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ORIGINAL PAPER

Growth recovery of mature Norway spruce and European beech from chronic O_3 stress

Hans Pretzsch[1] · Gerhard Schütze[1]

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Abstract

Elevated O_3 levels can strongly impair the health and vitality of forest ecosystems. Free-air exposure systems reveal that forest tree and stand growth can be reduced strongly under chronic O_3 stress. Detailed knowledge of the effect of O_3 exposure on photosynthesis, carbon sequestration, allometry and growth during chronic stress is available. However, knowledge of growth response after O_3 reduction is scarce. Here, we analyse the growth of mature Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica L.*) in the free-air O_3 fumigation experiment at Kranzberg Forest. We compare tree growth over a 9-year period (2008–2016) after exposure to O_3 (2000–2007). During $2 \times O_3$ exposure, the annual basal area growth of Norway spruce and European beech decreased by 24 and 32%, respectively. After cessation of $2 \times O_3$ exposure, the annual basal area growth of Norway spruce and European beech not only recovered but exceeded the growth of the trees in the control condition by 14 and 24%, respectively. The growth resilience and resistance of trees previously exposed to $2 \times O_3$ towards drought stress and late frost was hardly lower than that of the trees in the control condition. The capacity for growth recovery even after long-term chronic O_3 stress emphasizes the strong beneficial effect of air pollution control on the health of forest ecosystems and on the global land carbon sink.

Keywords O_3 fumigation · Stem diameter growth · Stem basal area growth · Growth losses · Stress resilience · Drought · Late frost

Introduction

Elevated O_3 can strongly reduce photosynthesis, carbon sequestration and growth of trees (Karnosky et al. 2007; Matyssek and Sandermann 2003; Sitch et al. 2007; Wittig et al. 2009). Tree growth is an indicator of vitality and of the susceptibility of trees to environmental stress (Dobbertin 2005). Growth of tree height may be increased by O_3 exposure and chronic stress in case of Norway spruce, white ash and yellow poplar (Kress et al. 1982; Pretzsch et al. 2010) or remain unaffected in several clones of aspen (Isebrands et al. 2001). Overall, however, many studies have predominantly reported a decrease in height and diameter growth in particular (Pääkkönen et al. 1993; Kress et al. 1982; Pretzsch et al. 2010). Karlsson et al. (2006) had reported a mean annual decline in basal area increment of 17% in 19- to 35-year-old Norway spruce at the tree level during a 9-year exposure with a range of 1800–8700 nmol mol^{-1} h AOT40. Braun et al. (2007) found a decrease in height growth of 4.7% in 60- to 180-year-old European beech stands when exposed between 0 and 10 ppm h^{-1} AOT40 (accumulated O_3 over threshold 40). Studies on black cherry and yellow poplar by Somers et al. (1998) have revealed O_3-induced stem radial growth losses of 8–12 and 30–43%, respectively, for trees with visible O_3 injuries; their study does not provide quantitative information of O_3 exposure. In a long-term study on black cherry, Vollenweider et al. (2003) had reported stem radial growth losses of 28% for conditions with SUM00 (ppm h^{-1}) 69–98 and SUM60 (ppm h^{-1}) 13–21 during the growing period. This prevalent pattern of response to

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✉ Hans Pretzsch
H.Pretzsch@lrz.tum.de

[1] Chair for Forest Growth and Yield Science, Center of Life and Food Sciences Weihenstephan, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

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chronic stress can be modified further by acute stress, growth velocity and size of the tree (Grantz et al. 2006; Pretzsch and Dieler 2011), tree age (Weinstein et al. 1998), environmental conditions (Alonso et al. 2001; Löw et al. 2006) and genotypes within a given species (Dickson et al. 2001; Karlsson et al. 1997).

In contrast to the wealth of research on the effect of chronic O_3 stress in trees, knowledge of the growth recovery after a reduction in O_3 exposure is limited. The potential of forest and urban trees to recover from O_3 exposure is highly ecopolitically relevant, as it emphasizes the effectiveness and benefit of air pollution control (Matyssek et al. 2013). Among the very few studies which have analysed the recovery from O_3 exposure, the majority found a significant growth recovery and dealt with tree seedlings or saplings in chambers (Botkin et al. 1972; Weber et al. 1993). However, results in young plants may not translate to mature plants, and growing conditions in chambers may not reflect the syn-ecological interactions prevalent in natural ecosystems (Chappelka and Samuelson 1998; Karnosky et al. 2007; Matyssek et al. 2010). McLaughlin et al. (1982, 2007) demonstrated the recovery from O_3 stress in southern Appalachian hardwood forest stands. Löw et al. (2006) found that European beech in Bavarian pre-alpine stands could recover from O_3 stress under water limitation, as drought protects plants from O_3 injury through stomatal closure. Elevated O_3 levels did not exacerbate drought effects in leaves or stem. Felzer et al. (2004) had further highlighted the ability of trees to recover from chronic O_3 stress in their simulation studies regarding hardwood and pines in the O_3 conterminous areas of the USA. This limited understanding warrants further research into the recovery process after O_3 stress, especially in relation to mature trees.

Nine years after completion of the free-air $2 \times O_3$ fumigation at Kranzberg Forest, this experimental plot (Häberle et al. 2012; Matyssek et al. 2010; Pretzsch et al. 1998) offers a unique opportunity to analyse the post-fumigation behaviour of trees. The growth in the post-fumigation period from 2008 to 2016 can be contrasted with the growth in the phase of double-ambient O_3 exposure ($2 \times O_3$) from 2000 to 2007. Studies of tree growth recovery from O_3 stress are scarce and virtually non-existent for mature trees such as the presently (reference year 2017) approx. 80-year-old Norway spruce and European beech in the Kranzberg Forest. From both species we sampled increment cores from trees formerly exposed to a double-ambient O_3 regime ($2 \times O_3$), and from trees growing under ambient O_3 concentration ($1 \times O_3$ = control). Based on the annual diameter and the basal area growth of the trees of the two groups we (1) quantified the growth losses caused by $2 \times O_3$ fumigation, (2) investigated growth recovery over 9 years following the cessation of long-term O_3 fumigation and (3) examined the formerly O_3-exposed trees in regard to resilience and resistance against stress caused by drought and late frost in the post-fumigation period.

Materials and methods

Applied $2 \times O_3$ regime

Details about the Kranzberg Forest experiment (Häberle et al. 2012; Pretzsch et al. 1998, 2014), the method of O_3 fumigation (Werner and Fabian 2002) and the scaffolding and crane system for dendrometric and ecophysiological measurements (Matyssek et al. 2010, 2014) have been published previously. Here, we stress that the free-air fumigation experiment Kranzberg Forest (Freising, Germany, 48°25′N, 11°39′E) was established in 1998 in an approx. 60-year-old mixed stand of Norway spruce and European beech. Norway spruce and European beech are mixed by single individuals or small groups. The stand stocks on fertile and moist tertiary soil where both species are close to optimal growing conditions. To avoid confounding of thinning reactions with O_3 fumigation effects, the stand has not been thinned from the age of 50 years till present.

Figure 1 depicts the course of ambient O_3 concentrations at the weather station in the Kranzberg Forest from 2000 to 2016. In addition, we show the O_3 concentrations measured at the DWD station Hohenpeißenberg 100 km southwest of Kranzberg, where the mean level was higher than that in the Kranzberg Forest. Except for the characteristic intra-annual variation, the ambient O_3 concentrations showed no significant trend (see mean trend line in Fig. 1 with slope equal to zero) at a mean level of 26.1 ppb in the Kranzberg Forest and of 38.1 ppb at the DWD station Hohenpeißenberg.

The local ambient O_3 concentration was used as a reference for the fumigation of the Norway spruces and European beeches in the Kranzberg Forest. From 2000 to 2007, a double-ambient O_3 regime was applied to the full crowns of a cluster of spruces and beeches (Häberle et al. 2012). Comparisons were made with a cluster of trees with unchanged ambient air ($1 \times O_3$ = control). $2 \times O_3$ fumigation was restricted to 150 nl O_3 l^{-1} to prevent risk of acute O_3 injury. Online O_3 analysis and 160 passive samplers distributed across the fumigated and non-fumigated canopy were installed for continuous O_3 monitoring (Werner and Fabian 2002).

Dendrometric measurements

Stand inventories (tree diameters, heights, crown sizes, stem coordinates, etc.) were started in 1998 and repeated several times until the present day. All trees were fitted with permanent girth tapes to record stem diameter growth. In 2016, we selected $n = 11$ spruces and $n = 11$ beeches from

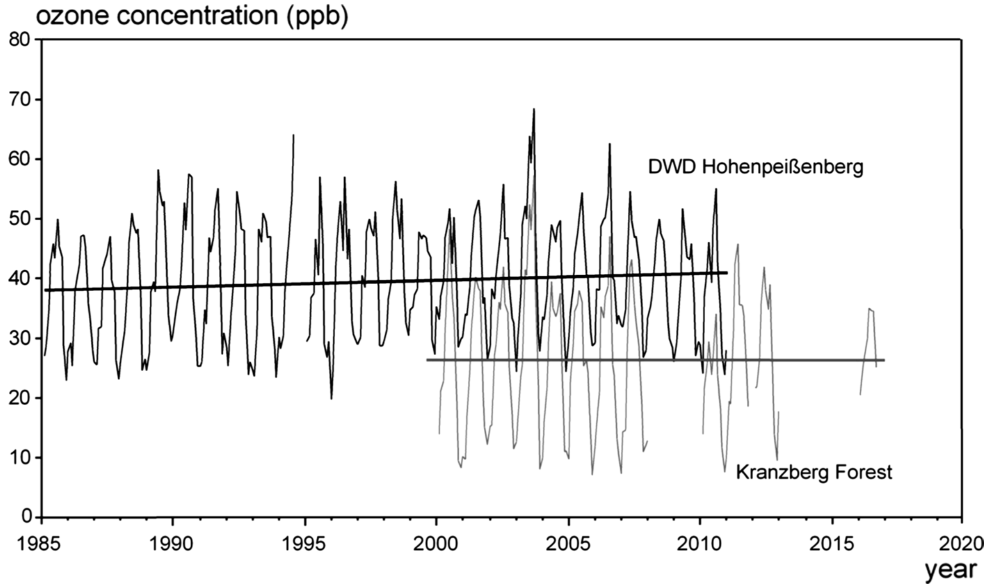

Fig. 1 Course of the ambient O_3 concentration in the Kranzberg Forest from 2000 to 2016 and at the DWD station Hohenpeißenberg from 1985 to 2011. The graph depicts the monthly values (oscillating curves) as well as the mean trend (straight lines) for both stations (courtesy of Häberle et al. (2012) and DWD Meteorologisches Observatorium Hohenpeißenberg)

the formerly $2 \times O_3$-exposed part of the stand, and equal numbers of trees in the control part ($1 \times O_3$) of the stand as a reference (Table 1). We only selected dominant trees of equal age and similar size, to avoid confounding of O_3 stress effects with age and size.

For retrospective analysis of the annual stem diameter and basal area growth, we sampled two increment cores from each tree: one from the northern and one from the eastern side of the stem. Given the main wind direction of southwest, this is also the direction with the widest tree diameter of the oval stem cross section. Therefore, the sampling from the northern and eastern direction stood in a 45° angle to this maximum diameter and avoided biased growth records. The cores were taken back to the pith in order to ensure a radial boring direction and to enable counting of the ring numbers to estimate the tree age (tree age ≅ number of tree rings at height 1.30 m + 5 years). The increment cores were obtained with the borer MORA CORETAX produced by Haglöf.

For further analyses, the increment cores were glued on wooden slides, ground and polished on a sanding machine using paper with 120 grits. Subsequently, they were cleaned by compressed air and analysed to the nearest 1/100 mm using a digital positioning table (Kutschenreiter and Johann; Digitalpositiometer, Britz and Hatzl GmbH, Austria). For cross-dating and synchronization the extremely narrow rings in 1976 and 2003 were most helpful. The radial increments, ir, of the two cores of a tree taken from north and east direction (ir_n, ir_e) were added to obtain a representative time series of stem diameter increment, id, for each tree ($\mathrm{id} = \mathrm{ir}_n + \mathrm{ir}_e$). Based on the stem diameter d_i at the beginning of each year i and the annual diameter growth id_i within the year i, the annual basal area growth $\mathrm{iba}_i = \pi/4 \times (d_i + \mathrm{id}_i)^2 - \pi/4 \times d_i^2 = \pi/4 \times (2 \times d_i \times \mathrm{id}_i + \mathrm{id}_i^2)$ can be calculated for further evaluation (Assmann 1961, p 52).

Table 1 Overview of the O_3-exposed and control trees of Norway spruce and European beech sampled for increment coring

Tree species	Treatment	Sample size n	Mean d_{1991} (± SD) cm	Mean d_{2000} (± SD) cm	Mean d_{2008} (± SD) cm	Mean ba_{1991} (± SD) m^2	Mean ba_{2000} (± SD) m^2	Mean ba_{2008} (± SD) m^2
N. spruce	$1 \times O_3$, control	11	23.9 (5.8)	28.9 (6.9)	32.4 (8.0)	0.045 (0.019)	0.070 (0.031)	0.089 (0.044)
N. spruce	$2 \times O_3$	11	26.6 (8.9)	31.6 (10.6)	34.2 (11.8)	0.060 (0.045)	0.086 (0.059)	0.103 (0.073)
N. spruce	Fum/control	–	1.11	1.09	1.06	1.33	1.24	1.16
E. beech	$1 \times O_3$, control	11	21.2 (6.0)	24.2 (7.8)	26.5 (8.8)	0.037 (0.024)	0.050 (0.033)	0.060 (0.039)
E. beech	$2 \times O_3$	11	23.6 (6.0)	25.9 (6.8)	27.1 (7.3)	0.047 (0.027)	0.057 (0.032)	0.063 (0.035)
E. beech	Fum/control	–	1.11	1.07	1.02	1.25	1.13	1.04

mean d (± SD) mean tree diameter at breast height (1.30 m) at the beginning of phase 1 in year 1991, phase 2 in 2000 and phase 3 in 2008; mean ba (± SD) mean tree basal area at breast height (1.30 m) at the beginning of phase 1 in year 1991, phase 2 in 2000 and phase 3 in 2008; fum/control ratios between the mean tree size of the O_3-exposed and control trees

Annual temperature, precipitation and Martonne index in the study period

To characterize the water supply and drought stress for each year, we calculated the index M of de Martonne (1926) [M = precipitation (mm)/(mean temperature °C + 10)]. This calculation was based on the precipitation (in mm) and mean temperature (in °C) in the whole year (M_y) and in the growing season from April to September (M_{gs}). The higher the index M, the better the water supply for plant growth.

Because of its minimal data requirement, this index has been widely used to describe the drought condition or aridity in a given region (Rötzer et al. 2012, Pretzsch et al. 2013; Quan et al. 2013). We selected this relatively simple drought index as it increases the ability to compare the weather conditions of our study to previous works. Moreover, the necessary basis data for more sophisticated indices were not available. Please note that we only used this index for characterization of the annual weather conditions and not for any further statistical analyses.

Figure 2 illustrates the variation of the water availability over the period of this study. On average, M_{gs} varied between 11.5 and 24.4 mm $°C^{-1}$ over the period of April–September and M_y between 29.7 and 64.5 mm $°C^{-1}$. The years 2001–2002 and 2005–2013 were moist, whereas 2003 and 2015 represent extremely dry years. In the O_3 fumigation period from 2000 to 2007, M_{gs} was 20.6 mm $°C^{-1}$ and M_y 47.4 mm $°C^{-1}$. In the year 2015, M_{gs} was 15.3 mm $°C^{-}$ and M_y was 34.8 mm $°C^{-}$. These meteorological data were obtained by the weather station Freising, which is located in a distance of about 2 km from the experimental stand also in the Kranzberg Forest and part of the Bavarian Environmental Monitoring System (LWF 2017).

We analysed the trees' growth resilience to late frost in the post-fumigation year 2011. The mean temperature in Bavaria in the year 2011 was 8.9 °C and thus above the long-term average from 1961 to 1990 (7.5 °C). The warm spring in 2011 triggered an early start of the growing season. However, in May 2011 after budbreak, a late frost with temperatures around − 7.0 °C affected tree growth in our study area (Zimmermann et al. 2012).

Evaluation of long-term growth decline and recovery

This analysis was based on the annual tree diameter increments, id, and annual basal area increments, iba, over the periods p_1 1991–1999 (pre-O_3 fumigation), p_2 2000–2007 (O_3 fumigation) and p_3 2008–2016 (post-O_3 fumigation). In the following we explain the evaluation on the basis of the annual tree diameter increments; the evaluation based on the annual basal area increments was carried out analogously.

Before the quantification of any growth depression or recovery, we removed the decreasing age trend from the course of tree diameter increment, so age would not confound stress or recovery effects. In line with the increment trend method (Association of German Forest Research Organizations 1988), the course of annual diameter increment of the control trees was used for this age trend removal. The control trees were used to derive the ratios $\overline{aid}_{c,p_2/p_1} = \overline{id}_{c,p_2}/\overline{id}_{c,p_1}$ and $\overline{aid}_{c,p_3/p_2} = \overline{id}_{c,p_3}/\overline{id}_{c,p_2}$ for removal of the age trend from period 1 (1991–1999) to period 2 (2000–2007) and

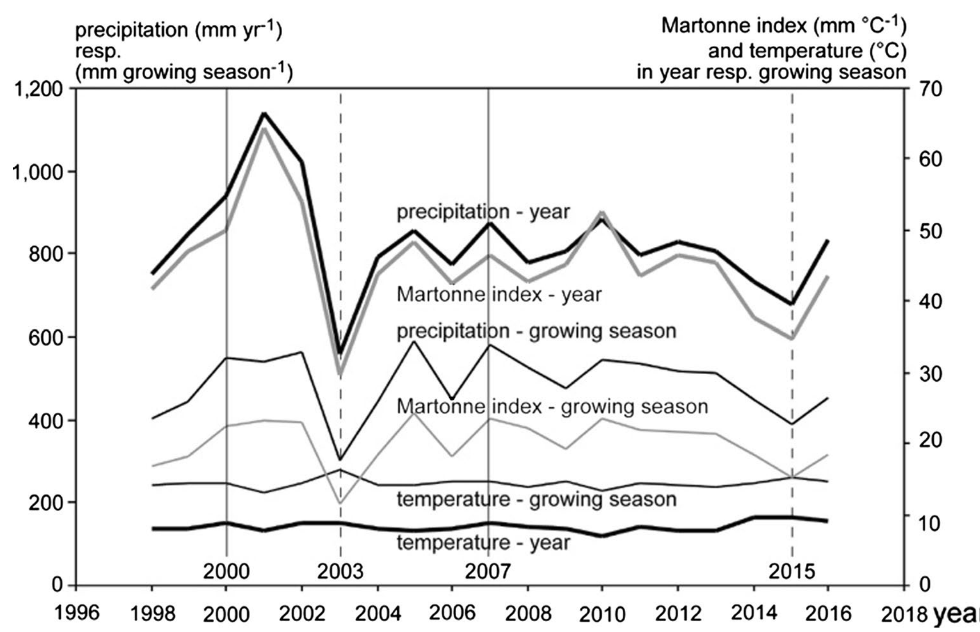

Fig. 2 Precipitation, mean temperature and Martonne index since 1998 in the whole year and in the growing seasons from May to September for the Kranzberg Forest experimental site. The years 2003 and 2015 are indicated by broken vertical lines and represent years with extremely low water availability. The solid vertical lines represent the beginning and termination of the 2 × O_3 fumigation

from periods 2–3 (2008–2016), respectively. In the ratios $\overline{\mathrm{aid}}_{c,p_2/p_1}$ and $\overline{\mathrm{aid}}_{c,p_3/p_2}$ (see columns 7 and 8 in Table 2), $\overline{\mathrm{aid}}$ represents the age trend factor, c the control trees, and p_1, p_2 and p_3 the periods 1–3. The ratios are based on the mean annual diameter increments $\overline{\mathrm{id}}_{c,p_1}$, $\overline{\mathrm{id}}_{c,p_3}$ and $\overline{\mathrm{id}}_{c,p_3}$ of the control trees in the periods p_1, p_2 and p_3. To quantify any growth reduction in period p_2 of the treatment trees, their growth in period p_1 was adjusted by $\overline{\mathrm{aid}}_{c,p_2/p_1}$ to the expected growth, i.e. $\hat{\overline{\mathrm{id}}}_{O,p_2} = \overline{\mathrm{id}}_{O,p_1} \times \overline{\mathrm{aid}}_{c,p_2/p_1}$. In $\hat{\overline{\mathrm{id}}}_{O,p_2}$ O stands for $2\times O_3$ treated trees. The ratio $\overline{\mathrm{id}}_{O,p_2}/\hat{\overline{\mathrm{id}}}_{O,p_2}$ yields the reduced or increased growth level in the fumigation period. The term 1-$\overline{\mathrm{id}}_{O,p_2}/\hat{\overline{\mathrm{id}}}_{O,p_2}$ quantifies the relative growth losses by O_3 exposure.

Any growth recovery was derived as follows: we first calculated the expected mean diameter increment in period 3 by applying age trend factor $\overline{\mathrm{aid}}_{c,p_3/p_2}$, i.e. $\hat{\overline{\mathrm{id}}}_{O,p_3} = \overline{\mathrm{id}}_{O,p_2} \times \overline{\mathrm{aid}}_{c,p_3/p_2}$. The ratio $\overline{\mathrm{id}}_{O,p_3}/\hat{\overline{\mathrm{id}}}_{O,p_3}$ indicates a recovery (ratio > 1.0), normality (= 1.0) or depression (< 1.0) below the expected normal age trend. The term 1-$\overline{\mathrm{id}}_{O,p_3}/\hat{\overline{\mathrm{id}}}_{O,p_3}$ quantifies the strength of recovery and depression, respectively.

In addition to the quantification of any growth depression or recovery, we tested any group differences between the observed and expected diameter increment at the individual tree level. The test of differences between observed and expected id in period p_2 was based on $id_{O,2}$ (observed) and $\hat{\mathrm{id}}_{O,p_2} = \mathrm{id}_{O,p_1} \times \overline{\mathrm{aid}}_{c,p_2/p_1}$ (expected) individual tree data. Analogously the test between observed and expected in p_3 was based on $id_{O,3}$ (observed) and expected growth $\hat{\mathrm{id}}_{O,p_3} = \mathrm{id}_{O,p_1} \times \overline{\mathrm{aid}}_{c,p_2/p_1}$ (expected).

Evaluation of stress resistance and resilience

To compare the previously O_3-exposed trees with the control trees under episodic drought and late frost stress, we used the indices for resistance and resilience (Rt, Rs). These indices have been introduced and explained in detail by Lloret et al. (2011). The indices were calculated individually on the basis of the annual tree diameter increment (mm yr^{-1}) and annual tree basal area increment ($cm^2\ yr^{-1}$) for all 44 sample trees. The following explanation of the calculation of the indices Rt, Rs is based on the diameter increment, id; we calculated them for the basal area increment, iba, analogously.

Basic components of the indices were the following values of the diameter increment: PreS is the mean diameter increment in a period of n_{PreS} years before the stress period,

Table 2 Mean annual diameter growth and mean annual basal area growth derived from increment cores of twice ambient O_3-exposed and control trees of Norway spruce and European beech in the three measurement phases, p_1 = 1991–1999 (pre-$2\times O_3$ exposure), p_2 = 2000–2007 ($2\times O_3$ exposure), p_3 = 2008–2016 (post-$2\times O_3$ exposure)

Tree species	Treatment	Sample size	Mean annual $\overline{\mathrm{id}}_{c,p_1}$ $\overline{\mathrm{id}}_{O,p_1}$ (± SD)	Mean annual $\overline{\mathrm{id}}_{c,p_2}$ $\overline{\mathrm{id}}_{O,p_2}$ (± SD)	Mean annual $\overline{\mathrm{id}}_{c,p_3}$ $\overline{\mathrm{id}}_{O,p_3}$ (± SD)	Ratio $\overline{\mathrm{aid}}_{c,p_2/p_1}=\overline{\mathrm{id}}_{c,p_2}/\overline{\mathrm{id}}_{c,p_1}$	Ratio $\overline{\mathrm{aid}}_{c,p_3/p_2}=\overline{\mathrm{id}}_{c,p_3}/\overline{\mathrm{id}}_{c,p_2}$	Mean annual $\overline{\mathrm{iba}}_{c,p_1}$ $\overline{\mathrm{iba}}_{O,p_1}$ (± SD)	Mean annual $\overline{\mathrm{iba}}_{c,p_2}$ $\overline{\mathrm{iba}}_{O,p_2}$ (± SD)	Mean annual $\overline{\mathrm{iba}}_{c,p_3}$ $\overline{\mathrm{iba}}_{O,p_3}$ (± SD)	Ratio $\overline{\mathrm{aiba}}_{c,p_2/p_1}=\overline{\mathrm{iba}}_{c,p_2}/\overline{\mathrm{iba}}_{c,p_1\,1}$	Ratio $\overline{\mathrm{aiba}}_{c,p_3/p_2}=\overline{\mathrm{iba}}_{c,p_3}/\overline{\mathrm{iba}}_{c,p_2}$
		n	mm yr^{-1}	mm yr^{-1}	mm yr^{-1}	(mm yr^{-1})/(mm yr^{-1})	(mm yr^{-1})/(mm yr^{-1})	$cm^2\ yr^{-1}$	$cm^2\ yr^{-1}$	$cm^2\ yr^{-1}$	($cm^2\ yr^{-1}$)/($cm^2\ yr^{-1}$)	($cm^2\ yr^{-1}$)/($cm^2\ yr^{-1}$)
N. spruce	$1\times O_3$, control	11	6.43 (2.80)	4.63 (2.73)	3.63 (2.62)	0.70	0.75	27.03 (1.65)	23.80 (2.07)	21.49 (2.10)	0.88	0.90
N. spruce	$2\times O_3$	11	6.48 (3.06)	3.57 (2.58)	3.31 (2.51)			30.78 (2.12)	20.73 (2.18)	21.29 (2.26)		
N. spruce	$2\times O_3/1\times O_3$	–	1.01	0.77	0.91			1.14	0.87	0.99		
E. beech	$1\times O_3$, control	11	3.81 (1.86)	2.85 (1.70)	1.94 (1.30)	0.73	0.68	14.64 (1.08)	12.58 (1.07)	9.39 (0.82)	0.86	0.75
E. beech	$2\times O_3$	11	2.98 (1.40)	1.67 (0.97)	1.39 (1.16)			12.30 (0.80)	7.24 (0.54)	6.71 (0.68)		
E. beech	$2\times O_3/1\times O_3$	–	0.78	0.59	0.72			0.84	0.58	0.71		

Mean diameter increments of the control trees (c) and O_3-fumigated trees (O) in periods 1…3, $\overline{\mathrm{id}}_{c,p_1}$, $\overline{\mathrm{id}}_{c,p_2}$, $\overline{\mathrm{id}}_{c,p_3}$, $\overline{\mathrm{id}}_{O,p_1}$, $\overline{\mathrm{id}}_{O,p_2}$, $\overline{\mathrm{id}}_{O,p_3}$ and age trend factors $\overline{\mathrm{aid}}_{c,p_2/p_1}$ $\overline{\mathrm{aid}}_{c,p_3/p_2}$. Mean basal area increment of the control trees (c) and O_3-fumigated trees (O) in periods 1…3, $\overline{\mathrm{iba}}_{c,p_1}$, $\overline{\mathrm{iba}}_{c,p_2}$, $\overline{\mathrm{iba}}_{c,p_3}$, $\overline{\mathrm{iba}}_{O,p_1}$, $\overline{\mathrm{iba}}_{O,p_2}$, $\overline{iba}_{O,p_3}$ and age trend factors $\overline{\mathrm{aiba}}_{c,p_2/p_1}$ and $\overline{\mathrm{aiba}}_{c,p_3/p_2}$

S is the mean diameter increment in the year n_S of episodic stress, and PostS is the mean diameter increment in a period of n_{PostS} years after the stress.

The resistance Rt = S/PreS quantifies the decrease from the pre-stress period to the stress period. Rt = 1 indicates complete resistance, with lower Rt marking lower resistance. Resilience Rs = PostS/PreS represents the ratio between post-stress and pre-stress diameter increment. Rs ≥ 1 indicates a full recovery or even an increase after the episodic stress, whereas values of Rs < 1 indicate a low resilience. For more details about the indices and their ecological foundation see Lloret et al. (2011).

To analyse growth in response to the drought stress in 2015, we used the mean diameter increment in the 3 years 2012, 2013 and 2014 before the drought period (PreS), the diameter increment in the dry year 2015 (S), and the diameter increment in 2016 after the drought period ($n_{PreS} = 3$, $n_S = 1$, $n_{PostS} = 1$).

To analyse the growth response to the late frost in 2011, we used the mean diameter increment in the 3 years 2008, 2009 and 2010 before the late frost (PreS), the diameter increment in the year with late frost 2011 (S) and the mean diameter increment in 2012, 2013 and 2014 after the late frost ($n_{PreS} = 3$, $n_S = 1$, $n_{PostS} = 3$).

To remove any age trends from this analysis, we repeated it analogously based on indexed annual growth records. As the course of growth in the post-fumigation period was linear, we fitted a straight line to the annual growth records of the years 2008–2016 and used this straight line to index the annual growth. Our subsequent analysis was based on the indexed annual growth records (ratios between absolute growth rate and trend represented by the straight line). Following this, the Rt and Rs values were calculated based on the indexed growth records. The trend removal and indexing were conducted for each tree individually. As there were hardly any differences between the Rt and Rs values based on absolute and indexed growth rates, we only report the results based on the indexed growth rates in the result section.

Statistical evaluation

We set up a linear mixed-effects model to test whether diameter growth or basal area growth of the twice ambient O_3-exposed trees differed significantly from the expected growth under ambient O_3 concentration during the period of O_3 fumigation from 2000 to 2007 ($id_{O,2}$ vs. $\widehat{id}_{O,p_2}$) and during the post-fumigation period 2008–2016 ($id_{O,3}$ vs. $\widehat{id}_{O,p_3}$). We introduce the statistical evaluation and model for the diameter growth; the evaluation was carried out for the basal area growth analogously. Values belonging to one tree in a stand can be dependent on each other (Crawley 2009, p 627) and thus do not meet the assumption of independence (Zuur et al. 2009, p 102). For this reason, a random effect b_i for the trees was added to the linear model. This way, autocorrelation within the data can be accounted for and potential "pseudoreplication" can be avoided (Crawley 2009, p 629). The model function was applied for both Norway spruce and European beech. The dependent variable id_{ij} was the diameter increment in period *i* of tree *j*, and the variable group ij indicates the belonging to the groups "observed" or "expected"

$$id_{ij} = a_0 + a_1 \times group_{ij} + b_{ij} + \varepsilon_{ij}.$$

For the application of linear mixed-effects models, the lme function of the nlme package in R (Pinheiro et al. 2016) was used.

Results

Before providing a detailed statistical evaluation, we show the course of the annual basal area increment in terms of absolute growth rates (iba in $cm^{-2}\ yr^{-1}$) (Fig. 3a, b). In the case of beech, the control trees already showed slightly (though not significantly) greater absolute basal area increment before the O_3 exposure. We display the annual growth rates in relation to the mean growth rate in the pre-fumigation period 1991–1999 ($iba/\overline{iba}_{1991-1999}$ in $cm^{-2}\ yr^{-1} / mm\ yr^{-1} cm^{-2}$) (Fig. 3c, d). To eliminate these baseline differences in the statistical analysis, we applied the increment trend method (Association of German Forest Research Organizations 1988). Figure 3c, d shows a clear age-related decline of the basal area growth in both species, and in both the control and the fumigated trees. In the case of Norway spruce (Fig. 3c) during the $2 \times O_3$ exposure from 2000 to 2007, the growth of the fumigated trees was distinctly lower than that of the control trees. In the drought year 2003, both groups dropped to a similarly low level. However, after the drought, the trees in both groups recovered quickly, and, in the post-fumigation period, the previously fumigated trees showed growth rates similar to those of the control trees. In the case of European beech (Fig. 3d) during the $2 \times O_3$ exposure, the basal area growth of the fumigated trees was distinctly lower than that of the control trees, but the growth reduction in the drought year 2003 was only marginal. In the post-fumigation period, similar to the findings on the Norway spruce, the previously fumigated European beech trees reached the growth rates of the control trees. Supplement Figure 1 shows the analogous courses of the annual stem diameter increment.

Growth reduction during double-ambient O_3 exposure

Due to their advanced age, both spruce and beech trees displayed a downward trend in basal area increment (Fig. 3) and diameter increment (Supplement Figure 1). Compared to the

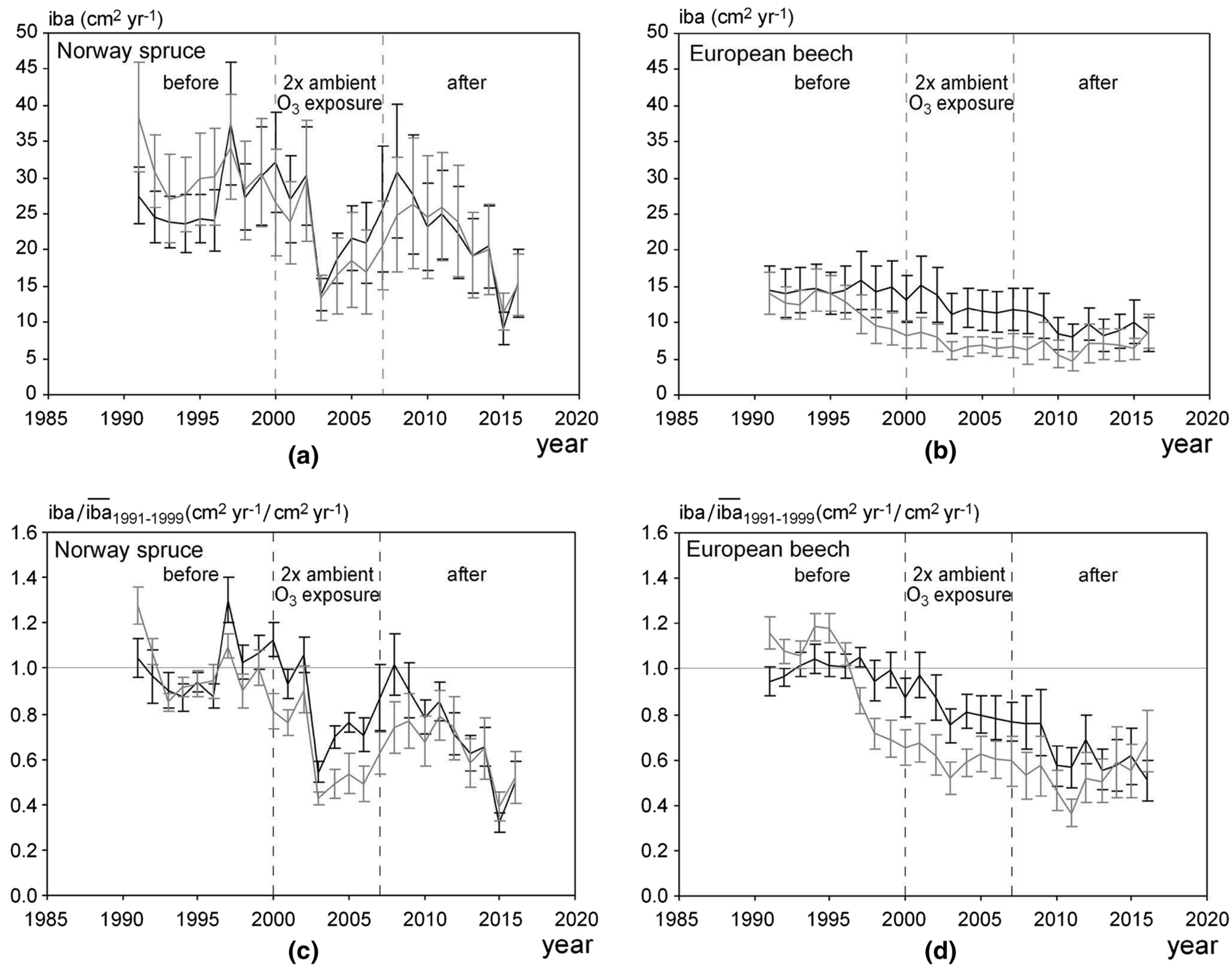

Fig. 3 Course of the annual basal area increment (mean ± SE) from 1991 to 2016 for Norway spruce (**a**, **c**) and European beech (**b**, **d**). The course of the annual basal area increment is shown in units of absolute growth rates (iba in $cm^{-2}\ yr^{-1}$) (**a** and **b**) and in terms of growth rates in relation to the mean growth rate in the pre-fumigation period 1991–1999 ($iba/\overline{iba}_{1991-1999}$ in $cm^{-2}\ yr^{-1}/cm^{-2}\ yr^{-1}$) (**c** and **d**). Growth of the control trees (black) and trees with $2\times O_3$ exposure from 2000 to 2007 (grey). The broken vertical lines separate the period with O_3 treatment (2000–2007) from the periods before (1991–1999) and after (2008–2016) the treatment

first period (1991–1999), in the second period (2000–2007) the growth of the control trees decreased to 0.88 (spruce) and to 0.86 (beech) (see $\overline{aiba}_{c,p_2/p_1}$ values in Table 2). There was a comparable age-related decline from period 2 (2000–2007) to period 3 (2008–2016) of 0.90 and 0.75 for the spruce and beech control trees, respectively (see $\overline{aiba}_{c,p_3/p_2}$ values in Table 2). After removal of the age trend using the increment trend method, the $2\times O_3$-exposed trees showed a clear negative growth response to O_3 exposure. Compared to the pre-exposure period 1, the basal area increment of spruce and beech was reduced to 0.76 and 0.68, respectively. This resulted in a twice ambient O_3 stress induced growth loss of 24 and 32%, respectively (Table 3). For both species, the growth reduction by O_3 was significant at the level $p<0.001$ (Table 3). Note that Tables 2 and 3 show the results for both diameter and basal area increment.

Strong recovery after cessation of the $2\times O_3$ fumigation

The removal of the age trend from the course of diameter increment in phases 2 to 3 revealed the behaviour of the trees after cessation of O_3 fumigation. After removal of the age trend, we found a diameter increment of spruce and beech of 1.14 and 1.24, respectively, in phase 3 compared to the increment in phase 2. Compared to the normal age trend reflected by the control trees, this marked a recovery reaction and increment gain of the previously O_3-exposed spruces and beeches of 14 and 24%, respectively. For both

Table 3 Diameter and basal area growth of the double-ambient O_3-exposed trees compared to their expected growth under ambient O_3 concentration within the period of O_3 fumigation from 2000 to 2007

Species	*n* per group	$\overline{\widehat{id}}_{c,p_2}$ exp. mean (±SE) mm yr^{-1}	$\overline{id}_{O,p_2}$ obs. mean (±SE) mm yr^{-1}	*p* value	Relation obs./exp. mm yr^{-1}/mm yr^{-1}	Diameter growth loss or benefit %	$\overline{\widehat{iba}}_{c,p_2}$ exp. mean (±SE) cm^2 yr^{-1}	$\overline{iba}_{O,p_2}$ obs. mean (±SE) cm^2 yr^{-1}	*p* value	Relation obs./exp. cm^2 yr^{-1}/cm^2 yr^{-1}	Basal area growth loss or benefit %
Norway spruce	11	4.67 (0.61)	3.56 (0.21)	**0.000**	0.76	−24	27.12 (5.50)	20.73 (2.18)	**0.000**	0.76	−24
European beech	11	2.23 (0.26)	1.67 (0.09)	**0.000**	0.75	−25	10.56 (1.69)	7.23 (0.54)	**0.000**	0.68	−32

n tree number per group (control and O_3-fumigated are both represented by the same tree number *n*); $\overline{\widehat{id}}_{c,p_2}$ and $\overline{\widehat{iba}}_{O,p_2}$ expected mean annual diameter and expected basal area growth of trees under ambient O_3; $\overline{id}_{O,p_2}$ and $\overline{iba}_{O,p_2}$ observed mean annual diameter and observed basal area growth of trees under twice ambient O_3; *p* value, result of the two-sided *t* test with significant differences in bold digits; relationship between observed and expected growth; loss and benefit of growth, respectively

species, the recovery reaction proved to be significant at $p < 0.01$ and $p < 0.05$ in spruce and beech, respectively (Table 4).

Stress resistance and resilience in the period after O_3 exposure

The indices of stress resistance and resilience for the untreated and $2 \times O_3$-fumigated trees were calculated with and without age trend removal. As the results were very similar, we only report the results based on growth standardized by age trend removal (Fig. 3). The much lower Rt and Rs values of spruce compared to beech reflect the well-known fact that drought affects spruce much stronger than beech (Pretzsch et al. 2013, Rötzer et al. 2017). Basal area growth of Norway spruce decreased in the drought year 2015 in both groups. Control trees displayed a growth loss of 31% (Rt = 0.69), and previously exposed trees a growth loss of 13% (Rt = 0.88). In the case of European beech, Rt values of 1.12 for control trees and 1.14 for previously exposed trees even indicate a trend towards a positive response. The resilience after drought was very similar for control (Rs = 1.14) and previously exposed (Rs = 1.16) spruces. In the case of beech, trees with former O_3 fumigation (Rs = 1.51) were even more resilient towards drought than the control trees (Rs = 1.06). Table 5 indicates the presence of these trends, while there were no significant between-group differences.

Norway spruce was very resistant against the late frost in 2011 (Rt = 1.16 and 1.22). In contrast, beech was much more affected (Rt = 0.87 and 0.64), losing 13–36% of its diameter increment in 2011. Compared to the control trees, the growth losses of the previously fumigated trees were significantly higher. However, beech was very resilient to late frost: in the period after the late frost, the basal area increment changed to 1.01 and 0.87 for control and O_3-exposed trees, respectively. This suggests a high ability of beech to recover after late frost (Table 5).

Discussion

Over the last decades, the ambient O_3 concentration displayed no trend in the Kranzberg Forest. It displayed the characteristic intra-annual variation, but, on average, remained at 26.1 ppb. During exposure to double-ambient O_3 from 2000 to 2007, basal area growth of Norway spruce and European beech decreased significantly by 24–32%. However, basal area growth recovered in the post-fumigation period. Moreover, the growth of previously O_3-fumigated trees exceeded that of the control trees in post-fumigation period. Furthermore, basal area growth resistance and resilience to drought and late frost was hardly modified by

Table 4 Diameter growth and basal area growth of the ambient O_3-exposed trees compared to the previously double-ambient O_3-exposed trees in the post-exposure period 2008–2016

Species	*n* per group	$\overline{\widehat{id}}_{c,p_3}$ exp. mean (±SE) mm yr^{-1}	$\overline{id}_{O,p_3}$ obs. mean (±SE) mm yr^{-1}	*p* value	Relation obs./exp. mean (±SE) mm yr^{-1}/mm yr^{-1}	Diameter growth loss or benefit %	$\overline{\widehat{iba}}_{c,p_3}$ exp. mean (±SE) cm^2 yr^{-1}	$\overline{iba}_{O,p_3}$ obs. mean (±SE) cm^2 yr^{-1}	*p* value	Relation obs./exp. mean (±SE) cm^2 yr^{-1}/cm^2 yr^{-1}	Basal area growth loss or benefit %
Norway spruce	11	2.80 (±0.60)	3.37 (±0.20)	**0.005**	1.20 (±0.07)	+20	18.72 (5.91)	21.29 (2.26)	**0.050**	1.14 (±0.06)	+14
European beech	11	1.14 (±0.23)	1.39 (±0.09)	**0.010**	1.22 (±0.09)	+22	5.40 (1.49)	6.71 (0.68)	**0.005**	1.24 (±0.11)	+24

n tree number per group (control and O_3-fumigated are both represented by the same tree number *n*); $\overline{\widehat{id}}_{c,p_3}$ and $\overline{\widehat{iba}}_{c,p_3}$ expected diameter and expected basal area growth of the previously double-ambient O_3-exposed trees in the post-fumigation period 2008–2016; $\overline{id}_{O,p_3}$ and $\overline{iba}_{O,p_3}$ diameter and basal area growth of the formerly twice ambient O_3-exposed trees in the post-fumigation period 2008–2016; *p* value, result of the two-sided *t* test with significant differences in bold digits; ratio between observed and expected growth; growth loss and benefit, respectively

Table 5 Resistance, Rt, and resilience, Rs, of trees in the post-O_3 fumigation period 2008–2015 to stress by drought in 2015 and to late frost in 2011

Stress	Species	*n*	Annual diameter growth						Annual basal area growth					
		Per group	Rt control mean (±SE)	Rt O_3 mean (±SE)	*p* value	Rs control mean (±SE)	Rs O_3 mean (±SE)	*p* value	Rt control mean (±SE)	Rt O_3 mean (±SE)	*p* value	Rs control mean (±SE)	Rs O_3 mean (±SE)	*p* value
Drought 2015	Norway spruce	11	0.70 (0.08)	0.88 (0.13)	0.260	1.18 (0.13)	1.19 (0.19)	0.981	0.69 (0.08)	0.87 (0.13)	0.244	1.14 (0.12)	1.16 (0.18)	0.911
Drought 2015	European beech	11	1.12 (0.09)	1.14 (0.14)	0.919	1.07 (0.11)	1.52 (0.24)	0.102	1.12 (0.09)	1.14 (0.14)	0.909	1.06 (0.11)	1.51 (0.23)	0.092
Late frost 2011	Norway spruce	11	1.15 (0.07)	1.22 (0.07)	0.478	1.06 (0.05)	1.07 (0.07)	0.963	1.16 (0.07)	1.22 (0.07)	0.518	1.07 (0.05)	1.07 (0.07)	0.999
Late frost 2011	European beech	11	0.86 (0.06)	0.65 (0.06)	**0.019**	1.00 (0.05)	0.87 (0.07)	0.162	0.87 (0.06)	0.64 (0.06)	**0.017**	1.01 (0.06)	0.87 (0.07)	0.144

Results of the tests comparing the behaviour of control trees with previously O_3-fumigated trees based on annual diameter growth and annual basal area growth

Stress, type of stress analysed; species, Norway spruce and European beech; *n*, tree number per group (control and O_3-fumigated are both represented by the same tree number *n*); Rt, resistance; Rs resilience; *p* value, result of the two-sided *t* test with significant differences in bold digits previous exposure to O_3 stress. Finally, as the tree height increment is still low at this tree age, the percentage of basal area growth loss reflects well the percentage loss of tree volume increment.

Growth decline under $2 \times O_3$ exposure

On average, Norway spruce (−24%) and European beech (−32%) displayed similar reductions in tree basal area growth during $2 \times O_3$ exposure from 2000 to 2007. While previous studies have only considered parts of the fumigation period (Wipfler et al. 2005), or focused on specific years (Löw et al. 2006), this present study provides a more comprehensive view, including the pre- and post-fumigation periods. The observed growth losses correspond well with previous studies, which have reported O_3-induced decreases in height, diameter and basal area growth. The studies mentioned in the introduction report significant losses of stem diameter and basal area increment caused by chronic O_3 stress. These empirical findings of reduced tree growth under chronic O_3 stress have been used to parameterize models in order to estimate growth and yield losses on larger bases (Constable et al. 1996, De Marco et al. 2013, Retzlaff et al. 1997, 2000).

As the height growth is only low at this stand age, the percentage of basal area growth losses reflects well the growth losses of tree volume growth. The sampled trees were dominant and represent large parts of the stand growth. Thus, we can conclude that $2 \times O_3$ exposure reduced stand volume growth of Norway spruce and European beech by about 24 and 32%, respectively. Over the period from 2000 to 2007, the mean annual stem volume stand growth per hectare of the control plots was 25.0 $m^3\ ha^{-1}\ yr^{-1}$ for Norway spruce and 20.3 $m^3\ ha^{-1}\ yr^{-1}$ for European beech (Pretzsch et al. 2010). A loss of 24 and 32% therefore translates into a loss of stand growth of 6 and 6.5 $m^3\ ha^{-1}\ yr^{-1}$ of stem volume per year, and a total loss of about 48 and 52 $m^3\ ha^{-1}\ yr^{-1}$ in the 8 years of double-ambient O_3 exposure in total. This represents a considerable loss in economical result for the forest owner. Additional potential ecological disadvantages include reduced tree vitality (Dobbertin 2005; Niinemets 2010), loss of structural stand heterogeneity (Pretzsch and Dieler 2011) and reduced variety of herbaceous species (Bassin et al. 2007; Barbo et al. 1998).

Recovery after $2 \times O_3$ exposure

Both species recovered quickly from the severe $2 \times O_3$-induced growth reduction. In the post-fumigation period, they exceeded the basal area growth of the control trees by 14 and 24%, respectively. Consequently, they almost caught up with the control trees regarding basal area growth. Furthermore, the previous chronic O_3 stress hardly reduced their resistance and resilience towards drought in the post-fumigation period. Moreover, with the exception of a slight reduction in late frost resistance in European beech, former O_3 fumigation did not modify the resistance and resilience to late frost. Here, we hypothesize that the growth decline in 2011 was mainly caused by late frost; other factors (e.g. fructification and herbivory) might also have contributed to the low growth in 2011 but were neither noticed nor measured.

Chronic O_3 stress can lead to oxidative damages or even cell death in the substomatal cavity of needles and leaves (Grünhage et al. 2012; Nunn et al. 2006). Photosynthesis, production of photosynthates and tree growth can be reduced, and needles or leaves may age quicker and be shed earlier (Manning 2005; Matyssek and Sandermann 2003). Trees may further change their assimilate partitioning (Cooley and Manning 1987) and allometry (Pretzsch et al. 2010) as a result of the reduced photosynthesis, but the direct damage is restricted to the tree foliage (Felzer et al. 2007; Günthardt-Goerg and Vollenweider 2007). After cessation of O_3 fumigation, the damaged foliage may be quickly replaced by the annual renewal of the youngest age class of needles (in the case of conifers) and of all leaves (in the case of deciduous trees). These new and undamaged one-year-old needles may contribute overproportionally to the annual growth in the case of conifers (Hom and Oechel 1983; Wang et al. 1995). This renewal of organs could contribute to large parts of the entire yield and thus can at least partly explain the quick recovery.

We further hypothesize that, after cessation of the O_3 fumigation, trees may boost their primary metabolism at the expense of their secondary metabolism. While O_3 fumigation triggered an increased investment into the anti-oxidation processes for defence, primary metabolism and carbon allocation to growth may be prioritized during the post-fumigation period (Matyssek et al. 2002; Nunn et al. 2006). In the post-fumigation period, trees might further benefit from the accumulation of nutrients, which were not captured and taken up during the fumigation period due to the trees' reduced growth. This could explain why the previously O_3-fumigated trees exceeded the growth of the control trees in the post-fumigation period. Our study also indicates that growth loss due to drought seems to be smaller in previously fumigated trees, which hints towards an adaptation towards faster stomata responses or improved anti-oxidative defences (which does not help against frost damages). This seems to be interesting because many studies (although not all) show beneficial effects of drought due to decreased ozone uptake (e.g. Gao et al. 2017).

Methods for detection of growth losses, recovery and resistance

In essence, the applied increment trend method uses the control trees to remove the age trend from the fumigated trees. It then compares growth in the fumigation period to that during the pre-fumigation period and that during the post-fumigation period. By using the increment trend method (Pretzsch and Utschig 1989), effects of age and O_3-fumigation can be separated. The increment trend method conforms to the recommendations of the Forest and Yield Science Section of the German Union of Forest Research Organizations (Association of German Forest Research Organizations 1988) for increment diagnoses in damaged forest stands. It has been applied routinely to the quantification of the effects of acid rain on tree growth (Pretzsch and Utschig 1989). In the case of beech, the control trees already displayed slightly, though not significantly, greater diameter increment before O_3 exposure. A direct between-group comparison would neglect those initial group differences in growth. The increment trend method avoids such flawed diagnoses by comparing growth during the stress period with the growth in the period before the stress period based on natural age trend removal. This methodological justification also applies to the quantification of recovery. The growth in the post-fumigation period was compared to the growth in the fumigation period, and the control trees were used for removal of the normal age trend before this comparison and evaluation.

The indices Rt and Rs for resilience and resistance are well-established approaches for quantifying the stress response of trees based on increment core data (Lloret et al. 2011; Thurm et al. 2016). In the present study, we were mainly interested in any difference in stress resistance and resilience between the control and exposed trees. Martínez-Vilalta et al. (2012), Merlin et al. (2015) and Pretzsch et al. (2012) had applied RT and Rs successfully to evaluate effects of drought on tree growth.

Conclusions

During $2 \times O_3$ exposure, basal area growth of Norway spruce and European beech decreased by 24 and 32%, respectively. After cessation of $2 \times O_3$ exposure, growth recovered and even exceeded the growth of the control trees by 14 and 24%, respectively. The growth resilience and resistance of previously $2 \times O_3$-exposed trees to drought stress and late frost was lower compared to that of the control trees. The excess recovery of growth loss even after long-term O_3 stress emphasizes the benefit and importance of air pollution control for the health of forest ecosystems. Reductions in O_3 concentration levels seem to quickly repair tree productivity and to remedy the significant suppression of the global land carbon sink caused by O_3 deposition.

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Authors' contributions HP initiated the study and wrote the manuscript. GS carried out the field work and the data analyses.

Compliance with ethical standards

Conflict of interest Both authors declare that they have no conflict interest.

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