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Intra-annual growth response of adult Norway spruce (*Picea abies* [L.] KARST.) and European beech (*Fagus sylvatica* L.) to an experimentally enhanced, free-air ozone regime

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Abstract Several findings indicate an impact of ozone on stem diameter growth leaving the question unanswered, if and how the intra-annual growth pattern is changed. In this study the hypotheses are tested, that (1) ozone will alter the absolute growth and (2) alter and shift the period of growth activity within a year. Our data originates from the free air ozone fumigation experiment 'Kranzberger Forst' in a mixed stand of Norway spruce and common beech near Freising/Germany. Annual and intra-annual growth reactions of a sample of five adult beech and five spruce trees, exposed to double ambient ozone were examined and compared to the same number of untreated reference trees. Diameter increments were measured with plastic diameter girth bands and high-resolution, automatically logging micro-dendrometers, mounted at breast height (1.3 m). We used the increment data from the growth periods 2000 to 2005. The high-resolution micro-dendrometer data were examined by fitting a Weibull function to the standardized annual growth profiles to obtain curve parameters for statistical tests. We estimated the parameters 'T' which represents the point of time, when 63% of the annual diameter increment is performed and the parameter 'm', the Weibull module, which was used as an indicator for the span of time needed to complete the annual growth. The statistical significance of these curve parameters, together with the absolute diameter increment, was tested by use of mixed regression models. The analysis of the growth curve parameters revealed a significantly altered intra-annual growth pattern of both species induced by ozone. Spruce under ozone showed reduced absolute annual diameter increment and a preponed growth activity compared to untreated trees. Beech's absolute diameter increment was not affected under ozone, but its growth activity was delayed. For both species, ozone fumigation did not alter the individual length of the annual growing season. These results are discussed with respect to drought, tree ring anatomy and tree allometry. The study shows that ozone is able to change growth behaviour of trees even if increment losses are not obvious.

Keywords Ozone · Norway spruce (*Picea abies*) · European beech (*Fagus sylvatica*) · Stem diameter increment · Intra-annual growth pattern · Stress reaction · Mixed models

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Introduction

The results of several research projects based upon empirical measurements as well as simulation models coincide in their prognoses of future increase of tropospheric ozone concentrations (Marenco et al. 1994; Stevenson et al. 1998; Stockwell et al. 1997; Ashmore 2005). Marenco et al. (1994) stated a yearly increase of 1.6% in ozone concentration, Vingarzan (2004) predicts 0.5–2%, which raises the question of how plants are affected by elevated ozone exposition.

In recent times the impact of ozone on growth of woody plants has been intensively examined in order to assess possible effects of future tropospheric ozone concentrations (Ashmore 2005; Karnosky et al. 2003; Matyssek and Innes 1999; Dittmar et al. 2003). This topic is of ecological as well as of economical interest, especially in respect to crop tree species. Although, the economic effect of ozone on trees seems not to be as severe as the effects on quality and yield of agricultural products (Ashmore 2005; Vollen-weider et al. 2003), recent results reveal significant impacts of ozone on woody plants. For trees, reactions have been observed on physiological level (Nunn et al. 2005), whole tree level (Oksanen and Saalem 1999; Karlsson et al. 1997; Wipfler et al. 2005; Somers et al. 1998) and stand level (Karnosky et al. 2003). The experiments have been per-formed on plants of the whole ontogenetic scale, on seedlings, young plants and adult trees. The experimental sites range from laboratories, where physiological reactions can be examined in detail under controlled conditions, up to field studies of whole stands, with the focus on whole plant reaction as the integral of all physiological processes. The majority of these studies were complemented by modelling approaches to link the results from experiments with various designs (Deckmyn et al. 2007; Kolb and Matyssek 2001; Samuelson and Kelly 2001). It turned out that results of studies on tree seedlings cannot be used for predictions about growth reactions of adult trees (Chapp-elka and Samuelson 1997; Skärby et al. 1998). The link between processes observed in leaves, shoots or roots and the whole-tree biomass allocation is not yet understood. The examination of the growth patterns of adult trees exposed to stress, which can be interpreted as results of known growth processes, could be a further step towards the understanding of the mechanism of stress reaction.

One of these well-examined growth processes is the formation of tree rings. It is usually accessed by measuring stem diameter or ring width on the lower end of the trunk. Stem diameter growth at breast height has proven to be sensitive to stress, obviously due to carbon allocation patterns under stress (Waring and Schlesinger 1985; Pret-zsch 1989; Kramer 1986; Sterba 1996). Growth profiles along the stem can therefore be affected by pollution, competition or other environmental conditions. In the stems of spruce even whole tree rings can be missing as a consequence of stress (Schweingruber et al. 1983; Athari 1980, 1983). Franz et al. (1990) observed a general decrease in diameter growth as well as altered intra-annual growth behaviour. Recent results in forest science also suggest that ozone damage can be detected via studies of the diameter growth (Wipfler et al. 2005; Karlsson et al. 2006). It is also debatable whether ozone induced growth decline is comparable with the phenomenon which was labelled 'new forest decline' in the 1980s.

A closer examination of intra-annual growth profiles may reveal the time span within the vegetation period, when these losses of stem growth at breast height occur. Patterns that deviate from the expected growth rhythm can be detected, because the pattern of tree ring formation during the vegetation period is well known. The growth period in Central Europe usually starts in April and ends at the end of August. The maximum growth rate is usually achieved in early summer; breast height diameter growth usually ends around the beginning of October, depending on growth conditions.

This study is based on measurements at stem diameter at breast height (dbh). To study intra-annual growth profiles, measurements of high temporal and spatial resolution of diameter of circumference are necessary. This can be provided by automatically logged micro-dendrometer bands. These systems have become more common in forest research, in order to understand tree ring formation (Downes et al. 2002; Wimmer et al. 2002). The high measurement frequency enables short-term effects to be detected as well as trends over the whole vegetation period. Water uptake, water adsorption and transpiration cause a short-term circumference fluctuation, which can be sepa-rated into three phases: shrinkage, recovery and increment (Deslauriers et al. 2003; Downes et al. 1999; Offenthaler et al. 2001). This fluctuation can be observed as daily cycles (short term) as well as mid- and long-term cycles (Deslauriers and Morin 2005). These cycles are strongly affected by climatic conditions, leading to different water storage states in bark and xylem (Zweifel et al. 2000, 2001; Downes et al. 1999). These short-term environmentally induced changes of stem form have to be separated from actual growth processes.

The aim of this study is to test in which way ozone affects tree ring formation of spruce and beech within an annual time span. In order to identify the ozone effect in this study, it is necessary to separate the ozone effect from other influences like competition and climate. We therefore formulated the subsequent hypotheses:

H I: Ozone limits the annual stem diameter increment of spruce and beech
H II: Ozone shifts and alters the annual time span of stem diameter growth activity

Methods

The Kranzberg Forest research site

The experimental plot 'Kranzberger Forst' is located 35 km north of Munich in the Bavarian tertiary midlands ('Ter-tiär—Hügelland'). It is a 0.5 ha section of a mixed stand,

mainly comprising of spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees with sporadic admixture of Scots pine (*Pinus silvestris*), European larch (*Larix decidua*), sycamore maple (*Acer pseudoplatanus*) and pedunculate oak (*Quercus robur*) (Table 1). The plot was established in 1994 as part of an age series in mixed stands of spruce and beech. The geometrical shape of the plot is rectangular with a size of 50 × 100 m. The mixture of spruce and beech is group-wise, i.e. two groups of beech are located within a spruce stand. One of these groups together with nearby spruces forms the centre of the ozone fumigation experiment and is also the most intensively investigated part of experimental site (Pretzsch et al. 1998).

Ten beech trees and ten spruce trees were selected as intensively examined trees (Table 2) and equipped with various measurement devices. Since 2000, five trees of each species are fumigated with ozone. They are exposed to double the ambient ozone concentration $2 * O_3$ where the maximum ozone concentration permitted was 150 nl l^{-1}. The rest of the trees provided reference data $(1 * O_3)$. The fumigation system and the monitoring system are described in detail in Werner and Fabian (2002).

In spring 2004 the spruce and beech trees' age of the experimental plot was determined by stem core analysis with approximately 52 ± 2 and 62 ± 4 years, respectively. Beech and spruce trees grow in a balanced

competitive situation. No thinning activities were performed on this plot until the harvest of some sample trees in 2004. The biggest part of the stand and especially the part with the ozone treatment remained untouched for a long time, and grew under self-thinning conditions. Therefore, the competition can be assumed to be distinct.

Measurements

In 1999 each tree in the plot was equipped with a plastic dendrometer girth band, mounted at breast height (1.3 m). Its scale represents the diameter and is equipped with a vernier scale to allow for records of 1 mm accuracy. The records are taken with a frequency of four weeks during the vegetation period and 8 weeks during winter. The annual diameter increment at breast height (id) was calculated by subtracting the diameter value after end of the vegetation period from the value before the vegetation period.

For 10 spruce trees and 12 beech trees, among them the fumigated and the reference trees, the change of circumference is recorded automatically in 30 min intervals. These measurements are performed with micro-dendrometers of the type D6, manufactured by UMS, Germany, allowing for measurements without stem wounding. These devices have a chord, applied around the stem with a temperature induced expansion coefficient of <4 μm/K.

Table 1 Stand properties of "Kranzberg Forest" in spring 2000 (Wipfler et al. 2005)

Date	Age	Species	N (ha)	h_o (m)	d_o (m)	h_o/d_o	h_g (m)	d_g (m)	h_g/d_g	G (m²/ha)	V (m²/ha)	iG	iV [m³/(ha year)]
2000	49	Norway spruce	506	27.9	41.4	67	25.5	28.4	89	32.1	398	1.0	14.4
2000	49	Scots pine	14	27.6	38.9	70	25.9	30.0	86	1.0	12	–	0.3
2000	49	European Larch	2				24.2	24.0	100	0.1	1	–	–
2000	56	Common beech	297	25.2	36.7	68	24.0	23.4	102	12.8	156	0.3	4.7
2000	56	Pedunculate oak	10	24.4	27.1	90	24.0	23.8	100	0.4	5	–	0.2
2000	49	Total	829							46.4	572	1.3	19.6

N number of trees per ha, h_o, d_o mean height (m)/diameter (cm) of the 100 thickest trees per ha, h_g, d_g basal area mean height (m)/diameter (cm), G basal area in m² per ha, V wood volume in m³ per ha, iG, iV annual basal area (m²)/wood volume increment (m³) per ha and year

Table 2 Properties of the sample trees in comparison with the whole stand in 2002

	dbh (2002) (cm)			Tree height (2002) (m)			Crown radius (1999) (m)		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Spruce									
1 × ambient O_3	34.88	27.40	38.90	25.79	23.79	27.64	2.02	0.71	2.55
2 × ambient O_3	30.55	23.42	42.26	25.61	22.17	29.33	1.56	1.28	1.76
Stand	28.68	7.91	53.11	24.63	6.00	31.70	1.90	0.10	5.10
Beech									
1 × ambient O_3	23.27	14.80	30.11	23.52	22.85	25.16	2.09	1.16	2.95
2 × ambient O_3	26.47	15.65	38.84	23.06	21.38	24.96	2.51	1.09	4.00
Stand	23.99	7.56	42.82	23.30	7.70	33.20	2.19	0.00	9.90

The chord is attached to a stirrup with an electric contact, due its position the change of circumference is measured. The signal is amplified by a measurement amplifier (MA-20) and recorded in data logger (Type Delta-T Logger DL2e).

Statistical evaluation

In order to evaluate H I, the absolute annual stem diameter increment data, taken from the plastic dendrometer girth bands, were examined. The effect of ozone fumigation on id was evaluated by means of a regression analysis with id values of all years of the sample period (6 years) as response variable and ozone as dependent variable.

To evaluate H II the high-resolution data of the diameter change, as delivered by the micro-dendrometer had to be prepared. The annual growth profiles were standardised as relative to the absolute circumference change within one year to separate tree specific differences in absolute growth from intra-annual effects. To achieve a better fit of the mathematical function the origin of the time scale was set to 90th day of the year. The separation of the short-term reversible changes in the circumference from the long-term growth trend was achieved by fitting the cumulative Weibull function to standardised circumference recordings (Fig. 1). Thus, the growth profiles were smoothed and the noise due to reversible shrinkage and swelling of the stem was filtered. The fit of the function provided a parametric description of the growth profile's shape that can be used for further statistical evaluation. Data were discarded when the end- or starting point of the growth profile was missing or when the fit was not satisfying ($R^2 < 0.9$).

We chose the cumulative Weibull function to describe a growth process, because its s-shaped form very well describes the annual growth profiles (Yang et al. 1978). In addition, its parameters are highly appropriate to identify ozone impacts on the period of growth activity.

The cumulative Weibull function has the form:

$$y = 1 - e^{-\left(\frac{t}{T}\right)^m} \tag{1}$$

with y, stem circumference change from the origin of the time scale (90th day of the year, 0:00 a.m.) up to time t relative to the total annual circumference change; t, time (days); T, characteristic lifetime; m, Weibull module; e, Euler's number.

According to the theory of the Weibull function the parameter T is the so-called characteristic lifetime. In our context it represents the point of time, when 63% of the annual diameter increment is performed. The parameter m is the so-called Weibull module, which in our context is small when the growth period is long and large when annual growth is performed during a short span of time.

The site conditions can be regarded as *ceteris paribus* conditions, equal for each tree. The social state was taken into account by using the three-dimensional distance dependent geometric competition index KKL (Pretzsch et al. 2002). The KKL competition index usually results in values from 0 (no competition) up to around 4 (high competition). It is well known that conifers and deciduous trees differ in the way they compete for light and water. For this reason another index, the 'KMA' (Pretzsch et al. 2002) is computed. This index expresses the fraction of competition that is due to coniferous trees. In a radius of double crown diameter of the tree under consideration the summed up crown surface areas of conifers is related to the sum of crown surface area of all species. Calculation of this index results in values from 0 (no conifers as competitors) to 1 (all competitors are conifers). This was assumed to be of importance, because the phenology of competitors has to be taken in account when studying the growth behaviour within the vegetation period.

The derived curve parameters were used in order to identify differences between the treated sample and the reference group. When analysing these data, random effects that might occur on tree or vegetation period level specifically had to be considered. This was possible by using mixed effects models (Pinheiro and Bates 2000).

The fit of the Weibull-function to the annual growth data was performed with the statistic software SPSS 14.0, using the Levenberg–Marquardt algorithm. The evaluation of the curve parameters with mixed models was performed with the free statistic software 'R version 2.5.1 (R Development Core Team 2008)'.

Before the evaluation of the intra-annual growth profiles could be started, it was to decide, on which grouping and nesting levels random effects should be considered. Possible levels were the individual tree and the vegetation
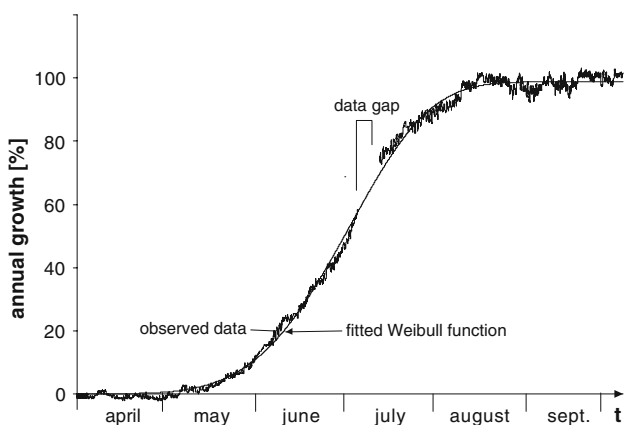

Fig. 1 Example of a Weibull function fit to standardised measurements from a micro-dendrometer during one growing season

period. A model with a random effect only with the grouping level 'vegetation period' outperformed more complicated grouping structures in terms of the Akaike information criterion (AIC). Based on that result, the 'vegetation period'—group structure was chosen, resulting in six groups (vegetation periods 2000–2005). An individual random effect term of each vegetation period appears plausible, because the climatic conditions are different for each year, but equal for each tree in a specific year.

Evaluation was started with models for predictions of the parameters id, T and m. The models were formulated in a general generic form for both tree species (Eq. 2). After model testing, all parameters, which were not significant for none of both species, were excluded.

$$y_{ijk} = \beta_1 * \text{treat}_k + \beta_2 * \text{dbh}_{ij} + \beta_3 * \text{KKL}_{ij} + \beta_4 * \text{KMA}_{ij} + \beta_0 + b_i + \varepsilon_{ijk} \qquad (2)$$

y, response variable (id, T, or m, respectively); treat, ozone treatment (0 = no ozone fumigation, 1 = ozone fumigation); dbh, diameter at breast height; KKL, competition index; KMA, competition species mixture index; index j, individual tree; index i, vegetation period; index k, treatment level; b_i, random effects on group i (vegetation period); ε_{ijk}, error term for each individual (j) in each group (i) under treatment k; β, regression coefficients.

Due to the high correlation between KKL and dbh, only one of both factors was included for the model. It was tested in each case which factor provided the better fit.

For evaluation of id, T and m the generic model was used without those elements, which were not significant for the focussed response variable.

The bivariate factor ozone is included as a dummy variable (treat), the tree dimension, expressed by the dbh and KKL and KMA are considered to determine the stem growth. KMA had to be discarded in the model predicting T (Eq. 4), because the number of cases was too low.

Results

For evaluation of H I, the generic model with mixed effects (Eq. 2) was modified. On a preliminary test, the significance of all parameters was tested. The parameter KKL performed worse than dbh and was therefore excluded. KMA turned out to be not significant and was also excluded. Subsequent model was applied:

$$\text{id} = \beta_1 * \text{treat}_k + \beta_2 * \text{dbh}_{ij} + \beta_0 + b_i + \varepsilon_{ijk} \qquad (3)$$

with id, annual stem diameter increment; treat, treatment; dbh, diameter at breast height; index j, individual tree; index i, vegetation period; index k, treatment level; b_i, random effects on group i (vegetation period); ε_{ijk}, error term; β, regression coefficients.

H I can be confirmed for spruce by the examination of the absolute annual growth using mixed effects models. The coefficient representing the treatment on spruce averages -0.071 cm year^{-1}, i.e. spruce fumigation with double ambient ozone looses 0.071 cm of its annual stem diameter increment at breast height. The average spruce of the sample collective, having a dbh of 30 cm, looses 13% of its diameter growth. Beside treatment, dbh with a coefficient of 0.011 was of significant positive effect on id (Table 3).

For European beech, hypothesis H I is rejected. No significant reaction from ozone fumigation can be found, when mixed models are applied. Here, only dbh with a coefficient of 0.014 was a factor of significant influence.

The parameters T and m of the fitted Weibull-function were investigated by use of the subsequent models (Eqs. 4, 5) in order to evaluate hypothesis H II. dbh proved to be not significant for both curve parameters. Because its significant influence on id, it can be stated, that the shape of the intra-annual growth curve is independent from the dbh and id. Instead of dbh, KKL as competition index was used for the regression analysis, because it was significant and lead to an improvement of the model in terms of AIC. The applied models had the subsequent forms:

$$T = \beta_1 * \text{treat}_k + \beta_3 * \text{KKL}_{ij} + \beta_0 + b_i + \varepsilon_{ijk} \qquad (4)$$

$$m = \beta_1 * \text{treat}_k + \beta_3 * \text{KKL}_{ij} + \beta_4 * \text{KMA}_{ij} + \beta_0 + b_i + \varepsilon_{ijk} \qquad (5)$$

with increment T, characteristic lifetime; m, Weibull-module; treat, treatment; KKL, competition index; KMA, competition species mixture index; index j, individual tree; index i, vegetation period; index k, treatment level; b_i, random effects on group i (vegetation period); ε_{ijk}, error term; β, regression coefficients.

H II is accepted for spruce. The point, T, when 63% of the annual growth is achieved, is reached nearly 6 days earlier when the tree is fumigated with ozone (Table 4). The Weibull module m represents the length of the growth

Table 3 Fit of the model for diameter increment id (Eq. 3) for Spruce ($n = 41$) and Beech ($n = 42$)

Coeffcients	Value	SE	df	t value	p value
Spruce[a]					
β_0	-0.054	0.069	33	-0.779	0.441
β_1	-0.071	0.027	33	-2.596	**0.014**
β_2	0.011	0.002	33	6.592	**0.000**
Beech[b]					
β_0	-0.167	0.097	34	-1.717	0.095
β_1	-0.041	0.046	34	-0.897	0.376
β_2	0.014	0.004	34	3.618	**0.001**

[a] $b_i \sim N(0, \hat{\sigma}^2 = 0.075^2), \varepsilon_{ijk} \sim N(0, \hat{\sigma}^2 = 0.075^2)$
[b] $b_i \sim N(0, \hat{\sigma}^2 = 0.043^2), \varepsilon_{ijk} \sim N(0, \hat{\sigma}^2 = 0.114^2)$

Table 4 Fit of the model for characteristic lifetime T (Eq. 4) for Spruce ($n = 41$) and Beech ($n = 42$)

Coeffcients	Value	SE	df	t value	p value
Spruce[a]					
β_0	87.976	8.387	33	10.490	**0.000**
β_1	−5.989	2.359	33	−2.539	**0.016**
β_3	−2.630	1.127	33	−2.334	**0.026**
Beech[b]					
β_0	90.494	5.273	34	17.162	**0.000**
β_1	5.874	2.178	34	2.696	**0.011**
β_3	−26.861	7.914	34	−3.394	**0.002**

[a] $b_i \sim N(0, \hat{\sigma}^2 = 19.934^2), \varepsilon_{ijk} \sim N(0, \hat{\sigma}^2 = 6.303^2)$

[b] $b_i \sim N(0, \hat{\sigma}^2 = 12.240^2), \varepsilon_{ijk} \sim N(0, \hat{\sigma}^2 = 5.481^2)$

Table 5 Fit of the model for Weibull module in (Eq. 5) for Spruce ($n = 41$) and Beech ($n = 42$)

Coeffcients	Value	SE	df	t value	p value
Spruce[a]					
β_0	2.890	0.870	32	3.322	**0.002**
β_1	0.673	0.369	32	1.824	0.078
β_3	0.177	0.151	32	1.168	0.251
β_4	0.328	0.617	32	0.531	0.599
Beech[b]					
β_0	0.758	1.556	33	0.487	0.630
β_1	0.088	0.614	33	0.143	0.887
β_3	1.370	0.589	33	2.324	**0.026**
β_4	8.694	3.449	33	2.520	**0.017**

[a] $b_i \sim N(0, \hat{\sigma}^2 = 1.631^2), \varepsilon_{ijk} \sim N(0, \hat{\sigma}^2 = 0.835^2)$

[b] $b_i \sim N(0, \hat{\sigma}^2 = 0.696^2), \varepsilon_{ijk} \sim N(0, \hat{\sigma}^2 = 1.551^2)$

period. A lower value of m indicates a longer growth period (Fig. 2). This did not change significantly due to ozone treatment (Table 5).

H II can be also accepted for beech. The results of the examination of the growth curve parameter T indicated a delaying effect of the ozone fumigation on the intra annual growth pattern. The point 'T' is reached nearly 6 day later under ozone fumigation. This pattern is also affected by the competition, which has, however, the opposite effect on the growth profile of beech and lessens T, thus, the growth activity is preponed (Table 4).

No significant effect of ozone on parameter m was observed, thus, the length of the growth period was not altered significantly by ozone. However, the Weibull module m was significantly affected by competition. Competition, especially with a high fraction of spruce trees, tends to shorten the growth period (Table 5).

The results for spruce and beech are visualized schematically in Fig. 2: while spruce suffers a general loss of the diameter increment, beech reacts in an altered intra-annual growth pattern without changing the absolute biomass allocation on the stem at breast height. Note, that the length of the growth period of both species is not affected by ozone.

Discussion

In this study diameter increment of spruce under ozone exposition was found to be lowered, whereas diameter increment of beech remained unaffected. These results for both species match well the results of Wipfler et al. (2005), who found no growth reaction—changes in stem diameter increment—on ozone of beech, but were able to detect a significant reaction of spruce. The sensitivity of spruce to ozone is also underpinned by Karlsson et al. (2006). The result in respect to beech, however, is contradictory to the diameter increment losses of adult beech that were found in other studies (Braun et al. 1999). However, the considerably higher ozone sensitivity of Norway spruce compared to beech regarding dbh growth does not fit well with the findings of several other studies on parameters other than stem growth (autumn senescence, exchange of various gases), where beech was found to react stronger to ozone than spruce (Nunn et al. 2005). In respect to the aspect of the growth and defence dilemma (Herms and Mattson 1992), one could argue whether the observed reaction of spruce is the consequence of redirection of assimilates

Fig. 2 Schematic visualisation of the growth reaction of spruce and beech on ozone during one growing season
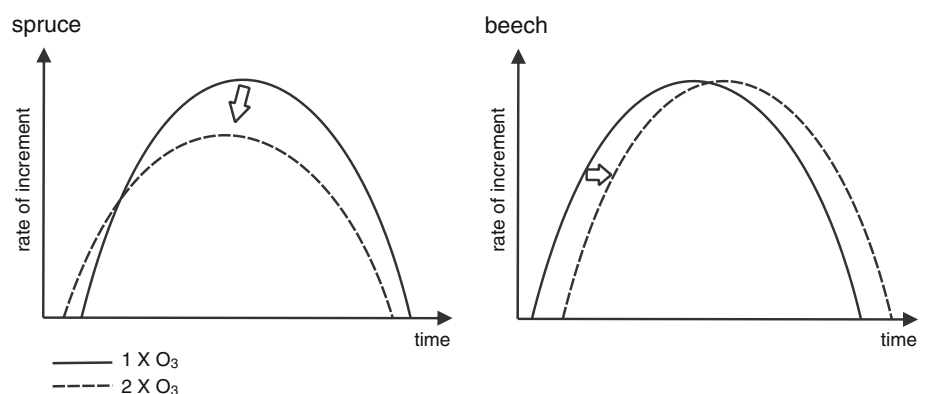
towards the defence related metabolism and therefore an expression of a successful defence strategy against the abiotic stress factor ozone, while beech maintains the growth without strengthening of the defence related metabolism.

When losses in stem diameter increment are found, it is debatable, whether this finding is a consequence of a shortened growth period or of limited increment in a certain phase of the intra-annual growth pattern. This is the background of H II, which asks for the intra-annual growth profile, represented by the function parameters T and m. For both spruce and beech, m is not affected by ozone; the growth period is therefore not shortened. Thus, the loss of diameter increment of spruce is not due to a shortened growth period, but is obviously due to a generally lowered growth rate throughout the vegetation period. The parameter T was significantly altered for both species. Spruce displayed earlier, beech later growth activity. The fact that parameter m does not change under fumigation makes interpretation of the growth patterns easier. A higher T value indicates that the growth period starts later and ends later if m does not change.

The distribution of the rate of increment over a vegetation period is probably strongly connected to the phenology and health state of the foliage. In field experiments, the relationship between foliage condition and ozone exposure is often ambiguous (Ferretti et al. 2007; Matyssek et al. 2006). Effects of ozone on foliage of spruce and beech were found by Nunn et al. (2005). On spruce, premature bud break was observed, which can explain the shift of the intra-annual growth pattern as detected in this examination. The premature cessation of stem growth, however, could not be explained by phenological observations. On beech, premature autumnal senescence of leaves was discovered in some years, whereas bud break was not affected by ozone (Nunn et al. 2002, 2005). This is somehow contradictory to the findings of this study. Here it was found that growth period length is not affected by ozone while the growth process is delayed, which would imply a delayed cessation of the annual growth process. However, no longer maintenance of foliage under ozone exposition was found (Nunn et al. 2002). This suggests that trees react differently in cambial growth and leaf maintenance.

The postponed stem diameter growth of beech is obviously not caused by altered phenology. The fact that bud break was not delayed indicates that photosynthesis starts 'regularly'. The assimilates possibly are used for repair and detoxification processes (Dizengremel 2001) or are directed to other organs or to carbon storage, as cellulose and sucrose content in leaves (Matyssek et al. 2007; Häberle et al. 2008). In respect to the inhibited photosynthesis and premature leaf loss under ozone and compensatory costs

for repair and respiration (Matyssek and Sandermann 2003), the delayed cessation of the stem growth of beech in fall remains puzzling. Answers may be found in tree ring anatomy (Schweingruber 1996; Bouriaud et al. 2005a, b) and possibly altered lignin formation under influence of ozone stress, as it was found in leaves (Matyssek and Sandermann 2003, Blumenröther et al. 2007; Betz et al. 2008).

It was already mentioned, that stress, as it is induced by ozone, can influence the tree's allocation pattern and hence its allometry (Matyssek and Sandermann 2003). It is therefore not possible to interpret reduction of stem growth at breast height as a general decline of overall biomass allocation; losses of carbon allocation as a consequence can occur in other parts of the organism. Even at the stem itself biomass allocation can be differ significantly at different heights depending on resource availability and stress level (Elling 1993; Pretzsch 1989; Schweingruber et al. 1983; Seifert et al. 2003), not to mention the possible changes in branch biomass allocation. However, the sensitivity of the lower end of a trunk should be used as an indicator rather than a predictor for loss of biomass allocation. Another consequence of ozone on allometric relationships of trees could be a change of crown development. Braun et al. (2006) as well as Stribley and Ashmore (2002) found for beech a significant shoot growth reduction. Thus, shoot growth—like the breast height diameter increment—can also be affected by ozone negatively. For seedlings Landolt et al. (2000) found, besides a loss of biomass, an altered root/shoot ratio of beech in favour of the roots, which calls for a very careful interpretation when scaling up from diameter growth at dbh to biomass while evaluating stress impact on trees.

For both spruce and beech no significant influence of the competition index KKL was found on total annual diameter growth. Probably, the effect of inter-tree competition is already represented by the dbh mathematically (cf. Wipfler et al. 2005). In this context, the result of Herbinger et al. (2005) on adult beech is to be considered. In this study a decline of foliage under ozone fumigation, especially of the light crown, is stated. That means, that ozone exposed trees are less effective in the use of light in relation to their biomass maintenance. For dominating trees, this could compensate the advantage of low competition and for suppressed trees shading could become weaker due to less foliage in the canopy layer. Thus, competition indices would become less explanatory as regression factors. In the regression analysis this correlation cannot be observed directly, but its effect may have attenuated the value of the ozone coefficient. Competition on the time course of growth could be observed on beech. The lower value of the parameter 'T' under competition indicates a preponement of the growth process. Suppressed trees start to grow earlier

at the beginning of the vegetation period. However, the growth soon is reduced by the influence of competitors. This is confirmed by the increased value of the Weibull-module *m* with increased competition, which indicates a shortened growth period.

This study is restricted only to the stem growth at breast height. Conclusions concerning the impact of ozone on growth of whole adult forest trees can only be drawn in concert with other studies dealing with growth of other organs of the tree (Wieser et al. 2006). This also has to include the partitioning in generative organs (Seifert and Müller-Starck 2008). On the other hand, ozone effects can occur without affecting stem growth. Matyssek et al. (2007) found numerous physiological effects on beech, while the stem growth remained unaffected. Among these effects where reactions which are clearly associated with ozone stress like the response of the antioxidative system (Herbinger et al. 2005) and the change of sucrose and starch concentrations in leaves (Blumenröther et al. 2007). The numerous possible climatic effects, like drought (Löw et al. 2006; Grulke et al. 2002), are not treated explicitly in this study, neither are the effects of atmospheric chemistry (except the presence of ozone) although future changes in the atmosphere such as the increase in CO_2 concentration are expected (Grams et al. 1999). Deslauriers and Morin (2005) found relations between cell production and minimum air and soil temperature during the growth period on conifers. Also bio-chemical processes as indicated by Herbinger et al. (2005) or Novak et al. (2005) need an analysis of a structural response in a higher temporal resolution, when they should be linked successfully to macro-scale processes like diameter increment. Further studies on this kind of data are recommended. The temporal shift of growth activities as shown in this study could be revealed only by means of high-resolution measurements. Stomata activity also plays a role in short-term stem increment changes, which are not actual growth processes but consequences of the water content of the xylem, which is regulated by stomata. Examination of these cyclic diameter changes could also help understanding the effect of ozone on function of stomata. In this context we can state that the micro-dendrometer data offers several promising possibilities for future exploration of ozone impact on tree growth apart from the analysis that is presented.

Although our sampled stand is representative of a huge fraction of Central European forests, our results must not be transferred to stands growing under different conditions, which may obviously be one of the reasons for contradictory results compared to other authors. The small number of sample trees per species and treatment means that it is only possible to generalise the results to a very limited extent. Although it is a finding of importance, that the period of

growth activity, as shown on stems of adult trees can shift, even if no integrated growth decline can be observed.

Conclusions

Ozone will be an important environmental factor in the future and its impacts on economically relevant tree species is of crucial importance. With appropriate statistical methods its impact on trees can be detected in field experiments, even on adult trees and on small samples, when experiments are designed to imitate chronic stress. Although only a limiting impact on stem growth was found on spruce, the analyses of the temporal diameter development during a growing season reveal an influence of ozone on the growth processes. It is still to be discussed, how these findings are to be interpreted in the context of other proven ozone impacts like leaf injuries or stomata function.

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