

Quantifying the impact of current and future tropospheric ozone on tree biomass, growth, physiology and biochemistry: a quantitative meta-analysis

VICTORIA E. WITTIG*, ELIZABETH A. AINSWORTH*†, SHAWNA L. NAIDU‡, DAVID F. KARNOSKY§ and STEPHEN P. LONG*

*Department of Plant Biology, University of Illinois at Urbana-Champaign, 190 ERML, 1201 W. Gregory Drive, Urbana, IL 61801, USA, †USDA/ARS Photosynthesis Research Unit, Urbana, IL 61801, USA, ‡Program in Molecular and Cellular Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA, §School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA

Abstract

The northern hemisphere temperate and boreal forests currently provide an important carbon sink; however, current tropospheric ozone concentrations ($[O_3]$) and $[O_3]$ projected for later this century are damaging to trees and have the potential to reduce the carbon sink strength of these forests. This meta-analysis estimated the magnitude of the impacts of current $[O_3]$ and future $[O_3]$ on the biomass, growth, physiology and biochemistry of trees representative of northern hemisphere forests. Current ambient $[O_3]$ (40 ppb on average) significantly reduced the total biomass of trees by 7% compared with trees grown in charcoal-filtered (CF) controls, which approximate preindustrial $[O_3]$. Above- and belowground productivity were equally affected by ambient $[O_3]$ in these studies. Elevated $[O_3]$ of 64 ppb reduced total biomass by 11% compared with trees grown at ambient $[O_3]$ while elevated $[O_3]$ of 97 ppb reduced total biomass of trees by 17% compared with CF controls. The root-to-shoot ratio was significantly reduced by elevated $[O_3]$ indicating greater sensitivity of root biomass to $[O_3]$. At elevated $[O_3]$, trees had significant reductions in leaf area, Rubisco content and chlorophyll content which may underlie significant reductions in photosynthetic capacity. Trees also had lower transpiration rates, and were shorter in height and had reduced diameter when grown at elevated $[O_3]$. Further, at elevated $[O_3]$, gymnosperms were significantly less sensitive than angiosperms. There were too few observations of the interaction of $[O_3]$ with elevated $[CO_2]$ and drought to conclusively project how these climate change factors will alter tree responses to $[O_3]$. Taken together, these results demonstrate that the carbon-sink strength of northern hemisphere forests is likely reduced by current $[O_3]$ and will be further reduced in future if $[O_3]$ rises. This implies that a key carbon sink currently offsetting a significant portion of global fossil fuel CO_2 emissions could be diminished or lost in the future.

Keywords: air pollution, angiosperms, global change, gymnosperms, ozone fumigation, root-to-shoot ratio

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Introduction

Tropospheric ozone (O_3) is not only a greenhouse gas with the third strongest radiative forcing on climate (Ehhalt *et al.*, 2001; Forster *et al.*, 2007), it is also the air

pollutant considered to be causing the most damage to plants (Ashmore, 2005; EPA, 2006; Karnosky *et al.*, 2007; Matyssek *et al.*, 2007; Paoletti *et al.*, 2007). Photochemical reactions involving nitrogen oxides (NO_x), largely of industrial origin, in the presence of volatile organic compounds (VOCs) of both natural and industrial origin, produce O_3 pollution (Fowler *et al.*, 1999b; Denman *et al.*, 2007; Forster *et al.*, 2007). Based on a

Correspondence: Dr Stephen P. Long, tel. +1 217 333 2487, fax +1 217 244 7563, e-mail: stevel@life.uiuc.edu

continuous 34-year record of low altitude O₃ measurements from the late 19th century, ambient background tropospheric ozone concentrations ([O₃]) in central Europe averaged 10 ppb (Volz & Kley, 1988). Model projections over large land areas for the late 19th century estimate slightly higher [O₃] ranging between 15 and 25 ppb in North America and Europe (Akimoto, 2003). As NO_x and VOCs have risen over the past century, surface ambient background [O₃] over land in the northern hemisphere has increased to levels that are damaging to vegetation (Chappelka & Samuelson, 1998; Skarby *et al.*, 1998; Fowler *et al.*, 1999a; Akimoto, 2003; EPA, 2006; Karnosky *et al.*, 2007; Matyssek *et al.*, 2007).

Tropospheric [O₃] is both temporally and spatially heterogeneous, depending on the distance from source pollutants, time of day and time of year, which complicates accurate projections of current regional trends or future concentrations. Contemporary daytime [O₃] in the temperate latitudes of the northern hemisphere range between 20 and 65 ppb (Akimoto, 2003; Vingarzan, 2004; Oltmans *et al.*, 2006), with an average of about 40 ppb (Ehhalt *et al.*, 2001). Concentrations are often higher in rural areas downwind of urban-source pollutants (Gregg *et al.*, 2003; Oltmans *et al.*, 2006). The largest projected increases this century are projected for the northern hemisphere (Karnosky *et al.*, 2005) due to increasing precursor concentrations in regions with high industrial development, transcontinental transport of O₃ pollution and changes in climate that increasingly favor O₃ formation (Meehl *et al.*, 2007). In the Third Assessment Report (TAR), the IPCC projected an average global increase in background [O₃] to approximately 68 ppb by 2050 and a further increase to 85 ppb by 2100 in the northern midlatitudes based on the A2 storyline from the Special Report on Emission Scenarios (SRES) (Ehhalt *et al.*, 2001). These are, however, averages and considerably higher levels are forecast for specific areas in the northern midlatitudes (Karnosky *et al.*, 2005; Sitch *et al.*, 2007).

Current and projected [O₃] are sufficient to cause chronic changes in trees [for reviews see Chappelka & Samuelson (1998); Skarby *et al.* (1998); Karnosky *et al.* (2007); Matyssek *et al.* (2007)], most notably reductions in photosynthesis (Long & Naidu, 2002; Wittig *et al.*, 2007), accelerated leaf senescence (Pell *et al.*, 1999; Karnosky *et al.*, 2005; Nunn *et al.*, 2005) and decreased productivity (Percy *et al.*, 2007). Forests are one of the most important global sinks for carbon (Geider *et al.*, 2001; Houghton, 2003; Sitch *et al.*, 2007). Without this sink, which offsets a significant proportion of current global CO₂ emissions, the rate of increase in atmospheric [CO₂] would be greater (Canadell *et al.*, 2007). Canadell *et al.* (2007) suggested that the observed strength of this sink might be declining. We have shown

previously that the rise in [O₃] since the Industrial Revolution has already resulted in a significant decrease in tree leaf photosynthesis (Wittig *et al.*, 2007), but does this translate into a loss in biomass and production? Percy *et al.* (2007) estimated a maximum 31% loss in productivity of *Populus tremuloides* in parts of its North American range between 2001 and 2003 due to O₃. How widespread are such decreases and can we assess whether there has been an overall loss and by what amount? Furthermore, what losses are possible if [O₃] continue to rise?

Most observations of O₃ effects on trees have been made on northern temperate species. Hundreds of peer-reviewed studies are available in literature reporting effects of [O₃] on tree biomass, along with components of that biomass and related physiological measures [for reviews see Chappelka & Samuelson (1998); Skarby *et al.* (1998); Karnosky *et al.* (2007); Matyssek *et al.* (2007)]. But, estimating the magnitude of the response of trees to O₃ is yet to be untangled from the many disparate experimental designs that limit a quantitative summary of the peer-reviewed literature. Meta-analytic techniques now provide an established means to summarize such disparate datasets and draw global conclusions (Curtis & Wang, 1998; Gurevitch & Hedges, 1999; Hedges *et al.*, 1999; Rosenberg *et al.*, 2000; Ainsworth *et al.*, 2007). This approach to analyzing prior studies has proved insightful in examining the effects of the global rise in [CO₂] (Curtis & Wang, 1998; Ainsworth & Long, 2005) and is now providing new insights into the effects of rising [O₃] (Morgan *et al.*, 2003; Grantz *et al.*, 2006; Valkama *et al.*, 2007; Wittig *et al.*, 2007; Ainsworth, 2008).

Meta-analytic techniques are used here to address the following questions. (1) By how much is current ambient [O₃] decreasing productivity relative to preindustrial [O₃]? (2) What further reductions in productivity may result from the expected increases in [O₃] within this century? (3) What is the underlying physiological basis for any decreases in productivity? (4) How might these reductions be affected by other atmospheric and climatic variables?

Materials and methods

Database

A database of the effects of O₃ on tree biomass, growth, physiology and biochemistry was compiled by surveying the peer-reviewed literature with the Web of Science (Thompson-ISI, Philadelphia, PA, USA) and SilverPlatter (Ovid Technologies, New York, NY, USA) citation indices following methodology previously described (Wittig *et al.*, 2007). Briefly, keyword searches covering

the period 1970 through October 2006 identified 313 articles that reported O₃ effects on tree biomass, growth, physiology and biochemistry, and each article identified was scanned for data. Articles and their observations were excluded if (1) the description of experimental design was insufficient to allow objective assignment to the categories of Table 1, (2) the data was previously or more completely reported in another article, (3) the leaf exposure period was less than 7 days. In total, 263 articles were included in the analysis of O₃ impacts on tree biomass, growth, physiology and biochemistry (Appendix A).

For each observation included for analysis, the value in the control and elevated [O₃] treatment (X_C and X_T), the standard deviations (SD_C and SD_T) and replication (N_C and N_T) were extracted from tables, text and/or figures of each primary article and then entered into a database together with the categorical information described in Table 1. Values given only in the figures of publications were digitized using data-extraction software (GRAFULA 3 v.2.10; Wesik SoftHaus, St. Petersburg, Russia). Three databases were compiled: (1) trees grown in charcoal-filtered (CF) control were compared with trees grown in ambient background [O₃], (2) trees grown in CF control were compared with trees grown in elevated [O₃] treatments and (3) trees grown in ambient background [O₃] were compared with trees grown in elevated [O₃] treatments.

Within each article, measures of final biomass (total dry weight, leaf dry weight, shoot dry weight, above-ground-woody dry weight, root dry weight), root-to-shoot ratio, height, diameter, leaf area and leaf nitrogen content on a mass basis recorded at the end of the experiment were considered independent if they were made on different species or distinct genotypes within a species, or if the measurements were made in different years. Seasonal measures of total chlorophyll content, chlorophyll *a* content, chlorophyll *b* content, chlorophyll *a/b*, Rubisco activity, Rubisco content, transpiration, leaf respiration, starch content and sugar content were considered independent if they were made on different species or distinct genotypes within a species, or if the measurements were made on different dates.

Sources of variation

Eight categories were identified as important potential sources of variation that could alter the response of trees to [O₃] (Table 1). Each observation was coded into the levels of each category as follows: (1) angiosperm vs. gymnosperm, (2) rooting volume, (3) fumigation method [e.g. FACE (free-air CO₂ enrichment) vs. open-top chamber], (4) duration of the entire experiment (total duration), (5) duration of the experiment in the current

Table 1 Categories and categorical levels describing the experimental conditions in studies of ozone (O₃) impacts on tree biomass, growth, physiology and biochemistry

Category	Categorical level	
Tree classification	Angiosperms	Gymnosperms
Rooting volume (L)	<5	5–10
Fumigation method	Growth chamber	Greenhouse
Total experiment duration (days)	<60	60–120
Current year duration (days)	<60	60–120
Experiment mean [O ₃] (ppb)	<40	40–60
Current year mean [O ₃] (ppb)	<40	40–60
Additional treatment	None	Elevated [CO ₂]
	Open-top chamber	Free-air enrichment
	≥ 10	240–300
	120–180	≥ 240
	120–180	300–360
	60–80	≥ 360
	60–80	
	Drought	Competition
	Air pollutant	
	Low nutrient	
	Ground	
	Branch chamber	
	180–240	
	180–240	
	≥ 80	
	≥ 80	

year (current year duration), (6) mean $[O_3]$ over the entire experiment (experiment $[O_3]$), (7) mean $[O_3]$ calculated over the current year of the experiment (current year $[O_3]$), (8) additional treatments (e.g. elevated $[CO_2]$ or drought) (Table 1). In addition to these categories, the different tree genera were examined. Because of limited observations of individual species, it was not possible to assess the impact of $[O_3]$ at the species level. Species within a genera were therefore combined although it is recognized that contrasting life-forms within a genus may obscure some differences. The mean $[O_3]$ in the control and treatment is defined as the hourly average concentration for the exposure period which varied from 4 to 24 h per day over a minimum duration of 7 days to durations greater than a year.

Meta-analyses

To calculate the effect of an $[O_3]$ treatment on trees as a proportionate change relative to a control, the natural log of the response ratio (r) was used, where r is the ratio of the mean in the experimental treatment (X_T) divided by the mean in the control (X_C). Effect sizes are reported as the antilog r converted to the mean percentage change from the control ($[(r-1) \times 100]$) as in previous analyses (Curtis & Wang, 1998; Ainsworth *et al.*, 2002; Morgan *et al.*, 2003; Ainsworth & Long, 2005; Wittig *et al.*, 2007). Trees unaffected by $[O_3]$ have an $r = 1$, and therefore, a 0% change from control. A negative percentage change indicates a decrease in response to $[O_3]$, while positive values indicate an increase. A meta-analytic software package was used to calculate all effect sizes, 95% confidence intervals (CI) and heterogeneity statistics (METAWIN 2.1.3.4; Sinauer Associates Inc., Sunderland, MA, USA; Rosenberg *et al.*, 2000). Three sets of analyses were conducted on each of the three databases described above: (1) X_C was the measure in CF air, and X_T in ambient $[O_3]$, (2) X_C was the measure in CF air and X_T was the measure in elevated $[O_3]$ treatments and (3) X_C was the measure in ambient $[O_3]$ and X_T in elevated $[O_3]$ treatments.

Approximately two-thirds of the studies did not report variance along with the mean effect and replication size, therefore an unweighted fixed-effects model was used to estimate the mean effect of $[O_3]$ relative to a control for all biomass, growth, physiological and biochemical parameters. Unweighted meta-analyses are advantageous because they are not restricted by the assumptions of normality in parametric tests nor by the need for an observed study variance (Hedges *et al.*, 1999) and have previously been used to study the effects of elevated $[CO_2]$ and $[O_3]$ on soybeans (Ainsworth *et al.*, 2002; Morgan *et al.*, 2003). An assumption of

the unweighted meta-analytic technique is that the variance in the treatment and control is equal to one (Rosenberg *et al.*, 2000). Under this assumption, it is not statistically possible to test for between-group heterogeneity (Q_B) and for this reason, the unweighted technique was not used to estimate differences between the categorical groups defined in Table 1. It was however possible to use bootstrapping techniques to generate 95% CI around the mean effect and determine the direction, magnitude and significance of the mean effect relative to control. To generate the bootstrapped CI, we used 64 999 iterations, the maximum allowed by the meta-analysis software, in order to minimize variation. If the 95% bootstrapped CI did not overlap zero, response to O_3 is considered significant (Ainsworth *et al.*, 2002; Morgan *et al.*, 2003).

A weighted random-effects model was used, where each individual response was weighted by the reciprocal of the observed pooled variance (Gurevitch & Hedges, 1999; Hedges *et al.*, 1999), to examine the effects of the categorical levels described in Table 1 on total biomass, leaf biomass, leaf area, aboveground-woody biomass, shoot biomass, root biomass, root-to-shoot ratio, height and diameter. Each of these variables had high degrees of freedom (df) even when observations without variance were excluded. Total heterogeneity (Q_T) was tested against a χ^2 distribution and CIs were generated using bootstrapping techniques, again with 64 999 iterations. The categorical analysis proceeded by partitioning the Q_T into the between-group heterogeneity (Q_B) and within-group heterogeneity (Q_W). Categories were determined to have at least one level significantly different from the others if the randomized P -value was < 0.05 , indicating that group membership was not random. Resampling techniques were used to generate randomized P -values because the data did not conform to the assumptions of parametric tests, (i.e. the data were not normally distributed). If the 95% bootstrapped CIs constructed around the mean effect size for each categorical level did not overlap, means were considered to be significantly different from one another (Curtis & Wang, 1998; Gurevitch & Hedges, 1999). Levels of each category were included in the analysis if there were at least 10 observations; however, if less than 10 observations were available, results were only discussed if they originated from at least three independent articles.

Results

Ambient $[O_3]$ relative to CF controls

Comparison of trees grown in current ambient $[O_3]$ with CF air provides a measure of how the elevation

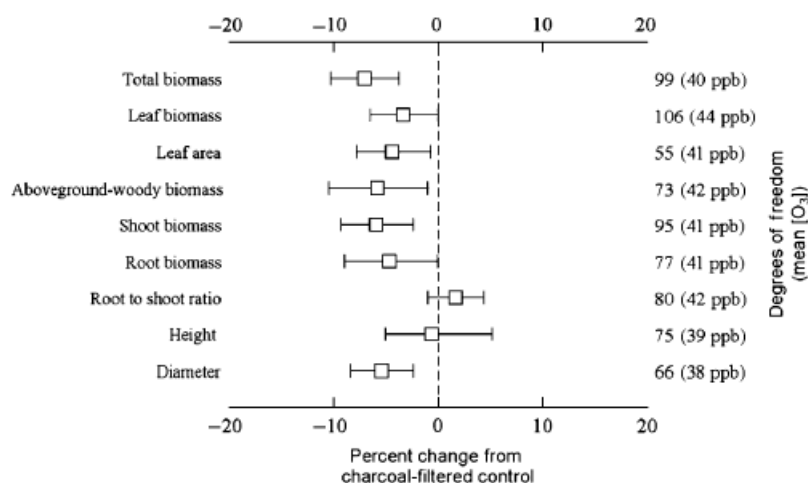


Fig. 1 Percent change in total biomass, leaf biomass, leaf area, aboveground woody biomass, shoot biomass, root biomass, root-to-shoot ratio, height and diameter of all trees exposed to ambient ozone concentrations ($[O_3]$) relative to charcoal-filtered controls. Symbols are bracketed by 95% bootstrapped confidence intervals; degrees of freedom and mean $[O_3]$ are given along the y -axis.

of $[O_3]$ that has occurred since the Industrial Revolution has reduced tree productivity. Across all studies, the average $[O_3]$ in the ambient air was 40 ppb (Fig. 1). Relative to CF air, this reduced the total biomass of trees across all studies ($df = 99$) significantly and on average by 7% (Fig. 1). Aboveground woody biomass, stem diameter and shoot biomass were similarly reduced by 6%, 5% and 6%, respectively (Fig. 1). Similar decreases were indicated for leaf and root biomass, but were not significant, whereas leaf area was reduced significantly by 4% (Fig. 1). Height and root-to-shoot ratio were not affected significantly (Fig. 1). There were no differences among the categories described in Table 1 nor for genera for total dry weight, leaf dry weight, shoot dry weight, aboveground woody dry weight, root dry weight or root-to-shoot ratio for trees grown in ambient $[O_3]$ relative to CF controls in the weighted meta-analysis (Appendix B1). In comparing ambient $[O_3]$ with CF, there were too few observations of different tree species to analyze variation between genera in the height and diameter studies (Appendix B2). Ambient $[O_3]$ relative to CF controls had no impact on transpiration or respiration rates or on chlorophyll, nitrogen, sugar or starch content (Appendix B3).

Elevated $[O_3]$ treatments relative to CF controls

Comparison of trees grown in air with elevated $[O_3]$ to trees grown in CF air provides a relative measure of how the elevation of $[O_3]$ to anticipated 2100 levels (Ehhalt *et al.*, 2001) will affect measures of productivity relative to preindustrial $[O_3]$. Elevation of $[O_3]$ between 81 and 101 ppb on average amplified all the effects on productivity reported in 'Ambient $[O_3]$ relative to CF

controls'. Total biomass was decreased by 17% at mean $[O_3]$ of 97 ppb averaged across studies compared with 7% at 40 ppb, and similar reductions were observed in all other measures of biomass examined (Fig. 2). In contrast, a significant reduction in root biomass was observed, which exceeded the decrease in shoot biomass, resulting in a significant 6% reduction in the root-to-shoot ratio, indicating decreased partitioning of carbon to roots. Height, which was not significantly affected by 40 ppb $[O_3]$, was decreased significantly by elevation of $[O_3]$ on average to 95 ppb (Fig. 2). Stem diameter was decreased by 10% and less than total biomass, consistent with the fact that biomass will be proportional to volume, of which diameter only represents one dimension.

Previous analyses reported the impact of elevated $[O_3]$ on light-saturated photosynthesis and stomatal conductance of trees (Wittig *et al.*, 2007) and are shown here for comparison. The reduction in leaf photosynthesis, 18% (Fig. 3), is almost identical to the reduction in biomass (Fig. 2). The impact of a decreased leaf photosynthetic rate on productivity would be amplified by the 20% decrease in leaf area (Fig. 2), but offset by the similar reduction in respiration (Fig. 3). Decreased chlorophyll *a* and *b* content resulted in decreased total chlorophyll content, but with no change in chlorophyll *a/b*, and very large decreases in Rubisco content (28%) and activity (21%) (Fig. 3). The significant 15% decrease in sucrose may indicate that decrease in photosynthesis is greater than decreases in utilization or sink activity, which is consistent with decrease in respiration (Fig. 3). Interestingly, nitrogen content was increased. This may result from the decreased size of the plant relative to the amount of nitrogen available, or to

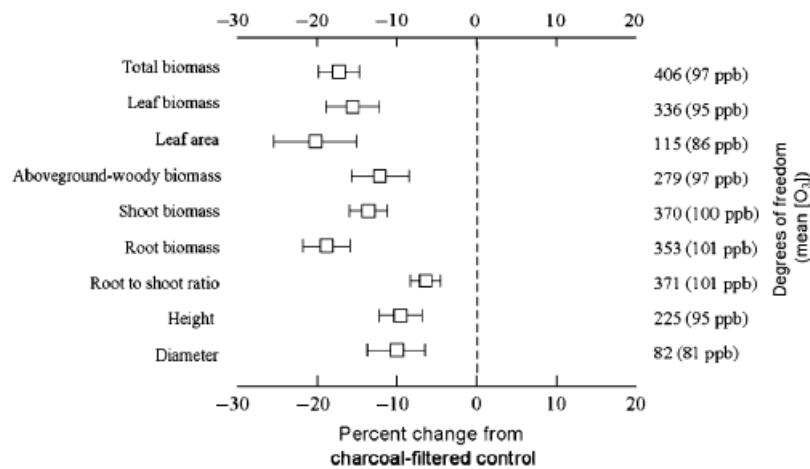


Fig. 2 Percent change in total biomass, leaf biomass, leaf area (per unit area), aboveground woody biomass, shoot biomass, root biomass, root-to-shoot ratio, height and diameter of all trees exposed to elevated ozone concentrations ([O₃]) relative to charcoal-filtered controls. Symbols are bracketed by 95% bootstrapped confidence intervals; degrees of freedom and mean [O₃] are given along the y-axis.

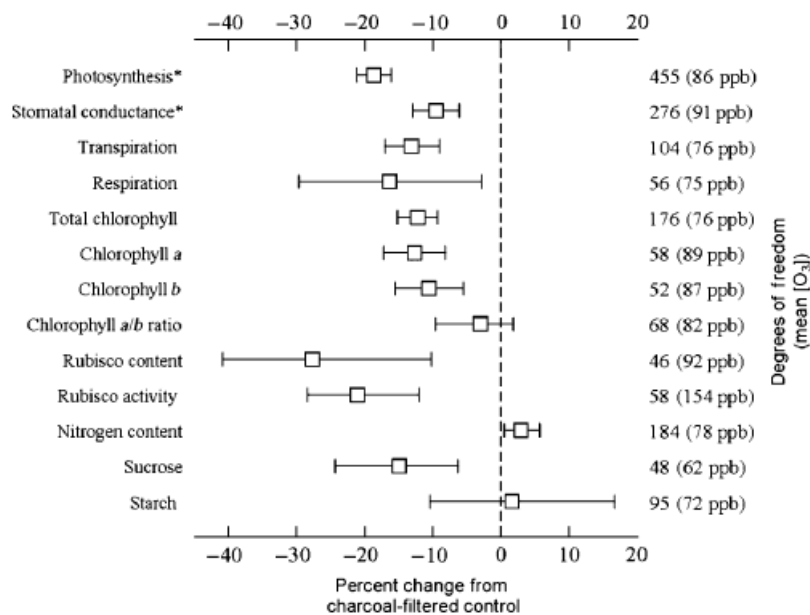


Fig. 3 Percent change in transpiration, respiration, total chlorophyll content, chlorophyll a content, chlorophyll b content, chlorophyll a/b ratio, Rubisco content, Rubisco activity, leaf nitrogen content, sucrose content and starch content ± 95% bootstrapped confidence intervals for all trees exposed to elevated ozone concentrations ([O₃]) relative to charcoal-filtered controls. Degrees of freedom and mean [O₃] are given along the y-axis. *Photosynthesis and stomatal conductance values have been taken from Wittig *et al.* (2007).

nitrogen retranslocation from prematurely senescing leaves under O₃ exposure.

Gymnosperms were less sensitive to elevated [O₃] than angiosperms (Fig. 4; Table 2). Total biomass of angiosperms was reduced by 23% at an average elevated [O₃] of 74 ppb, while total biomass of gymnosperms was reduced by just 7% at a higher mean [O₃] of 92 ppb (Fig. 4). The reduction in gymnosperm total biomass was largely driven by significant decreases

in root biomass; the reductions in gymnosperm shoot and leaf biomass were not significant (Fig. 4). Elevated [O₃] significantly decreased both above- and belowground biomass in angiosperms (Fig. 4), and also caused a 22% decrease in the root-to-shoot ratio (Fig. 4).

Although four gymnosperm genera, *Abies*, *Picea*, *Pinus* and *Sequoiadendron* were included in the meta-analysis of all trees, only *Picea* and *Pinus* had enough

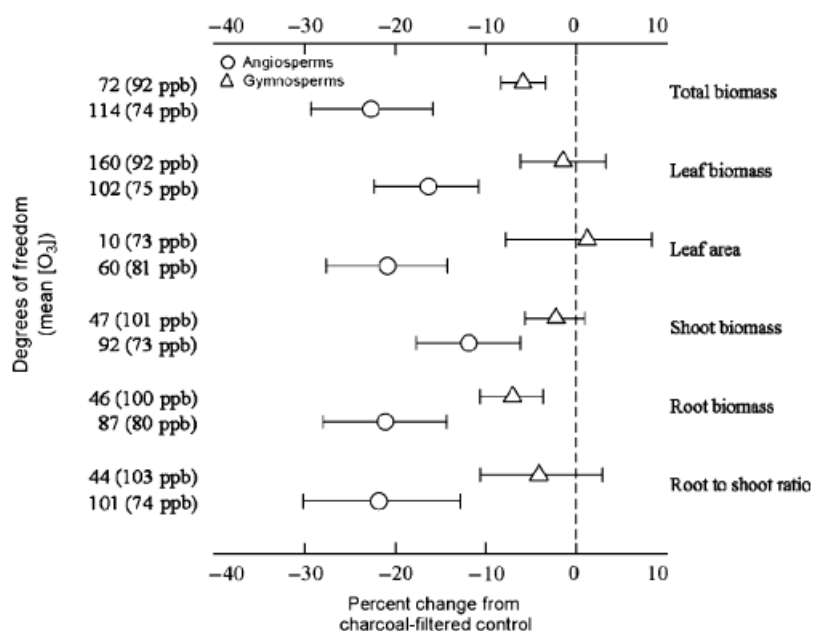


Fig. 4 Percent change in total biomass, leaf biomass, leaf area, shoot biomass, root biomass and root-to-shoot ratio for gymnosperms and angiosperms exposed to elevated ozone concentrations ($[O_3]$) relative to charcoal-filtered controls. Symbols are bracketed by 95% bootstrapped confidence intervals; degrees of freedom and mean $[O_3]$ are given along the y -axis.

Table 2 The between-group heterogeneity (Q_B) evaluated using resampling tests with 64 999 iterations to generate a randomized probability value for the total biomass, leaf biomass, aboveground woody biomass, shoot biomass, root biomass, root-to-shoot ratio, height and diameter of all trees exposed to elevated ozone concentrations ($[O_3]$) relative to charcoal-filtered controls in a weighted random-effects meta-analysis with categorical structure

Variable	Genera	Tree classification	Rooting volume	Fumigation method	Total experiment duration	Current year duration	Experiment mean $[O_3]$	Current year mean $[O_3]$	Additional treatment
Total biomass	70.356*	33.190***	5.367	5.599	27.933	4.930	15.371	15.613	7.087
Leaf biomass	24.825	10.322***	7.520*	0.392	23.025*	4.266	3.268	3.325	0.793
Leaf area	17.921	5.6787*	23.132	6.671	16.574	7.919	0.105	0.105	0.993
Aboveground woody biomass	41.028*	0.272	7.528	0.088	0.657	0.646	17.422*	17.333*	0.401
Shoot biomass	44.417**	8.514*	6.710	5.967	1.958	3.325	9.277	9.057	1.542
Root biomass	49.407**	12.270**	4.642	3.874	6.638	2.074	9.381	9.748	6.618
Root-to-shoot ratio	37.533	15.394*	21.749*	6.314	5.481	6.060	13.042	12.716	16.640
Height	37.067***	0.890	1.067	14.415*	4.715	1.432	2.668	1.365	5.951
Diameter	17.7139*	0.027	1.248	7.048*	15.588*	4.534	2.067	2.201	2.474

P -values <0.05 are considered significant.

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$.

observations to be included in the categorical analysis. Both *Picea* and *Pinus*, showed very similar responses to elevated $[O_3]$ (Table 3). Eleven angiosperm genera were included in the meta-analysis of the total biomass of all trees: *Acer*, *Alnus*, *Betula*, *Fagus*, *Fraxinus*, *Liquidambar*, *Liriodendron*, *Quercus*, *Platanus*, *Populus* and *Prunus*. Of those, four angiosperm genera were included in the categorical analysis (Table 3). *Liriodendron* did not show any reduction in total biomass at elevated $[O_3]$ (83 ppb)

in contrast to *Betula*, *Populus* and *Prunus*, which were all significantly reduced (Table 3).

As treatment $[O_3]$ increased, total angiosperm biomass was progressively reduced (Table 4; Fig. 5). $[O_3]$ less than 40 ppb had no significant effect on total biomass, while concentrations between 40 and 60 ppb decreased angiosperm biomass by $\sim 20\%$ and concentrations greater than 80 ppb decreased biomass by $\sim 40\%$ (Fig. 5). Other categories of studies did not

Table 3 Effect sizes, 95% bootstrapped confidence intervals (CIs), degrees of freedom (df) and mean ozone concentrations in the treatment and control ($[O_3] X_T/X_C$) for the total biomass of angiosperms, gymnosperms and the different genera exposed to elevated $[O_3]$ relative to charcoal-filtered controls

Genera	Percentage change	95% CI	df	$[O_3] X_T/X_C$	Q_B	P -value
Gymnosperms	-6	-8 to -3	72	92/12	0.607	0.819
<i>Picea</i>	-2	-8 to 4	8	45/12		
<i>Pinus</i>	-6	-9 to -4	59	96/12		
Angiosperms	-23	-29 to -16	114	74/10	24.010	0.133
<i>Betula</i>	-20	-42 to -1	14	84/2		
<i>Liriodendron</i>	1	-15 to 23	8	83/15		
<i>Populus</i>	-27	-36 to -17	71	74/9		
<i>Prunus</i>	-27	-44 to -7	6	62/10		

The between-group heterogeneity (Q_B) and associated P -values are presented for gymnosperm and angiosperm genera.

Table 4 The between-group heterogeneity (Q_B) evaluated using resampling tests with 64 999 iterations to generate a randomized probability value for the total biomass of angiosperms and gymnosperms exposed to elevated ozone concentrations ($[O_3]$) relative to charcoal-filtered controls in a weighted random-effects meta-analysis with categorical structure

Category	Gymnosperms		Angiosperms	
	Q_B	P -value	Q_B	P -value
Genera	0.607	0.819	24.010	0.133
Rooting volume	3.793	0.185	23.959	0.018*
Fumigation method	3.085	0.215	0.926	0.495
Total experiment duration	7.015	0.418	20.530	0.069
Current year duration	5.124	0.306	7.625	0.234
Leaf fumigation duration	5.065	0.307	7.625	0.231
Experiment mean $[O_3]$	5.656	0.208	46.096	0.002**
Current year mean $[O_3]$	3.729	0.622	40.312	0.009**
Additional treatment	6.226	0.284	2.575	0.438

P -value <0.05 is considered significant.

* P <0.05; ** P <0.01.

consistently affect the biomass response of trees to elevated $[O_3]$ (Table 2; Appendix C).

Elevated $[O_3]$ treatments relative to ambient $[O_3]$ controls

Comparison of trees grown in air with elevated $[O_3]$ of an average of 64 ppb to the current ambient $[O_3]$ of an average of 40 ppb, provides a measure of how the elevation of $[O_3]$ to anticipated 2050 levels (Ehhalt *et al.*, 2001) will affect measures of productivity relative to today. All measures of biomass, as well as root-to-shoot ratio, leaf area, height and diameter show significant reductions (Fig. 6). These parallel with those observed when comparing an average elevation of about 97 ppb with CF, although are smaller in magni-

tude. Importantly, these studies suggest that while elevation from preindustrial $[O_3]$ of <10 to 40 ppb decreased biomass by 7%, a further increase from 40 to 64 ppb will decrease production by 11%.

Paralleling the findings for the comparison of elevated $[O_3]$ vs. CF air, the large decrease in leaf photosynthetic rate would be amplified by a large decrease in leaf area, but possibly partially offset by an indicated, but not significant, decrease in respiration. Also, in parallel with elevated $[O_3]$ vs. CF there were significant decreases in chlorophyll and Rubisco content, even though nitrogen content per unit mass increased (Fig. 7). Transpiration was reduced by 9%; starch and sucrose were not different from controls (Fig. 7).

Gymnosperms were much less affected by an increase in $[O_3]$ from ambient concentrations relative to angiosperms (Fig. 8). Gymnosperms were largely unaffected by elevated $[O_3]$ (Fig. 8); however, angiosperm total biomass was reduced by 15% (Fig. 8). Angiosperm leaf area, leaf biomass and diameter were all significantly reduced relative to controls and different from gymnosperms (Fig. 8). There was no difference between the two gymnosperm genera examined (Table 6). Eight angiosperm genera were included in the analysis of all trees: *Acer*, *Betula*, *Fagus*, *Fraxinus*, *Liriodendron*, *Populus*, *Prunus* and *Quercus*. Of those, five were included in the categorical analysis after exclusion criteria were assessed. Although *Liriodendron* increased total biomass in elevated $[O_3]$ relative to ambient $[O_3]$, interpretation of this finding is limited by large uncertainty and low df (Table 6). In contrast, *Populus*, *Prunus* and *Quercus* all showed significant decreases in total biomass in elevated $[O_3]$ while *Betula* was not different from ambient $[O_3]$ controls (Table 6). Other differences in leaf biomass, root biomass and diameter reported in Table 5 are presented in full in Appendix D.

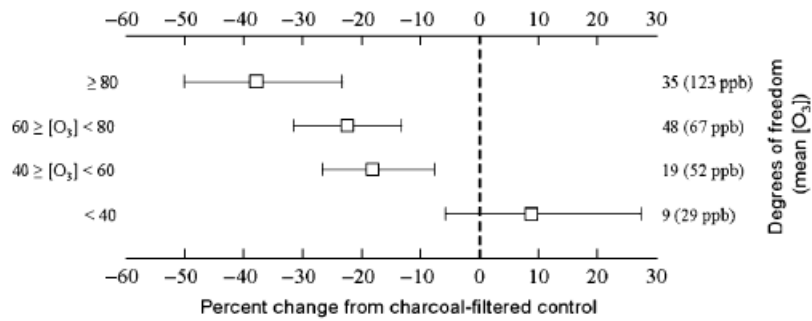


Fig. 5 Percent change in total biomass of angiosperms in elevated ozone concentration ($[O_3]$) categories relative to charcoal-filtered controls. Symbols are effect sizes bracketed by 95% bootstrapped confidence intervals; degrees of freedom and mean $[O_3]$ are given along the y -axis.

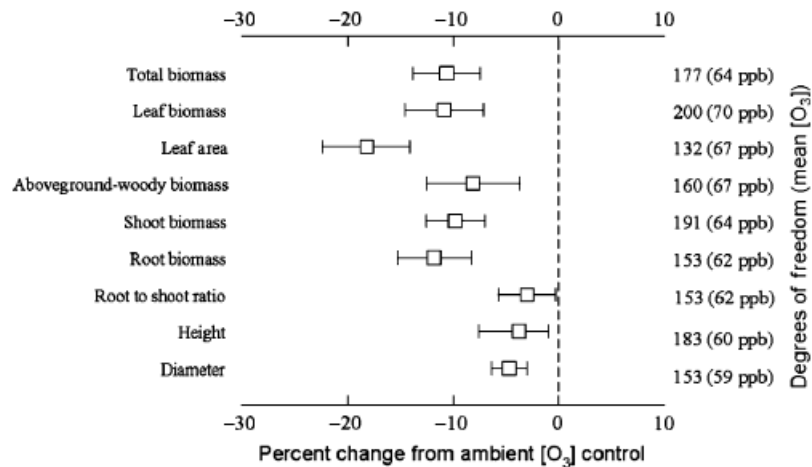


Fig. 6 Percent change in total biomass, leaf biomass, leaf area (per unit area), aboveground woody biomass, shoot biomass, root biomass, root-to-shoot ratio, height and diameter of all trees exposed to elevated ozone concentrations ($[O_3]$) relative to ambient $[O_3]$ controls. Symbols are bracketed by 95% bootstrapped confidence intervals; degrees of freedom and mean $[O_3]$ are given along the y -axis.

Discussion

Is current ambient ozone decreasing tree productivity relative to preindustrial $[O_3]$?

The best available ground level measurements of tropospheric $[O_3]$ before the Industrial Revolution in the northern temperate zone, suggest an average concentration of 10 ppb (Volz & Kley, 1988). Today, summer daytime surface background concentrations in the northern temperate zone may average 40 ppb (Fowler *et al.*, 1999b; Ehhalt *et al.*, 2001). Several modeling studies, based on limited datasets suggest that this increase in $[O_3]$ is likely to decrease carbon uptake into forests (Ollinger *et al.*, 1997; Felzer *et al.*, 2004). A meta-analysis of measured leaf photosynthetic rates showed an 11% average decrease due to elevation of $[O_3]$ to 47 ppb (Wittig *et al.*, 2007). Is this inferred decrease detectable in the actual measurements of biomass and

productivity? This meta-analytic review of 263 peer-reviewed articles reporting O_3 impacts on tree biomass shows that ambient $[O_3]$ of 40 ppb averaged across all studies resulted in a statistically significant 7% reduction (CI 4–10%, $df = 99$; Fig. 1). This decrease is relative to CF controls, which had a mean $[O_3]$ of 17 ppb across all studies, and so was slightly higher than the assumed preindustrial $[O_3]$. Therefore, even this 7% loss may be a slight underestimate. The species examined in the meta-analysis were from 10 genera including *Abies*, *Acer*, *Betula*, *Fagus*, *Liriodendron*, *Picea*, *Pinus*, *Populus*, *Prunus* and *Quercus* and there was no significant difference detected between them (Appendix B1). The species represented by these genera include many of the major or co-dominant species of the forests of the temperate and boreal regions of the northern midlatitudes. Sitch *et al.* (2007) projected from a modeling study that the northern forest carbon sink is depressed by current ambient $[O_3]$. Despite being based on measurements

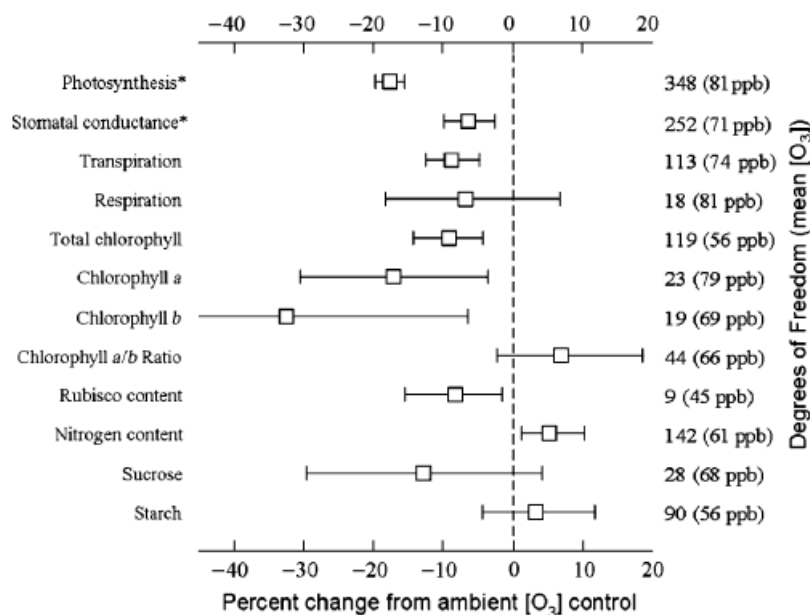


Fig. 7 Percent change in transpiration, respiration, total chlorophyll content, chlorophyll *a* content, chlorophyll *b* content, chlorophyll *a/b* ratio, Rubisco content, leaf nitrogen content, sucrose content and starch content ± 95% bootstrapped confidence intervals for all trees exposed to elevated ozone concentrations ([O₃]) relative to ambient [O₃] controls. Degrees of freedom and mean [O₃] are given along the *y*-axis. *Photosynthesis and stomatal conductance values have been taken from Wittig *et al.* (2007).

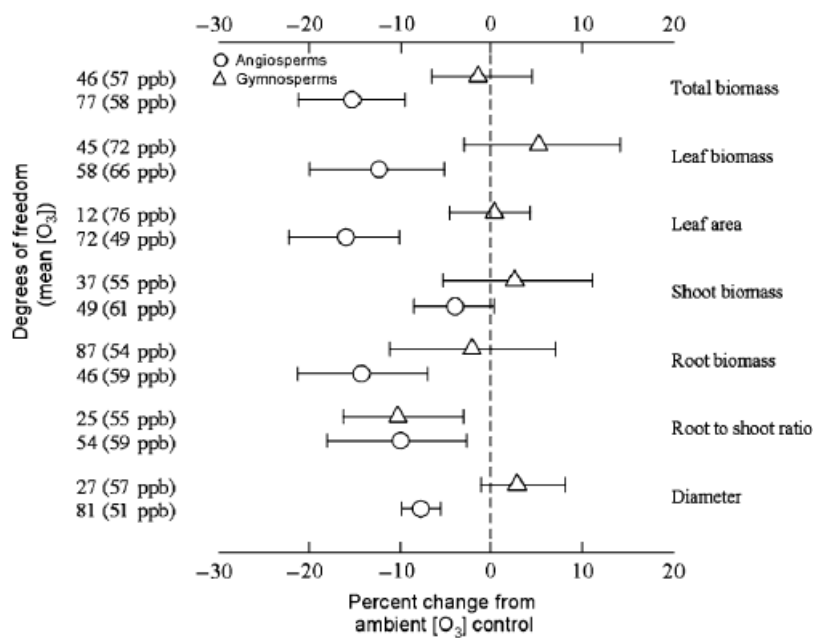


Fig. 8 Percent change in total biomass, leaf biomass, leaf area, shoot biomass, root biomass, root-to-shoot ratio and diameter for gymnosperms and angiosperms exposed to elevated ozone concentrations ([O₃]) relative to ambient [O₃] controls. Symbols are bracketed by 95% bootstrapped confidence intervals; degrees of freedom and mean [O₃] are given along the *y*-axis.

from young trees in controlled environments, the current study provides the strongest experimental evidence to date, given both its statistical significance and the fact that it is based on 100 independent measurements, for the hypothesis of Sitch *et al.* (2007).

Ollinger *et al.* (1997) predicted net primary productivity (NPP) of the northeastern US forest by coupling a simple model of ambient [O₃] effects on leaf photosynthesis to a forest ecosystem model (PnET-II). They projected that ambient [O₃] could be reducing NPP by

Table 5 The between-group heterogeneity (Q_B) evaluated using resampling tests with 64 999 iterations to generate a randomized probability value for the total biomass, leaf biomass, aboveground woody biomass, shoot biomass, root biomass, height and diameter of all trees exposed to elevated ozone concentrations ($[O_3]$) relative to ambient $[O_3]$ controls in a weighted random-effects meta-analysis with categorical structure

	Tree		Rooting	Fumigation	Total	Current year	Experiment	Current year	Additional
	Genera	classification	volume	method	experiment	duration	mean $[O_3]$	mean $[O_3]$	treatment
Total biomass	20.150**	4.702**	3.033	1.266	3.994	0.441	0.939	1.212	1.502
Leaf biomass	4.303	1.693**	2.730	0.277	8.649	0.699	0.732	0.698	0.711
Leaf area	10.104	2.078	6.834	0.854	3.461	3.088	1.976	0.660	1.904
Aboveground woody biomass	5.292	0.012	2.503	0.790	0.171	0.152	2.637	2.826	1.369
Shoot biomass	10.827	1.826	5.720	0.177	4.874	3.957	3.985	2.835	9.408
Root biomass	19.173*	3.449	6.779	3.251	4.640	0.501	0.882	1.080	2.128
Root-to-shoot ratio	16.114	0.007	3.834	2.682	1.067	0.392	7.648	7.338	1.762
Height	12.657	2.779	4.135	6.646	7.936	2.623	1.890	4.390	0.704
Diameter	21.298**	13.662***	18.624**	9.499*	9.549	2.987	6.064	6.405	0.103

P-values <0.05 are considered significant.

P* < 0.05; *P* < 0.01; ****P* < 0.001.

Table 6 Effect sizes, 95% bootstrapped confidence intervals (CIs), degrees of freedom (df) and mean ozone concentrations in the treatment and control ($[O_3] X_T/X_C$) for the total biomass of all trees, angiosperms, gymnosperms and the different genera exposed to elevated $[O_3]$ relative to ambient air controls

Genera	Percentage change	95% CI	df	$[O_3] X_T/X_C$	Q_B	<i>P</i> -value
Gymnosperms	-1	-7 to 4	46	57/31	0.417	0.208
<i>Picea</i>	5	-9 to 20	10	49/27		
<i>Pinus</i>	-4	-8 to 2	35	59/32		
Angiosperms	-15	-21 to -10	77	59/36	19.357	0.014*
<i>Betula</i>	-7	-17 to 4	13	46/28		
<i>Liriodendron</i>	23	14 to 36	7	79/48		
<i>Populus</i>	-22	-31 to -15	29	60/40		
<i>Prunus</i>	-24	-37 to -10	8	57/36		
<i>Quercus</i>	-23	-52 to -1	5	58/27		

P-value <0.05 (*) is considered significant.

3–16% and that the greatest losses were in aboveground woody biomass in comparison with leaf or root biomass. The present meta-analysis provides experimental and statistically significant support to both these projections (Fig. 1). It was not, however, possible to provide conclusive insight into the interaction of drought and O_3 as was done in the Ollinger *et al.* (1997) modeling study. Ollinger *et al.* (1997) show that periods of high $[O_3]$ are associated with hot, dry weather that reduces stomatal conductance and offsets $[O_3]$ impacts. In theory, any environmental condition that reduces stomatal conductance will reduce O_3 uptake and lessen any subsequent damage. Because of gaps in observations of this interaction in literature, it is uncertain from the meta-analysis what the magnitude or significance of this interaction is under contemporary $[O_3]$.

Modeled estimates of carbon sequestration by forests of the Great Smoky Mountains National Park attribute a 50% loss (0.9 Tg) to ambient $[O_3]$ between 1971 and 2001 (Zhang *et al.*, 2007). This ecosystem process model also suggested that pine forests were less affected than angiosperms (Zhang *et al.*, 2007). A meta-analysis of the impact of current ambient $[O_3]$ on the photosynthesis and stomatal conductance of trees reported large, significant reductions in both parameters for angiosperms, whereas pine and other gymnosperms were unaffected (Wittig *et al.*, 2007). However, in the present study, no differences were detected between the biomass of angiosperms and gymnosperms in response to ambient $[O_3]$ relative to CF (Table 2; Fig. 1). This differs from Wittig *et al.* (2007) that showed a significant loss of leaf photosynthesis in angiosperms due to ambient $[O_3]$

Table 7 The between-group heterogeneity (Q_B) evaluated using resampling tests with 64999 iterations to generate a randomized probability value for the total biomass of angiosperms and gymnosperms exposed to elevated ozone concentrations ($[O_3]$) relative to ambient $[O_3]$ controls in a weighted random-effects meta-analysis with categorical structure

Category	Gymnosperms		Angiosperms	
	Q_B	<i>P</i> -value	Q_B	<i>P</i> -value
Genus	0.417	0.208	19.357	0.014*
Rooting volume	5.452	0.029*	14.806	0.007**
Method	0.114	0.484	3.426	0.174
Total duration	2.487	0.168	12.026	0.103
Current year duration	0.180	0.631	2.947	0.206
Leaf fumigation duration	0.233	0.550	2.947	0.208
Experiment $[O_3]$	4.931	0.037	3.116	0.390
Current year $[O_3]$	0.786	0.501	5.051	0.186
Additional treatment	8.595	0.055	2.377	0.588

P-value <0.05 is considered significant.

P* < 0.05; *P* < 0.01.

but not gymnosperms. However, decreased biomass does not depend only on decreased leaf photosynthesis, but could also result from decreased leaf area (Fig. 1) and/or increased diversion of resources within the leaf to detoxifying O_3 and tissue repair (Wieser & Matyssek, 2007).

It has been suggested that ability to project from $[O_3]$ studies using small trees in chambers to $[O_3]$ impacts on large forest trees is limited (Samuelson & Kelly, 2001; Karnosky *et al.*, 2005, 2007). This is relevant because most studies are short-term experiments on long-lived organisms in varied artificial chamber environments, which may limit the conclusions from this meta-analysis. However, in the Aspen-FACE experiment, biomass loss after 6 years of growth and treatment appeared proportionally similar to the loss at 2 years (King *et al.*, 2005). Although arguably still young after 6 years of growth, the continuous open-air fumigation from planting through canopy closure and beyond at Aspen-FACE provides unique and critical insight into the potential response of an intact, mature forest. Furthermore, while the bias of most experiments to juvenile trees must remain a concern, the meta-analytic results are in good agreement with previous model estimates derived from young tree data (Hogsett *et al.*, 1997; Ollinger *et al.*, 1997).

What further reductions in productivity may result from the expected increases in ozone within this century?

If $[O_3]$ in the northern hemisphere progressively increases over this century, as projected (Ehhalt *et al.*, 2001), then it may reach 68 ppb by 2050 and 85 ppb by

2100. Elevation from current to an average 64 ppb $[O_3]$ resulted in an average decrease in tree biomass of 11% (CI 7–14%, df 177; Fig. 7). By the close of this century, the meta-analysis suggests that biomass losses may reach 17% (CI 15–20%, df 406; Fig. 2), relative to preindustrial $[O_3]$ and therefore a further 10% reduction relative to today. Open-air daytime fumigation of trees with tropospheric $[O_3]$ at approximately 50 ppb at the Aspen-FACE facility in Rhinelander, Wisconsin, caused 21%, 13% and 14% reductions in NPP of aspen, aspen-birch and aspen-maple communities, respectively, after 7 years of fumigation (King *et al.*, 2005). The value for aspen (*P. tremuloides*) is similar to the mean response of *Populus* in this meta-analysis (21% cf. 22%, Table 6). However, the mean treatment level in Aspen-FACE was 50 ppb, while the 22% average decrease observed here was from an average exposure level of 60 ppb. This suggests a greater impact of $[O_3]$ when applied in an open-air treatment and is consistent with recent findings that soybean biomass was decreased more under open-air treatment in FACE than in chamber experiments (Morgan *et al.*, 2003, 2005). While this is limited to two studies, it should be of concern that the large and significant losses projected across the chamber studies may be underestimates of what will occur under open-air and over longer, more realistic growth periods. Clearly, more and longer duration open-air studies like those conducted by King *et al.* (2005) in different forest types are critical if we are going to understand future changes to temperate and boreal forest productivity.

While the impact of current ambient $[O_3]$ relative to CF was not significantly different when comparing gymnosperms with angiosperms (Appendix B1), elevation from present ambient to expected levels for 2050 and 2100 affected angiosperms significantly more than gymnosperms (Figs 4 and 8, Tables 2 and 5). Gymnosperm biomass was not significantly reduced by elevated $[O_3]$ to an average 57 ppb relative to ambient $[O_3]$ of 31 ppb in contrast to a 15% reduction in angiosperms at an average $[O_3]$ of 58 ppb relative to ambient $[O_3]$ of 36 ppb. However, relative to CF air, at an average elevation of $[O_3]$ to 92 ppb, gymnosperm biomass was significantly decreased, but only by 6% compared with 23% in angiosperms at an average of 74 ppb (Figs 4 and 8). As all the gymnosperms studied were evergreen while the majority of angiosperms were deciduous, it was therefore not possible to determine whether this difference was due to leaf longevity or phylum. Evergreen leaves as a rule have lower stomatal conductance than deciduous leaves (Samuelson & Kelly, 2001), which would decrease O_3 uptake and subsequent damage. Whatever the basis, this finding suggests that rising $[O_3]$ might not only decrease the productivity of forests, but also give gymnosperms an advantage in mixed

deciduous forest, which would potentially lead to changes in community composition.

It is also clear from the present study that some genera are more sensitive than others. For example, *Liriodendron* biomass was not different from CF control when exposed to average elevated $[O_3]$ of 83 ppb, while *Populus* biomass was reduced by 27% (CI 17–36%) under elevated $[O_3]$ of 74 ppb (Table 3). It may be of relevance that *Liriodendron* is a basal angiosperm, and while deciduous, of the angiosperms examined, is the closest relative to the gymnosperms. Although the genus-level analysis provides additional insight into angiosperm and gymnosperm responses, it is also recognized that within species, there are sensitive and tolerant genotypes that are not accounted for at the genus scale (Karnosky *et al.*, 2007).

Some individual studies found that elevated $[O_3]$ reduced root biomass more than aboveground biomass (Coleman *et al.*, 1996). Grantz *et al.* (2006) conducted a meta-analysis of $[O_3]$ impacts on the root-to-shoot allocation coefficient (k) and relative growth rate (RGR) of plants. Although predominantly based on herbaceous species, it included seedlings of five tree species, from three studies. Results from their meta-analysis suggest that k for three of the five tree species, *Pinus sylvestris*, *Picea abies* and *Quercus petraea*, were reduced by elevated $[O_3]$. Grantz *et al.* (2006) suggest that leaves lower in the canopy are the preferential sources of assimilates for roots while leaves in the upper canopy are preferential sources of assimilates for shoots. It thus follows that the older leaves lower in the canopy which are undergoing accelerated senescence might be the cause of the lower root-to-shoot ratio (Grantz *et al.*, 2006). The much larger dataset examined here shows a 15% reduction (CI 10–21%) in root-to-shoot ratio across 78 independent measures of angiosperm trees in response to a mean elevation of $[O_3]$ to 59 ppb (Fig. 8). *Quercus* was among those included in the 78 observations and although the CI was large (1–52%), a significant reduction was detected (Table 6). In contrast to Grantz *et al.* (2006), the 47 independent measures of gymnosperm root-to-shoot ratios, representing *Picea* and *Pinus*, at mean elevation of $[O_3]$ to 57 ppb did not reveal a significant effect, relative to an ambient $[O_3]$ of 31 ppb (Fig. 8). The dramatic 15% decrease in allocation to angiosperm roots found in the current analysis has broad negative implications both for community persistence and carbon sequestration. A smaller root system, relative to shoot size, is likely to increase vulnerability to drought, storm damage and nutrient stress. This effect differs between angiosperms and gymnosperms (Table 2) and so may also cause long-term changes in community composition by disadvantaging angiosperms more than gymnosperms. Overall,

the highly significant decrease in angiosperm root-to-shoot ratio suggests that the losses of biomass due to elevated $[O_3]$ observed here, may be a minimum of the actual losses, given that these effects could be amplified by these secondary effects that may well decrease tree fitness.

What is the underlying physiological basis for any decreases in productivity?

A previous meta-analysis, limited to photosynthesis and stomatal conductance, showed significant reductions in both parameters by elevated $[O_3]$ relative to CF and air with current ambient $[O_3]$ (Wittig *et al.*, 2007). The present analysis shows parallel large decreases in leaf area of 18% and 20% at elevated $[O_3]$ of 67 and 86 ppb, respectively (Figs 3 and 7) compared with the 18% and 19% reductions in light-saturated photosynthesis at 81 and 86 ppb averaged across elevated $[O_3]$ studies, respectively (Wittig *et al.*, 2007). While it has been shown that threshold O_3 metrics such as the SUM06 and AOT40 as well as cumulative O_3 flux are effective at relating damage and exposure (Martin *et al.*, 2000; Low *et al.*, 2006; Matyssek *et al.*, 2007), the only way to place every study in the meta-analysis on a common framework was to group them by $[O_3]$. The similarity in the magnitudes of decrease in photosynthesis, stomatal conductance, and leaf area across elevated $[O_3]$ studies indicates that the grouping by $[O_3]$ in the meta-analysis was effective. These results have clear implications for the carbon sink capacity of these trees. Reductions in stomatal conductance, along with the significant decreases in transpiration reported in this analysis (Figs 3 and 7), also imply reduced transfer of water to the atmosphere, decreasing humidity and potentially altering regional rainfall patterns in temperate and boreal forests. Integration of leaf physiological effects into General Circulation Models has shown that such decreases in transpiration can significantly increase continental surface temperatures, humidity and atmospheric circulation (Sellers *et al.*, 1996).

Several individual studies have shown that elevated $[O_3]$ causes accelerated senescence and earlier loss of Rubisco, which leads to a remobilization of resources to younger tissue (reviewed: Long & Naidu, 2002). This quantitative summary of 47 independent observations show a significant 28% (CI 10–41%) reduction in Rubisco content for leaves fumigated with a mean elevated $[O_3]$ of 92 ppb. A decrease in Rubisco content could be the result of increased protein degradation from oxidative damage or decreased synthesis (Long & Naidu, 2002). Brendley & Pell (1998) showed a premature loss of Rubisco from older leaves, and corresponding increases in Rubisco in leaves at the top of hybrid poplar

canopies. This type of compensatory response might explain the increase in nitrogen content in leaves, as shown in the present analysis (Figs 3 and 7). However, it could also reflect the fact that total biomass per unit land area is decreased, while the nitrogen nutrient resource is unchanged.

A recent meta-analysis of studies published between 1990 and 2005 reported $[O_3]$ impacts on total leaf nutrient concentrations, total carbohydrate concentrations and insect herbivore performance alone and in combination with elevated $[CO_2]$ (Valkama *et al.*, 2007). Valkama *et al.* (2007) grouped all leaf nutrients, for example, N, P, K, Ca, etc., together and the results based on 125 independent measures showed no overall difference in total nutrients due to elevated $[O_3]$ relative to ambient $[O_3]$. However, this absence of an overall effect resulted because decreases observed in some species were offset by increases in others. In our meta-analysis of 185 independent observations of leaf nitrogen content alone for trees grown in elevated $[O_3]$ of 78 ppb relative to CF air, nitrogen content was increased significantly by 3% (CI 1–6%; Fig. 3). Furthermore, across 143 independent observations of leaves grown in elevated $[O_3]$ of 61 ppb relative to ambient $[O_3]$ of 34 ppb, nitrogen content was significantly increased by 5% (CI 1–10%; Fig. 7). The difference in the two studies might result from the larger sample size used here, and/or from the fact that nitrogen was separated out in the present study.

Valkama *et al.* (2007) also found that total leaf carbohydrate concentrations, including sugars, starch and total nonstructural carbohydrates, were significantly reduced for angiosperms but there was a lack of response in gymnosperms. The separate meta-analysis of sucrose and starch concentration in leaves in the current study suggests that starch content is unchanged while sucrose content is reduced in elevated $[O_3]$ relative to CF air (Fig. 3). Such a decrease might be expected to lead to decreased leaf respiration. However, small increases in hybrid poplar leaf respiration were reported between 7 and 35 days of exposure to high $[O_3]$ (~ 125 ppb) in growth chambers (Reich, 1983). However, when examined across all 57 independent observations, a significant decrease in respiration of 16% (CI 3–30%) due to elevated $[O_3]$ of 75 ppb relative to CF air was found (Fig. 3). This is, therefore, consistent with the observed decrease in sucrose content.

How might these reductions be affected by other atmospheric and climatic variables?

Although it is expected that the impacts of elevated $[O_3]$ may not be as pronounced under elevated $[CO_2]$ due to decreased stomatal conductance and decreased O_3 up-

take, no significant interaction was evident across the studies. This may be the result of the small sample size and, therefore, inadequate statistical sensitivity (Tables 2 and 5). However, no significant interaction between elevated $[O_3]$ and elevated $[CO_2]$ in assessing biomass and NPP has been found in the Aspen-FACE study (Valkama *et al.*, 2007). As O_3 uptake is also decreased by other factors that decrease stomatal conductance such as drought and low nitrogen, these might also be expected to lessen impacts of rising $[O_3]$. While this may be the case, averaged across all peer-reviewed studies of these interactions, there was no evidence for such an offset (Tables 2 and 5). This lack of evidence, when the data is viewed as a whole, does suggest the need for caution in assuming that increasing $[CO_2]$ and drought incidence will provide protection against rising $[O_3]$ – because as shown here, field evidence is lacking. Long-term investigations on mature trees grown in open-air conditions centered on elucidating the interaction of O_3 with other changing climatic variables such as elevated $[CO_2]$, drought and temperature are essential to develop more accurate projections of the impacts of rising $[O_3]$ on forest trees.

Conclusion

While model projections have suggested that rising tropospheric $[O_3]$ will decrease the ability of temperate forests to act as a continuing sink offsetting net emissions of CO_2 to the atmosphere, experimental evidence has been uncertain due to variation between locations, species and methods. Here, by examining the entirety of the peer-reviewed literature, it is shown that current $[O_3]$ is already decreasing biomass growth by 7% and therefore carbon storage, relative to clean air. As $[O_3]$ continues to rise, further decreases of 11% and 17% are predicted to occur by 2050 and 2100, respectively. As the northern temperate forest is considered, the major current terrestrial sink partially offsetting net CO_2 emissions, $[O_3]$ will therefore accelerate the rate of rise in $[CO_2]$. Almost all studies of $[O_3]$ effects on trees have considered species and habitats north of the tropics. While the northern temperate zone is projected to see some of the highest future levels of $[O_3]$, large increases in the tropics are also forecast across this century. If effects parallel to those observed in temperate trees, then there is the risk that the world's forest ecosystems may change from net sink to net source of CO_2 .

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Appendix A

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Appendix B

The between-group heterogeneity (Q_B) evaluated using resampling tests with 64 999 iterations to generate a randomized probability value for the total biomass, leaf biomass, above-ground woody biomass, shoot biomass, root biomass, height and diameter of all trees exposed to ambient [O₃] relative to charcoal filtered controls in a weighted random-effects meta-

analysis with categorical structure. *P*-values < 0.05 are considered significant.

Table B1

Results of the categorical meta-analysis of the effects of ambient ozone concentrations ([O₃]) relative to charcoal filtered controls on height and diameter including the degrees of freedom (df), mean [O₃] in the treatment and control (mean [O₃] X_T/X_C), effect sizes and upper and lower confidence intervals (CI).

Table B2

The percent change in transpiration, respiration, total chlorophyll content, chlorophyll *a* content, chlorophyll *b* content, chlorophyll *a/b* ratio, leaf nitrogen content, sucrose content and starch content ± 95% bootstrapped confidence intervals for all trees exposed to ambient ozone concentrations ([O₃]) relative to ambient [O₃] controls. Degrees of freedom and mean [O₃] are given along the *y*-axis.

Table B3

Appendix C

Results of the categorical meta-analysis of the effects of elevated ozone concentrations ([O₃]) relative to charcoal filtered controls on leaf biomass, aboveground woody biomass, shoot biomass, root biomass, height and diameter including the degrees of freedom (df), mean [O₃] in the treatment and control (mean [O₃] X_T/X_C), effect sizes and upper and lower confidence intervals (CI).

Table C1

Appendix D

Results of the categorical meta-analysis of the effects of elevated ozone concentrations ([O₃]) relative to ambient [O₃] controls on leaf biomass, shoot biomass, root biomass and diameter including the degrees of freedom (df), mean [O₃] in the treatment and control (mean [O₃] X_T/X_C), effect sizes and upper and lower confidence intervals (CI).

Table D1

Table B1

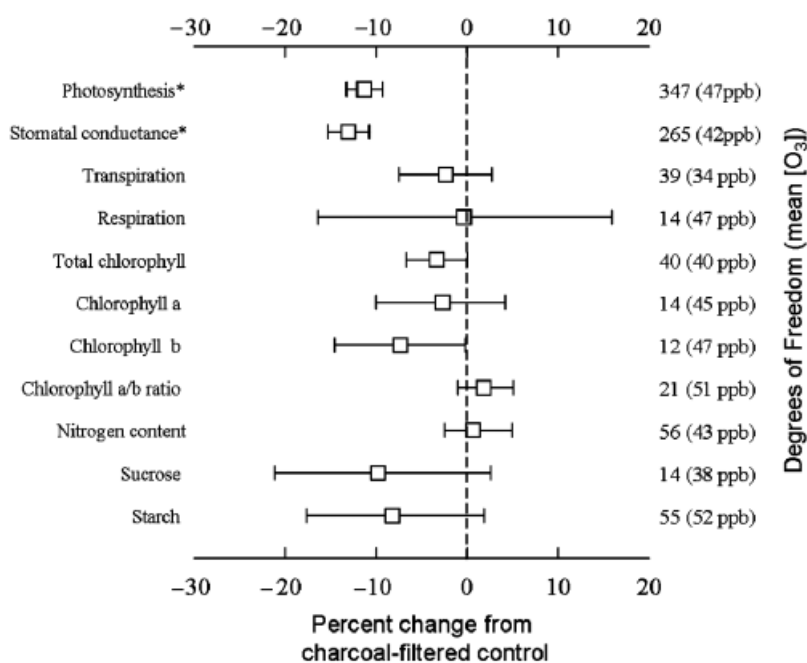
	Genera	Tree classification	Rooting volume	Fumigation method	Total experiment duration	Current year duration	Additional treatment
Total biomass	6.085	0.228	1.030	0.066	3.297	1.424	0.569
Leaf biomass	8.523	4.630	0.150	0.009	2.341	2.954	0.010
Leaf area biomass	0.653	0.476	0.006	0.265	17.371	2.594	0.099
Aboveground woody biomass	3.920	3.317	3.729	–	1.392	1.610	1.052
Shoot biomass	8.329	2.868	2.898	0.002	2.022	3.909	0.602
Root biomass	16.239	3.174	8.019	0.250	3.622	0.969	1.201
Root-to-shoot ratio	6.118	1.379	2.945	0.134	1.592	0.307	0.115
Height	29.284**	0.844	3.311	0.017	9.816	4.504	–
Diameter	29.625*	2.100	2.378	–	6.309	4.434	–

P* < 0.05; *P* < 0.01; ****P* < 0.001.

Table B2

Variable	Category	Categorical level	df	Mean [O ₃] X _T /X _C	Effect size	Lower CI	Upper CI
Height	Genera	<i>Acer</i>	1	41/14	2.577	1.063	4.032
		<i>Betula</i>	1	24/5	0.963	0.890	0.978
		<i>Liriodendron</i>	7	43/19	1.051	0.935	1.168
		<i>Picea</i>	3	24/5	0.894	0.792	0.983
		<i>Pinus</i>	19	36/18	1.000	0.936	1.043
		<i>Populus</i>	2	42/20	0.785	0.738	0.916
		<i>Prunus</i>	8	42/19	1.073	0.919	1.094
		<i>Quercus</i>	1	45/18	1.045	1.021	1.220
Diameter	Genera	<i>Acer</i>	1	41/14	1.145	1.144	1.200
		<i>Betula</i>	1	24/5	0.861	0.824	0.872
		<i>Liriodendron</i>	7	43/19	0.946	0.871	1.001
		<i>Picea</i>	2	24/5	1.170	0.600	1.250
		<i>Pinus</i>	16	35/18	1.010	0.946	1.058
		<i>Populus</i>	2	42/20	0.835	0.769	0.871
		<i>Prunus</i>	8	42/19	1.081	0.847	1.105

Table B3



*Photosynthesis and stomatal conductance values taken from Wittig *et al.* (2007).

Table C1

Variable	Category	Categorical Level	df	mean [O ₃] X _T /X _C	Effect size	Lower CI	Upper CI	
Leaf biomass	Genera	<i>Alnus</i>	2	57/25	0.764	0.594	0.984	
		<i>Betula</i>	11	82/12	1.031	0.923	1.130	
		<i>Citrus</i>	3	82/10	0.867	0.767	0.936	
		<i>Liriodendron</i>	6	94/17	0.885	0.845	0.932	
		<i>Persea</i>	1	82/10	0.650	0.400	0.818	
		<i>Picea</i>	7	64/21	1.122	1.096	1.152	
		<i>Pinus</i>	49	81/15	0.955	0.908	1.005	
		<i>Populus</i>	60	71/9	0.789	0.690	0.881	
		<i>Prunus</i>	8	79/26	0.844	0.668	0.981	
		<i>Quercus</i>	1	86/18	0.957	0.921	0.978	
		<i>Sequoiadendron</i>	1	150/0	1.074	1.057	1.091	
	Tree classification	Angiosperm	102	75/12	0.837	0.777	0.892	
		Gymnosperm	57	83/16	0.985	0.939	1.033	
	Rooting volume (RV, in L)	<5	57	70/6	0.903	0.839	0.965	
		5 ≥ RV <10	26	93/20	0.747	0.681	0.805	
		≥ 10	33	80/6	0.858	0.724	0.962	
		Ground	39	76/26	0.948	0.879	1.022	
	Total experiment duration (TD, days)	<60	51	69/5	0.896	0.830	0.962	
		60 ≥ TD <120	29	103/19	0.822	0.713	0.904	
		120 ≥ TD <180	12	83/17	0.666	0.460	0.904	
180 ≥ TD <240		4	77/17	0.810	0.740	0.861		
240 ≥ TD <300		5	82/10	0.811	0.669	0.915		
300 ≥ TD <360		17	59/3	0.953	0.886	1.018		
360 ≥ TD	36	77/26	0.986	0.927	1.048			
Aboveground woody biomass	Genera	<i>Alnus</i>	2	57/25	0.696	0.536	0.889	
		<i>Betula</i>	7	97/2	1.111	1.048	1.202	
		<i>Liriodendron</i>	6	94/17	1.017	0.820	1.200	
		<i>Picea</i>	1	64/21	1.000	0.976	1.024	
		<i>Pinus</i>	28	85/14	0.968	0.930	1.009	
		<i>Populus</i>	56	72/9	0.902	0.806	1.007	
		<i>Prunus</i>	4	60/9	1.310	0.525	1.982	
		<i>Sequoiadendron</i>	1	150/0	1.062	1.052	1.072	
		Experiment mean [O ₃] (ppb)	<40	7	27/5	1.304	1.031	1.631
	40 ≥ [O ₃] <60		20	50/6	0.959	0.811	1.179	
	60 ≥ [O ₃] <80		43	65/5	0.911	0.801	1.009	
	80 ≥ [O ₃]		41	118/20	0.899	0.823	0.968	
	Current year mean [O ₃] (ppb)	<40	7	27/5	1.304	1.031	1.632	
		40 ≥ [O ₃] <60	19	49/5	0.956	0.804	1.180	
		60 ≥ [O ₃] <80	44	65/5	0.914	0.805	1.010	
	80 ≥ [O ₃]	41	118/20	0.899	0.823	0.968		
Shoot biomass	Genera	<i>Alnus</i>	2	57/25	0.734	0.569	0.935	
		<i>Betula</i>	7	97/2	1.090	1.019	1.192	
		<i>Ceratonia</i>	1	52/12	0.817	0.762	0.899	
		<i>Liriodendron</i>	6	97/17	0.932	0.809	1.096	
		<i>Picea</i>	1	64/21	1.118	1.083	1.141	
		<i>Pinus</i>	45	98/10	0.970	0.937	1.002	
		<i>Populus</i>	58	72/9	0.837	0.747	0.934	
		<i>Prunus</i>	4	60/9	0.845	0.668	1.000	
		<i>Quercus</i>	4	65/13	0.878	0.817	0.947	
		<i>Sequoiadendron</i>	1	150/0	1.071	1.061	1.080	
		Tree classification	Angiosperm	92	73/10	0.881	0.824	0.939
	Gymnosperm		47	102/10	0.978	0.944	1.009	
	Root biomass	Genera	<i>Alnus</i>	2	57/25	0.734	0.581	0.866

Continued

Table C1. (Contd.)

Variable	Category	Categorical Level	df	mean [O ₃] X _T /X _C	Effect size	Lower CI	Upper CI		
Height	Tree classification	<i>Betula</i>	12	117/1	1.011	0.886	1.136		
		<i>Liriodendron</i>	6	97/17	0.903	0.820	1.054		
		<i>Picea</i>	1	64/21	1.008	0.955	1.059		
		<i>Pinus</i>	42	99/9	0.930	0.893	0.965		
		<i>Populus</i>	56	72/9	0.747	0.655	0.842		
		<i>Prunus</i>	4	60/28	0.618	0.507	0.771		
		<i>Quercus</i>	1	86/18	0.932	0.917	0.937		
		<i>Sequoiadendron</i>	1	150/0	0.979	0.960	0.998		
		Angiosperm	87	80/10	0.789	0.721	0.857		
		Gymnosperm	46	100/9	0.930	0.894	0.964		
		Diameter	Genera	<i>Acer</i>	1	72/14	1.916	1.000	3.395
				<i>Betula</i>	19	91/5	1.056	1.020	1.096
				<i>Liriodendron</i>	1	63/10	1.227	1.003	1.441
				<i>Pinus</i>	23	97/15	0.994	0.956	1.028
				<i>Populus</i>	28	86/13	0.872	0.833	0.908
				<i>Prunus</i>	4	60/9	0.997	0.788	1.012
<i>Quercus</i>	1			86/18	1.090	1.083	1.090		
Fumigation method	Growth chamber			17	116/1	1.093	1.023	1.158	
	Greenhouse			3	170/0	0.992	0.935	1.026	
	Open-top chamber			58	75/16	0.995	0.965	1.016	
Diameter	Genera			<i>Acer</i>	1	72/14	1.063	0.880	1.068
				<i>Betula</i>	1	62/8	1.129	1.082	1.167
				<i>Liriodendron</i>	1	63/10	1.053	1.005	1.076
				<i>Pinus</i>	17	85/18	0.976	0.936	1.015
				<i>Populus</i>	18	62/3	0.950	0.901	0.996
				<i>Prunus</i>	4	60/9	0.899	0.735	0.971
		Fumigation method	Growth chamber	3	131/4	1.101	0.726	1.153	
			Open-top chamber	43	66/11	0.960	0.929	0.990	
			Total experiment	18	64/3	0.994	0.941	1.049	
		Diameter	duration (TD, days)	<60	5	95/5	0.983	0.880	1.099
				60 ≥ TD < 120	4	81/14	0.820	0.676	0.995
				120 ≥ TD < 180	7	70/19	0.969	0.862	1.089
				180 ≥ TD < 240	1	38/10	0.667	0.125	3.576
				240 ≥ TD < 300	1	74/21	0.954	0.337	2.706
		Diameter	duration (TD, days)	300 ≥ TD < 360	6	70/21	1.014	0.897	1.147
				360 ≥ TD	6	70/21	1.014	0.897	1.147

Table D1

Variable	Category	Categorical level	df	Mean [O ₃] X _T /X _C	Effect size	Lower CI	Upper CI	
Leaf biomass	Tree classification	Angiosperm	58	66/36	0.876	0.8004	0.9483	
		Gymnosperm	45	72/37	1.0518	0.9699	1.142	
Root biomass	Genera	<i>Betula</i>	20	42/27	0.8668	0.7638	0.9838	
		<i>Liriodendron</i>	4	92/51	1.2304	1.0853	1.6096	
		<i>Picea</i>	9	47/26	0.9762	0.8039	1.1698	
		<i>Pinus</i>	20	57/31	0.9794	0.9051	1.059	
		<i>Populus</i>	15	64/44	0.8875	0.8161	0.9585	
		<i>Prunus</i>	4	60/34	0.6174	0.4908	0.7629	
		<i>Quercus</i>	1	86/45	1.0095	1.0047	1.0185	
		<i>Acer</i>	1	72/41	0.9255	0.7333	0.9338	
Diameter	Genera	<i>Betula</i>	22	40/26	0.9366	0.8847	0.9943	
		<i>Liriodendron</i>	1	63/40	1.1182	1.0899	1.1723	
		<i>Picea</i>	7	23/43	1.0308	0.9921	1.0763	
		<i>Pinus</i>	19	63/34	1.0269	0.9756	1.1037	
		<i>Populus</i>	48	53/37	0.9134	0.8919	0.9367	
		<i>Prunus</i>	4	60/34	0.8434	0.7868	0.9069	
		Tree classification	Angiosperm	81	51/34	0.9221	0.901	0.9442
			Gymnosperm	27	57/31	1.0283	0.9892	1.0811
	Rooting volume (RV, in L)	<5	3	51/30	0.8429	0.7797	0.9016	
		5 ≥ RV < 10	14	49/31	1.0181	0.9865	1.0516	
		≥ 10	17	67/36	1.0267	1.0004	1.0544	
	Fumigation method	Ground	Ground	72	50/33	0.9218	0.8987	0.9479
			Growth chamber	2	36/28	1.0283	0.9916	1.0672
			Open-top chamber	46	59/33	0.9746	0.9337	1.0186
			Free-air enrichment	58	48/33	0.917	0.8954	0.9413