2000). It is also known that both nitrogen and ozone stimulate shoot growth to the disadvantage of root growth (Matyssek, 1998). This could explain reduced ecological fitness and stability, although aboveground growth potential simultaneously increases on many sites. But only very few studies deal with root biomass and its probable changes due to recent environmental influences (Eichhorn, 1995). This aspect should be investigated by specific studies.

Dendroecological investigations with temporal and spatial comparisons can offer an important tool to prove environmental impacts on forest growth and vitality, as demonstrated by this presentation and earlier studies (Eckstein et al., 1984; Kienast, 1985; Greve et al., 1986; Elling, 1987, 1993). These methods should be applied more often in the future and coordinated with forest condition surveys (e.g. ICP-LEVEL II monitoring), eco-physiological investigations and modelling of risk assessment.

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