Growth of Adult Norway Spruce (*Picea abies* [L.] Karst.) and European Beech (*Fagus sylvatica* L.) Under Free-Air Ozone Fumigation

P. Wipfler[1], T. Seifert[1], C. Heerdt[2], H. Werner[2], and H. Pretzsch[1]

[1] Chair of Forest Yield Science, Technische Universität München, Am Hochanger 13, 85354 Freising-Weihenstephan, Germany
[2] Chair of Ecoclimatology, Technische Universität München, Am Hochanger 13, 85354 Freising-Weihenstephan, Germany

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Abstract: **This study attempted to detect the impact of ozone on adult trees of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in an experimental mixed stand in Southern Bavaria, Germany. The aim was to examine whether there is a decrease in growth when trees are exposed to higher than atmospheric concentrations of ozone. This exposure was put into effect using a free-air fumigation system at tree crown level. Growth analysis was carried out on a group of 47 spruce and 36 beech trees, where radial stem increment at breast height – a sensitive index for stress – was measured. The ozone monitoring system allowed values to be obtained for the accumulated ozone exposure (SUM_{00}) of each individual tree, so that their radial increment over three years could be correlated with the corresponding ozone exposure for the same time period. Correlation and regression analysis were then carried out to test the influence of ozone on diameter increment. In both spruce and beech, the initial stem diameter was the most influential factor on radial increment in the following year. A linear model was applied, including the diameter of the preceding year and the ozone exposure of the current year as predicting factors. For spruce trees, a significant negative influence of ozone exposure was found. In contrast, no significant ozone effect on diameter increment of beech was detected. The effect of ozone stress on a large spruce tree can lead to a decrease in potential radial increment of 22%. The results are discussed in relation to other stress factors such as drought and lack of light.**

Key words: **Ozone, free-air ozone fumigation, stem diameter increment, permanent increment tapes, increment decrease, Norway spruce, European beech.**

Introduction

Few results on the impact of ozone on plants have been gained from field experiments. Most results have come from chamber experiments, although there are several field experiments in which ozone stress was estimated with low spatial resolution or radial increment was related to visible ozone damage (Somers et al., 1998; Vollenweider et al., 2003; McLaughlin and Dowing, 1995). Because of the enormous financial and personnel outlay, field experiments with controlled ozone exposure of tree species are rare (Karnosky et al., 2003) or have been limited to seedlings and young plants (Bäck, 1999; Samuelson, 2001; Oksanen and Saalem, 1999). In addition, such studies have mainly dealt with chemical, physiological, and anatomical aspects of stress and not growth reactions as a result of biochemical processes at lower hierarchic levels.

Considering the global aspect of increasing ozone concentrations in the atmosphere, reactions of forest stands – as important carbon sinks and natural resources – are crucial for ecological and economical prognoses (Ashmore, 2005). According to Broadmeadow (1998), transferring results obtained from chamber experiments to forest stands leads to high levels of uncertainty.

The most promising approach to detect growth reactions of trees on ozone exposure should be analysis of stem increment of the lower end of a tree trunk. Compared to the formation of new buds, leaves, shoots, and fine roots, carbon allocation to stem wood has a relatively low priority (Waring and Schlesinger, 1985). Allocation to stem wood only becomes essential if new sapwood is required for water supply to leaves or for maintenance of mechanical integrity of the stem. Due to its low priority in the allocation hierarchy, diameter increment in breast height is particularly sensitive – even though unspecific – in terms of a tree's resource availability.

In trees of equal size, a high diameter increment indicates a reasonable balance in carbon allocation, whereas a low increment indicates shortage of building materials, and a limitation on carbohydrates for storage or defence (Waring and Schlesinger, 1985). Kramer (1986), Pretzsch (1985), and Sterba (1996) have shown that Norway spruce, Scots pine, and silver fir reduce radial increment during stress, particularly in the lower third of the stem. Somers et al. (1998) found symptoms of ozone pressure in basal area increment of yellow poplar, contrary to findings for other variables such as height or relative crown length. Although the crowns of silver fir, Scots pine, and Norway spruce did not always show unambiguous stress symptoms, Elling (1993), Pretzsch (1998), and Schweingruber et al. (1983), using tree ring analysis, detected up to 20 missing tree rings at breast height. Therefore, increment at stem base is appropriate for early detection of stress and decline in tree

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vitality, however, increment decrease at stem base is not representative of the whole stem and least of all for the whole tree. Under stress, tree rings in the lower part of the stem can be missing or rather narrow, whereas rings in the stem's upper part and branches are still normal, i.e., trees become top-heavier. Therefore, use of a particular increment decrease at breast height with reference to the whole stem or even tree would result in an overestimation of growth decrease.

The subsequent evaluation is based on a free-air ozone fumigation experiment in an adult mixed stand of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.), which has been described by Grote and Pretzsch (1998). Norway spruce and European beech are the most important tree species in Middle Europe. Norway spruce and European beech account for nearly 75% of the harvested timber in Germany (BWI, 2005). Forests dominated by European beech cover 14.8%, while Norway spruce-dominated forests cover 28.2% of absolute forest land in Germany. There is also a considerable area containing mixed stands, with 84.7% beech and 32.7% spruce.

In this study, recordings of ozone exposure and annual diameter increment from 2002 to 2004 are used to test the following hypotheses:

- H I: Exposure to ozone has no effect on the stem diameter increment of Norway spruce and European beech. In case of H1's falsification we pose H2.
- H II: Both considered species react similarly to ozone exposure in terms of radial increment of the stem.

Materials and Methods

Kranzberg Forest

The growth response to ozone fumigation of adult Norway spruce and European beech trees was analyzed at the experimental site "Kranzberger Forst" (Grote and Pretzsch, 1998), where a group of trees was fumigated with ozone in a unique free-air O_3 experiment (Häberle et al., 1999; Werner and Fabian, 2002; Nunn et al., 2002). Every eight weeks, diameter at breast height (1.3 m) was measured to examine a potential influence of ozone on diameter growth.

The experimental site was established in 1994, based on an existing mixed stand of Norway spruce and European beech with other tree species of less importance. The experimental site

Table 1 Site characteristics of the experimental plot "Kranzberg Forest"

Parameter	Value	Reference
Altitude	490 m above sea level	
Mean annual temperature	7.0 – 7.5 °C	
Precipitation	730 – 890 mm	
Temperature during vegetation period	14.0 – 15.0 °C	
Soil	luvisol derived from loess over tertiary sediments	Grote and Pretzsch, 1998
Natural vegetation	Galio-odorati-Fagetum	Walentowski et al., 2004

"Kranzberger Forst" is located 35 km northeast of Munich in the "Tertiäres Hügelland" (Tertiary Hill Region) in southern Bavaria, Germany. The site conditions are summarized in Table **1**. The plot is rectangular, with a size of 50 × 100 m. Most of the beech trees are situated in two groups, where one group forms the centre of the ozone fumigation experiment.

In spring 2004 the age of the trees in the experimental plot was approximately 52 ± 2 years for spruce and 62 ± 4 years for beech. Both species grow in a balanced competitive situation. While spruce shows prominent height growth, beech typically tends to expand more horizontally and effectively closes crown gaps. Table **2** illustrates the characteristics of the whole stand for spring 2000, just before ozone fumigation started.

Ozone fumigation experiment in Kranzberg Forest

To gain knowledge of the reaction of adult trees to chronic ozone exposure, the "Kranzberg Ozone Fumigation Experiment" (KROFEX) was established. This system provides continuous and controlled free-air fumigation of adult tree canopies with twice ambient ozone concentration (Werner and Fabian, 2004; Nunn et al., 2002).

The ambient ozone concentraton is measured by an O_3 analyzer (MONITOR LABS, 8810) positioned above the canopy, away from the fumigated area, thus providing a background control. The maintenance of double ozone concentration with respect to ambient ozone concentration is controlled by eight

Table 2 Stand characteristics of the experimental plot "Kranzberg Forest" for spring 2000

Species	Age	Number of trees	Average height of 100 dominant trees	Average diameter of the 100 dominant trees	Height of mean basal area tree	Diameter of mean basal area tree	Basal area	Volume	Annual volume increment
Norway spruce	47	506	27.9	41.4	25.5	28.4	32.1	398	14.4
Scots pine	47	14	27.6	38.9	25.9	30.0	1.0	12	0.3
European larch	47	2			24.2	24.0	0.1	1	–
European beech	57	297	25.2	36.7	24.0	23.4	12.8	156	4.7
Pedunculate oak	57	10	24.4	27.1	24.0	23.8	0.4	5	0.2
Total		829					46.4	572	19.6

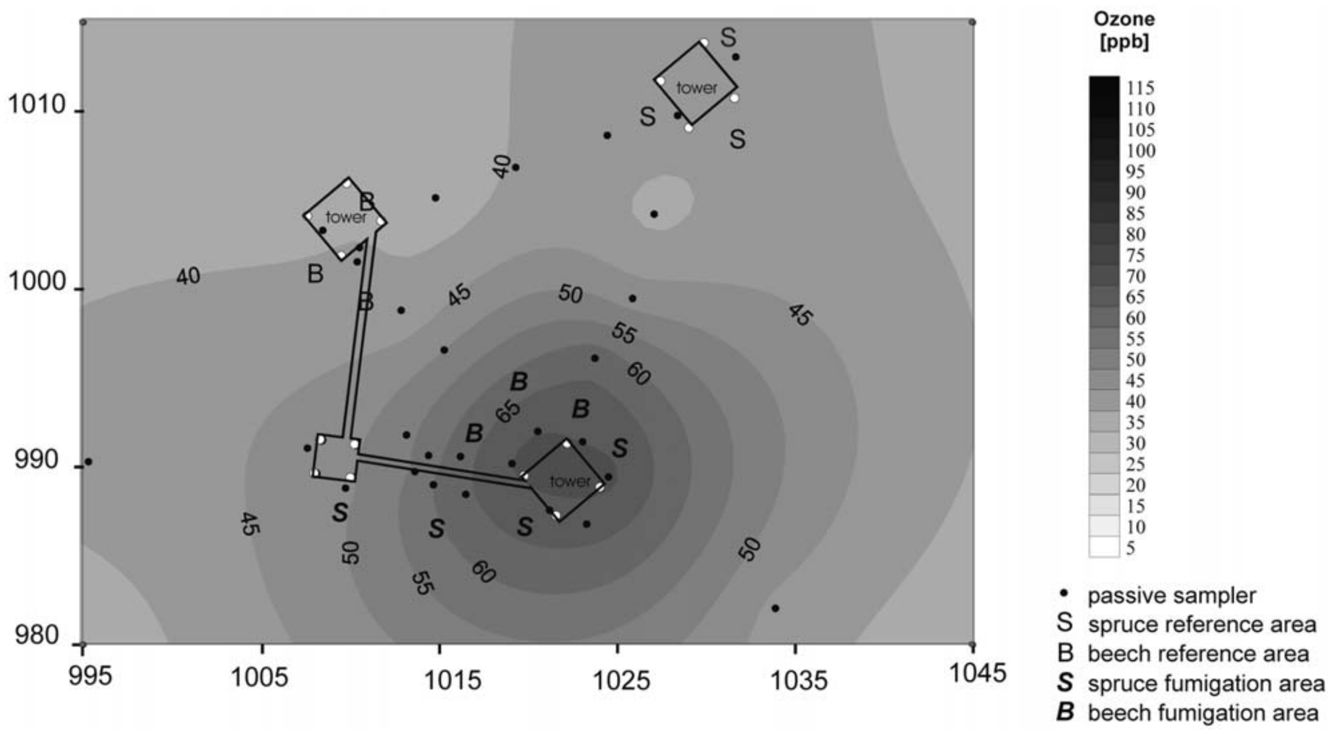

Fig. 1 Ozone distribution in "Kranzberg Forest". Sun crown = 20 m above ground exposed from 2.9.–9.9.2003.

Table 3 Ozone exposure to trees in "Kranzberg Forest" during the years 2002–2004. The minimum values can be regarded as ambient ozone concentration

Year	Period of ozone fumigation			All samplers SUM_{00} (ppbh) on the plot		
	Begin	End	Days	Mean (ppbh)	Min. (ppbh)	Max. (ppbh)
2002	2002-24-04	2002-29-10	185	146.293	101.733	255.047
2003	2003-04-04	2003-04-11	210	242.200	184.417	393.428
2004	2004-18-05	2004-03-11	165	160.978	126.355	223.214

O_3 analyzers at different heights and positions. Maximum ozone levels were limited to 150 ppb. The ozone is generated from 90% oxygen to avoid uncontrolled NO_X production. The ozone is transported by means of 120 PTFE tubes hanging from a grid (120 m^2) above the canopy.

The eight O_3 analyzers (logging interval 10 s) and 101 rope-mounted passive samplers (changing interval 1 week) are positioned at four levels whose heights are adjusted to reflect the stand's properties. These heights are 6 m (stems), 14 m (shade crowns), 21 m (sun crowns), and 26 m (above canopy). The isoplots are based on 25 passive sampler points (level 6 m, 14 m, and 21 m) and 18 samplers at the 26-m level (Fig. **1**). Eight samplers are mounted as near as possible to the continuous ozone analyzers, for calibration purposes. The plots show a clear concentration of ozone in the fumigation area. Further, the decreasing ozone concentration with increasing distance from the fumigation area is quite obvious.

For this study the SUM_{00} value of defined periods, as shown in Table **2**, was calculated. SUM_{00} is the sum of all hourly average ozone concentrations above 0 ppb expressed in ppb · h. SUM_{00} was used instead of a threshold value such as AOT_{40}, which needs hourly values of ozone concentrations. AOT_{40} (accumulated dose over a threshold of 40 ppb) is the sum of the differences between the hourly mean ozone concentration (in ppb or µl/l) and 40 ppb (or µl/l) for each hour when the concentration exceeds 40 ppb, accumulated during the time of day when global clear sky radiation is above 50 W/m^2. Fumigation started in the year 2000. The newly developed passive sampler deployed in this research was only available in spring 2002. For calculation of the influence of ozone on radial stem growth, SUM_{00} values were taken from the 21-m aboveground level, to cover ozone exposure of the biologically efficient sun crown of the stand.

Table **3** shows the variability of the ozone sum between the study years. These differences are related to two factors: varying length of the vegetation period and different environmental conditions. In the exceptional drought year of 2003, with its high radiation during the summer months, the ambient ozone level and therefore also the ozone level maintained by the fumigation system was higher than in other years.

Table 4 Properties of sample trees

	Quantity	Mean diameter	Mean height	Mean crown length	Minimum diameter	Maximum diameter	Minimum height	Maximum height
Norway spruce								
	47	30.2	24.5	12.3	8.8	51.8	13.0	30.0
Standard deviation		8.2	3.1	3.1				
European beech								
	35	23.9	23.3	13.7	14.3	38.3	21.8	25.8
Standard deviation		7.2	1.1	2.7				

The selection process for the sample trees

The sample trees were selected according to their distance from the ozone passive samplers to ensure that these trees were exposed to defined ozone concentrations. The distance between each tree and the samplers was calculated. The projected crown area was estimated for each tree as a regression function from stem diameter based on measured crown projection. A tree was selected if the crown was less than 3 m away from the next sampler.

The applied permanent girth tapes are made of temperature-insensitive plastic and were successfully tested by Spelsberg (1986), Franz et al. (1990), and Nüsslein (1995). Compared with repeated measurements by calliper or girthing tape, the permanent installation ensures a considerably higher accuracy of diameter increment recordings (Prodan, 1965; Pretzsch, 2002). Accuracy is additionally increased by using a vernier scale. On the experimental plot, FRE 813/1 tapes were installed on 330 Norway spruces and 196 European beeches at 1.30 m height and read from 1997 to 2004 at 2-month intervals with a precision of 1 mm. Recordings of annual diameter increment from 2002 to 2004 are used for this study.

Sample of trees

The group of trees studied consists of 47 spruces and 35 beeches (Table **4**). Both species have a wide diameter range. The spruce group consists of trees from 8.8 cm to 51.8 cm diameter at breast height (dbh), with a mean diameter of nearly 30.0 cm. The distribution maximum is between the 25-cm and 40-cm diameter class, with 19 trees. The maximum height of spruce is 30 m. These trees are thus among the highest on the experimental plot. The smallest tree is 13 m high and is probably under strong competitive pressure. The diameter of beech trees varies from 14.3 cm to nearly 40 cm, with an average of 24 cm. The dominant diameter class here is about 20 cm, comprising 12 trees. The average height, as well as the maximum height, of spruce is considerably higher than that of beech, whereas the average dbh of both species hardly differs. Considering the tendency of beech to spread its crown rather than to grow in height, it can be assumed that, despite the presence of small spruce, every plant is represented in the canopy of the stand. Due to the wide range of tree sizes, competition effects cannot be excluded. The crown lengths of trees are 13 m and 12 m, respectively, and therefore about half the total tree height.

To identify the role of dbh and SUM_{00}, a partial correlation analysis was performed. Any coincidental correlation between diameter and ozone exposure was tested with a correlation analysis. To test the interrelation between the diameter increment and ozone exposure, a regression analysis based on a linear model was used, which included the diameter as an additional factor. The statistical software SPSS 12.0 was used for all analyses.

Results

The aim of this study is to identify the role of ozone in the process of diameter increment of two tree species and to quantify and correlate this with other factors. The most influential factor is the absolute size of the tree, represented by diameter at breast height. Because the sample groups of the two species, as a result of the selection process, do not necessarily correspond to each other in size, nor represent the stand's size distribution, diameter should be used as a covariate to account for different competitive situations of the trees.

Fig. **2** shows the diameter increment in relation to diameter and ozone exposure, the latter being the main object of interest. The considerably higher diameter increment of spruce compared to that of beech corresponds well with its higher initial average diameter. In contrast, the exposure to ozone is very similar for the sample groups representing the two species. This finding allows us to use diameter as covariate when studying the influence of ozone to account for differences in the absolute level of diameter increment between trees, which is mainly a result of different competition and growth history.

The correlation between the ozone exposure as SUM_{00} value of three years and the diameter increment for the same period was tested with dbh (2001) as covariate. The test was highly significant for spruce, with a negative value indicating an obviously depressing influence of ozone on the stem diameter increment of the sample trees (Table **5**). The coefficient for beech is nearly zero and not significant. Thus, an influence of ozone on the growth of beech trees was not detected.

The findings of the correlation analysis were resumed in a regression model for the diameter increment (id) over a period of three years. The model included ozone exposure as accumulated SUM_{00} values over three years, the diameter as a known important factor, and an intercept term resulting in $\mathrm{id} = a + b \cdot \mathrm{d} + c \cdot SUM_{00}$ with id = diameter increment at breast

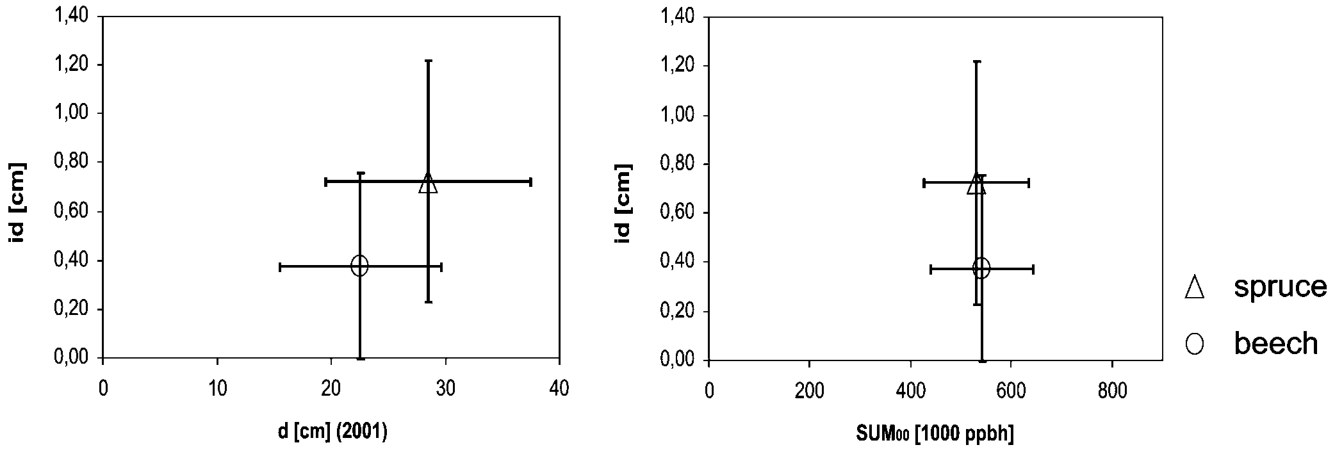

Fig. 2 Growth of spruce and beech in relation to diameter and ozone exposure. Error bars show standard deviation.

height (cm), d = diameter at breast height at the beginning of the period (cm), and SUM_{00} = ozone exposure (ppb).

A competition index was used to check the residuals of the model for any additional influence of competition which was not accounted for by the diameter. The application of the index KKL (Pretzsch, 1992) showed no correlation. Also, the insertion of the KKL as an independent variable in the regression showed no significant additional influence. Consequently, the models with diameter and ozone as independent variables were applied for spruce and beech and proved to be statistically significant (Table **6**). The model reveals that diameter has the strongest influence on growth. In the case of Norway spruce, the coefficient for ozone has a negative value and is significant, while no significant effect of ozone was found on stem diameter increment of beech.

Fig. **3** shows the model. The slope on the diameter scale demonstrates that diameter increment is mostly determined by the diameter itself. Spruce, therefore, needs a minimum stem diameter of 10 cm to achieve a minimal diameter increment in the experimental stand, whereas spruce of about 60 cm diameter can increase approximately 2 cm in diameter in three years. Diameter increment of spruce is also influenced by ozone exposure, as indicated by the slope over the SUM_{00} axis. According to the model, a difference in ozone exposure of 300 000 ppbh can cause a difference of 0.3 cm in diameter growth in three years.

Due to the high spread of the observed values, the model fit for beech is not satisfying, although it is significant. Results for beech must therefore be interpreted carefully. However, beech obviously shows a dependence of radial increment on absolute diameter. Because of the low value of the stability index, quantifiable conclusions would be inappropriate. An influence of ozone could not be detected.

To evaluate the adjustment of the model to the observed values, the residuals of the predicted values and the observed values were plotted (Fig. **4**). The predicted and the observed growth values show no tendency in any direction. This can be interpreted as the fact that no other important influential factor was left out of the model.

Table 5 Correlation between radial increment over 3 years and ozone exposure, with diameter in the year 2001 as covariate

	Degrees of freedom	Value of the coefficient	Degree of significance
Norway spruce	45	– 0.306	0.036
European beech	33	0.032	0.853

Table 6 Significance and parameters of the model id = a + b · d + c · SUM_{00} with id = diameter increment at breast height (cm), d = diameter breast height at the beginning of the period (cm), and SUM_{00} = ozone exposure (ppbh)

	F	R^2	Significance	df
Norway spruce				
Model	34.939	0.591	0.000	47
Parameter		*Standard error*		
a	0.112	0.281	0.693	
b (diameter)	0.041	0.005	0.000	
c (ozone)	0.000	0.000	0.036	
European beech				
Model	4.223	0.156	0.023	35
Parameter		*Standard error*		
a	– 0.213	0.359	0.556	
b (diameter)	0.024	0.008	0.007	
c (ozone)	0.000	0.000	0.853	

On the basis of these results Hypothesis I is rejected for Norway spruce and accepted for European beech. As a consequence of the difference between these species, Hypothesis II has to be rejected.

Discussion

With the background of global change and increasing exposure of plants to air pollutants, ozone research has become an essential part of contemporary botany. The reactions of plants

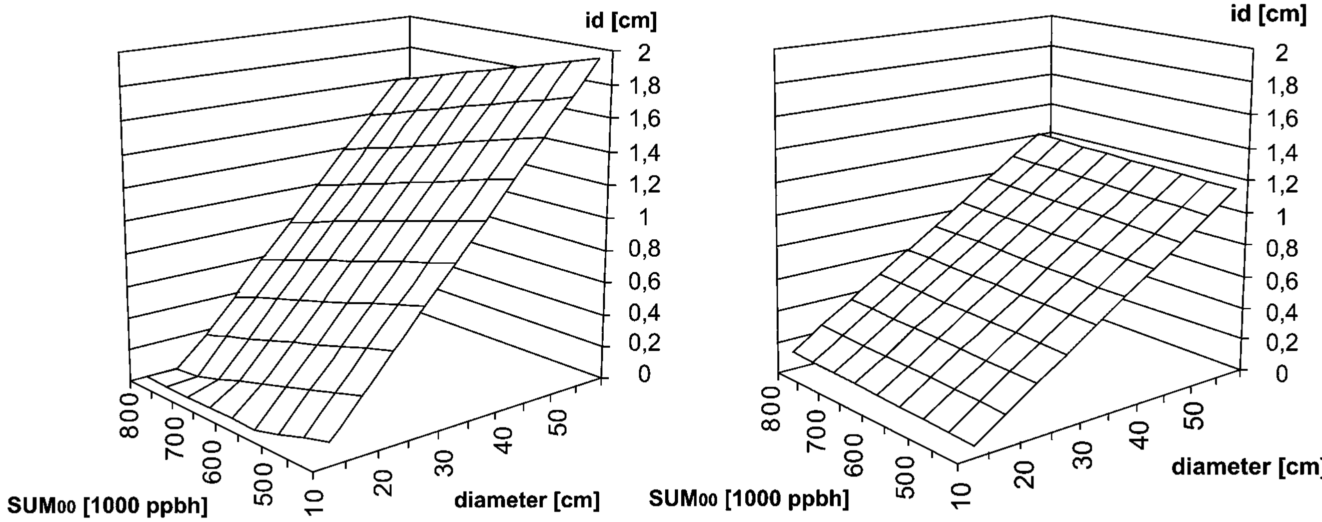

Fig. 3 The growth of Norway spruce (left) and European beech (right) in relation to diameter and ozone, according to the model.

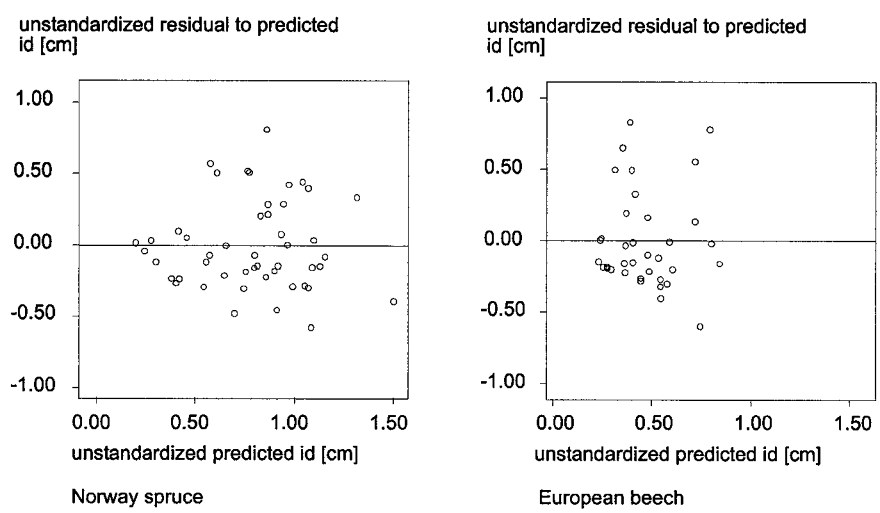

Fig. 4 Residuals between predicted and observed diameter increment (id).

to changing environmental factors are of crucial interest in respect to social, economic, and ecological questions. The Kranzberg Forest Experiment is among a small number of experiments which test the reaction of adult Norway spruce and European beech trees under field conditions.

The diameter increment of sample trees was analyzed in relation to their initial diameter and ozone exposure. No influence of ozone on diameter growth of European beech could be found, either by applying a partial correlation analysis, or by means of linear regression. Thus, we reject Hypothesis I with respect to European beech. The correlation coefficient was hardly above zero and, furthermore, was not significant. Also, the model derived from the regression analysis, which was significant, displayed no slope on the SUM_{00} axis. In contrast, we accept Hypothesis I for Norway spruce, where both correlation analysis and regression analysis displayed a significant negative coefficient for ozone exposure. According to the regression analysis, stem diameter growth of spruce is lowered by ozone by 0.42 cm in three years compared to trees without added ozone. For example, a spruce tree of 50 cm stem diameter would lose 24% of its potential stem growth, a smaller tree of 20 cm stem diameter would lose about 77%. These significant differences between spruce and beech lead to rejection of Hypothesis II, which states that the reactions to ozone of spruce and beech are similar.

The response of adult trees to ozone has been observed previously, especially in coniferous trees (Vollenweider et al., 2003; Karnosky et al., 2003; Somers et al., 1998). As mentioned above, stem diameter increment can be considered a stress-sensitive variable. The decrease in carbon allocation of a whole tree must not be deduced from the decrease in stem growth.

To estimate the role of ozone in the growth process of plants, it is necessary to understand its interaction with other environmental factors. Ozone has been described as a "major secondary air pollutant" (Ashmore, 2005) and a "secondary stress factor" (Muzika, 2004). Ozone has also been considered to predispose trees to further stress (Matyssek, 2003). Its main impact on trees appears to be the lowering of resilience towards other stress factors (Skärby et al., 1998).

What other stress factors, beside ozone, are the trees of the Kranzberg Forest exposed to? The site provides growing conditions without climatic extremes, as well as a good nutrient and water supply. In 2003, however, the stand suffered an exceptional drought period during the summer. In that year, we observed a general decrease in growth, especially of spruce trees. Is it likely that the higher sensitivity of spruce is related to its higher sensitivity towards drought stress? Both limiting and promoting effects of ozone on trees under drought stress have been reported. Partial stomatal closure caused by moisture deficits can limit the uptake of ozone and therefore moderate its impact. However, ozone seems to affect stomatal closure during moisture deficits. In fact, stomatal conductance in 2003, and therefore the ozone taken up by the trees under heavy ozone exposure may not have been that much higher than that of those trees which were less exposed to ozone (Nunn, 2005). Unlike mild drought stress, severe drought is assumed to "protect" trees from ozone by reducing stomatal conductance (Matyssek, 2003; Karlsson et al., 1997).

The interaction of radiation and ozone is also ambiguous. With seedlings, Bäck (1999) found more senescence under low light treatment. Assuming that this is also valid for adult trees, it corresponds well with the model presented here. The larger decrease in diameter increment of small trees could therefore be explained by a stronger ozone impact enforced by low light conditions. This interrelation, however, is still to be tested experimentally.

In stands of competing trees, light is considered as the determining factor for growth. Therefore, the ability to occupy space despite ozone stress will be decisive for survival of individual trees and species. Thus, the elongation of shoots and increased height growth, rather than enhanced stem diameter growth, are important factors. Though stem growth may indicate general biomass growth of the whole tree, crown development cannot be deduced from stem growth. It must be tested whether allometric functions, which work quite well under known conditions, change under abiotic stress. Corresponding studies are still to be conducted.

The model of initial stem diameter and ozone exposure proved to be sufficient and free of additional influence from competition effects. This is true for the unthinned sample stand. In recently thinned stands the competitive status of a tree may contribute to its diameter increment. The removal of competitors creates newly available growing space which would not yet seriously effect the initial diameter while it would already effect the current increment. So our results may be restricted to stands under self-thinning conditions.

Results from a field experiment cannot consider all possible influencing factors. It is nevertheless important to test stress factors during *"ceteris paribus"* conditions, especially in long living creatures and over long time periods. We chose a 3-year period to detect the chronic impact of ozone rather than acute effects. This is in line with other experiments dealing with ozone (Karnosky, 2003; Schmieden and Wild, 1995).

Because of the technical limitations of the ozone monitoring system, no hourly values of the ozone concentration were available. Thus, no threshold value considering a biological relevant ozone level like AOT_{40} could be used. The ozone exposures applied to the sample trees range from ambient concentration to nearly double ambient concentration of ozone. Some models do in fact suggest future ozone concentrations of more than 60 ppb in some regions, including Middle Europe (Emberson et al., 2003).

For statistical analysis a linear model was chosen because of its plausible results and ease of interpretation. Nevertheless, there are still limitations. First, the model predicts negative stem diameter change for small spruce trees under high ozone exposure, which is not possible and results from the specific parameterization of the experimental site. Moreover, a linear model does not allow a proportional increase in growth per additional unit ozone exposure, which would be more plausible than just a linear increase. Furthermore, the model does not allow different slopes in the growth scale at the high diameter and the low diameter end of the diameter scale. Therefore, small trees suffer a higher percentage of increment decrease in the model results. To avoid this calculation effect, a term describing the interrelation between ozone and size (dbh) was tested as an additional parameter, but it was not found significant. It must be noted that a class of high diameter of beech, though it was included in the model, was not represented in the sample group. This model, even though it is useful to illustrate the findings of this specific study, is not suitable for estimation of ozone damage in general.

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H. Pretzsch

Lehrstuhl für Waldwachstumskunde
Faculty of Forest Science and Resource Management
Technische Universität München
Am Hochanger 13
85354 Freising-Weihenstephan
Germany

E-mail: hans.pretzsch@lrz.tum.de

Guest Editor: R. Matyssek