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Interannual climatic variation mediates elevated CO_2 and O_3 effects on forest growth

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Abstract

We analyzed growth data from model aspen (*Populus tremuloides* Michx.) forest ecosystems grown in elevated atmospheric carbon dioxide ([CO_2]; 518 μL L^{-1}) and ozone concentrations ([O_3]; 1.5 $\times$ background of 30–40 nL L^{-1} during daylight hours) for 7 years using free-air CO_2 enrichment technology to determine how interannual variability in present-day climate might affect growth responses to either gas. We also tested whether growth effects of those gasses were sustained over time. Elevated [CO_2] increased tree heights, diameters, and main stem volumes by 11%, 16%, and 20%, respectively, whereas elevated ozone [O_3] decreased them by 11%, 8%, and 29%, respectively. Responses similar to these were found for stand volume and basal area. There were no growth responses to the combination of elevated [$CO_2 + O_3$]. The elevated [CO_2] growth stimulation was found to be decreasing, but relative growth rates varied considerably from year to year. Neither the variation in annual relative growth rates nor the apparent decline in CO_2 growth response could be explained in terms of nitrogen or water limitations. Instead, growth responses to elevated [CO_2] and [O_3] interacted strongly with present-day interannual variability in climatic conditions. The amount of photosynthetically active radiation and temperature during specific times of the year coinciding with growth phenology explained 20–63% of the annual variation in growth response to elevated [CO_2] and [O_3]. Years with higher photosynthetic photon flux (PPF) during the month of July resulted in more positive growth responses to elevated [CO_2] and more negative growth responses to elevated [O_3]. Mean daily temperatures during the month of October affected growth in a similar fashion the following year. These results indicate that a several-year trend of increasingly cloudy summers and cool autumns were responsible for the decrease in CO_2 growth response.

Keywords: air pollution, carbon dioxide, FACE, global change, ozone, *Populus tremuloides*, relative growth rate, trembling aspen

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Introduction

There are two points of intersection between climate and the carbon (C) cycle. First, atmospheric CO_2 concentration ([CO_2]) absorbs long-wave radiation, thus, global climate models use atmospheric [CO_2] concentration to force predictions of future warming (Cicerone *et al*., 2001). Climatologists have begun to incorporate source–sink fluxes of C into some global climate models (Cox *et al*., 2000; Cramer *et al*., 2001; Friedlingstein *et al*., 2003). For example, some include elevated [CO_2] effects on photosynthesis to estimate the fraction of anthropogenic CO_2 emissions remaining in the atmosphere. This is important because increases in atmospheric CO_2 concentration directly affect photosynthetic fixation of CO_2 and terrestrial C storage (Pendall *et al*., 2004). This leads to the second linkage between climate and the C

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cycle: that changes in climate can affect the function of C sources and sinks, both abiotic (e.g. carbonate rock weathering and reprecipitation, Liu & Zhao, 1999) and biotic (e.g. photosynthesis and respiration, Lenton, 2000). However, relatively little is known about the second linkage, thus few have coupled the reverse process of climate change with potential effects on terrestrial C exchange, particularly as C exchange is modified in a CO_2-enriched atmosphere (Hurtt *et al*., 2002; Friedlingstein *et al*., 2003).

C exchange by terrestrial ecosystems is affected by interannual variability in climate variables, particularly temperature, moisture, and growing season duration (Arain *et al*., 2002; Law *et al*., 2002). This has also been recognized on a global scale with the observation that global atmospheric [CO_2] seems to vary annually with climatic events such as the El Niño/Southern Oscillation (Schimel *et al*., 2001). In terms of long-range global climate change, however, interannual climatic variation will be superimposed upon changes in atmospheric chemistry that also have direct effects on plant physiology and growth.

Stimulation of photosynthesis and growth of C-3 plants by increasing atmospheric [CO_2] has been known for some time (Ceulemans & Mousseau, 1994). Earlier results have been confirmed in a number of free-air CO_2-enrichment (FACE) experiments on both existing and aggrading forest systems (Isebrands *et al*., 2001; Hamilton *et al*., 2002; Norby *et al*., 2002; Calfapietra *et al*., 2003; King *et al*., 2005). Across several forest FACE experiments, an increase of 200 ppm CO_2 produced about an 23% increase in net primary productivity (Norby *et al*., 2005).

In addition to increasing [CO_2], tropospheric ozone (O_3) is increasing in abundance and is considered the most significant air pollutant negatively affecting forest productivity worldwide (Taylor *et al*., 1994). Historical increases in background [O_3] may have already decreased plant productivity by up to 13% (Felzer *et al*., 2004). Whereas, increased [CO_2] stimulates plant productivity, O_3 reduces tree growth and vigor and may result in mortality, particularly if other stressors are present (Karnosky *et al*., 1996, Krupa *et al*., 2001).

As climate changes, in what manner will plant responses to elevated [CO_2] and [O_3] also change (cf. Norby & Luo, 2004)? Future effects of climate change on forest productivity are uncertain because many potential interacting processes affecting terrestrial C sink activity are not clearly understood (Adams & Piovesan, 2002; Hurtt *et al*., 2002; Friedlingstein *et al*., 2003; Beedlow *et al*., 2004), especially long-term growth responses to elevated CO_2 interacting with climate variables (Schimel *et al*., 2001; Friedlingstein *et al*., 2003). Insights into these important issues may be inferred from the effects of year-to-year variability in present day climate on plant responses to elevated [CO_2] and [O_3]. However, there is a paucity of field data linking interannual climate variability with long-term forest growth responses to changes in atmosphere (Cicerone *et al*., 2001; Schimel *et al*., 2001; Adams & Piovesan, 2002). Therefore, in this study, we closely examine relationships between interannual climatic variability and CO_2 and O_3 effects on forest growth over a 7-year period.

Methods

The Aspen FACE experiment

A detailed description of the Aspen FACE experiment is given in (Dickson *et al*., 2000). The Aspen FACE experiment was initiated in 1996 on a 32 ha USDA Forest Service experimental farm in Cassian Township, Oneida Co., Wisconsin (45.6°N, 89.5°W). Soil is a mixed, frigid, coarse loamy Alfic Haplorthod with a 30 cm clay loam plow layer grading into a sandy loam above stratified sand and gravel. More thorough descriptions of the soils and nutrients are reported in Dickson *et al*. (2000). The site was cultivated for agricultural crops from the 1920s until 1972 when it was converted to a tree research facility.

In 1996–1997, we constructed 12, 30 m diameter rings to deliver elevated concentrations of atmospheric CO_2 and O_3 to the interior of the rings at canopy height (Hendrey *et al*., 1999). The 12 rings were spaced approximately 100 m apart to avoid cross-contamination of atmospheric treatments. Design of the experiment was a full-factorial (current ambient control, elevated [CO_2], elevated [O_3], and elevated [CO_2] + [O_3]), randomized complete block design with three replicates. In 1997, we planted the rings to model communities of trembling aspen (*Populus tremuloides* Michx.) at $1 \times 1\,m^2$ spacing. The east half of each ring (focus of this study) was an aspen monoculture consisting of five clones.

The first full year of fumigation treatments occurred in 1998. Each year, CO_2 and O_3 fumigation began about mid-May with initiation of bud burst and continued through leaf senescence in mid-to-late October. Both CO_2 and O_3 were dispensed only during daylight hours. Target elevated [CO_2] was $560\,\mu L\,L^{-1}$. The 90% confidence interval for elevated [CO_2] was $395 \leqslant 518 \leqslant 642\,\mu L\,L^{-1}$ based on the daytime (07:00–20:00 hours) hourly means for the life of the experiment. Target elevated [O_3] was $1.5 \times$ that of ambient air. Ozone was not dispensed on overcast days. A detailed description of the O_3 fumigation protocol is given in Dickson *et al*. (2000). The daytime, 90% confidence intervals were $14 \leqslant 36 \leqslant 57\,nL\,L^{-1}$ for background [O_3], and $12 \times 48 \times 84\,\mathrm{nL\,L^{-1}}$ for elevated [O_3], based on the hourly means for the life of the experiment including days when ozone was and was not actively dispensed.

Annual growth measurements and volume calculations

We defined a core area in each ring, buffered from the vent pipes by five rows of trees and where elevated [CO_2] and [O_3] were most stable. In September–October of each year, we measured height (using height poles) and diameter (using diameter tape or digital caliper) on every tree in the core area of each ring (3656 trees in 1997 declining to 3226 trees in 2004). From 1997 to 2001, we measured diameters at 3 cm above the soil surface. Because of basal flare, we measured diameters at both 3 and 10 cm above the soil in 2001, and at 10 cm, thereafter. We calculated stem volume from height and diameter measurements assuming the main stem was shaped like a cone. For 2001, we used the mean of the 3 and 10 cm above-soil diameter measurements.

On a subsample of trees from each ring, we calculated the volume of each stem annual height growth increment as that of a frustum and then summed them for each tree. On those same trees, we calculated total tree stem volume simply as that of a cone. The two sets of volume calculations (the frustum summations and the simple cone calculations) had a 1 : 1 relationship and a paired *t*-test indicated no significant difference ($P = 0.81$). Pearson product–moment correlation between individual tree main stem volume (using the simple cone calculations) and tree biomass (above and belowground biomass determined from two destructive harvests of a subsample of trees; King *et al*., 2005) was 0.97. Also, there were no significant treatment-induced changes in above- vs. belowground allocation (King *et al*., 2005). Thus, we used main stem volume calculated as a cone as an appropriate surrogate for total tree biomass in all treatments.

We calculated stand basal area (BA) by converting tree diameters to tree BA, summing for each ring, and dividing by the area occupied by the core trees of each ring. Similarly, we summed tree volumes for each treatment ring and divided by area of ring cores for stand volume.

We treated height, diameter and volume of individual trees as subsamples in each ring. Ring means were the experimental units in a fixed effects, two-factor, complete block ANOVAs ($n = 3$). We analyzed annual tree height, diameter and volume growth curves, and stand BA and volume curves using orthogonal polynomials in repeated measures ANOVA for a fixed-effects, two-factor, complete block experiment with three replicate blocks (Steel & Torrie, 1980; Meredith & Stehman, 1991). We used least-squares regression to fit third-order polynomials to tree and stand volume growth curves for each treatment ring. We used third-order polynomials because they fit the data extremely well and have two inflection points to accommodate sigmoid growth patterns. More traditional exponential growth functions did not fit the data. To determine how growth was changing from year to year, we computed the first and second derivatives of the polynomials and compared among years and treatments using fixed effects ANOVA for a split-plot, two-factor, complete block design ($n = 3$) with year treated as the split-plot factor.

Growth can be considered compound interest on biomass invested; therefore, for meaningful comparisons among treatments in different years, tree and stand volume growth was relativized based on tree size at the beginning of the year. Annual relative volume growth increment (RGI) of each tree was calculated as (Niklas, 1994):

$$\ln(\text{volume at year } t) - \ln(\text{volume at year } t-1). \quad (1)$$

Stand RGI was calculated using stand volume ($\mathrm{m^3\,ha^{-1}}$). Both tree and stand RGI were analyzed with ANOVA for a fixed-effects, two-factor, experiment with three replicate blocks following $\log(y + 1)$ transformation (Steel & Torrie, 1980), with year as a covariate. We were interested in comparing RGI of the treatments to the current ambient control treatment from year to year. Because of large year-to-year changes in the magnitude of RGI, we determined the percent difference between treatment RGI and that of current ambient control:

$$\%\mathrm{RGI_E} = (\mathrm{RGI_E} - \mathrm{RGI_A})/\mathrm{RGI_A} \times 100\%, \quad (2)$$

where $\mathrm{RGI_A}$ is the RGI of the current ambient control treatment and $\mathrm{RGI_E}$ is the RGI of the elevated [CO_2], [O_3] or [$CO_2 + O_3$] treatment. In further discussion, we refer to $\%\mathrm{RGI_E}$ as $\%\mathrm{RGI_{CO_2}}$, $\%\mathrm{RGI_{O_3}}$, or $\%\mathrm{RGI_{CO_2+O_3}}$ depending upon treatment.

Total leaf nitrogen

We harvested one of each aspen clone from each ring in 2000 and 2002 and determined their total leaf N content (see details in King *et al*., 2005). A homogenized subsample of leaves from each tree were oven dried, ground to a powder, and their total N determined using a Carlo Erba CN analyzer (Carlo Erba, Milano, Italy). We then calculated total tree leaf N using the conversion of leaf fresh weight to leaf dry weight and the measured total fresh mass of leaves of each tree.

Growth-meteorological relationships

Meteorological monitoring occurred at a 20 m instrumented tower located on the north end of the site. In the present study, we utilized the following meteorological variables: temperature, relative humidity, and vapor pressure deficit at 5 m; photosynthetic photon flux (PPF); soil temperature at −10 cm, and rainfall. PPF was measured every 5 s, and air temperature, relative humidity and soil temperature were measured every 5 min. Total rainfall was recorded every 30 min. Thirty minute mean values of these measurements were used. Atmospheric vapor pressure deficit was calculated from air temperature and relative humidity. Soil moisture content was recorded every 2 h at −5 to −35, −50 to −80, and −100 to −130 cm in the aspen monoculture of four rings. We stratified meteorological and soil moisture data by day vs. night (daytime defined as 05:30–20:00 hours) and by month (May–October). We calculated mean daytime and nighttime temperature, relative humidity, vapor pressure deficit, wind speed, and soil temperature at −10 cm, mean daytime integrated PPF, and monthly total rainfall. We also calculated annual values of these variables.

We obtained the 30-year mean (1971–2002) monthly values of air temperature and rainfall from the US National Oceanic and Atmospheric Administration data recorded at the Rhinelander-Oneida County Airport, approximately 12 km east of the experiment.

We examined relationships of stratified meteorological data with $\%RGI_{CO_2}$ and $\%RGI_{O_3}$ using scatterplots of all possible combinations. Least-squares regression analysis, with $\%RGI_{CO_2}$ and $\%RGI_{O_3}$ as the dependent variables, confirmed statistical significance of relationships ($P < 0.05$). Regressions with PAR and temperature as the independent variables were forced through zero assuming no growth when they equal zero. In cases where a particular stratum of meteorological data correlated well with $\%RGI_{CO_2}$ or $\%RGI_{O_3}$ we statistically compared it with RGI of the other treatments to eliminate chance relationships. We found that a second-order polynomial equation provided the best fit for all significant relationships. We did not consider polynomials above second order because R^2 approaches 1 as the power of the polynomial approaches $n-1$.

Results

Tree and Stand Growth

After 7 years of growth in the treatments, elevated $[CO_2]$ increased ($P < 0.05$) mean height, diameter and stem volume of aspen trees by 10.9%, 15.7%, and 20.1%, respectively, whereas elevated $[O_3]$ decreased ($P < 0.05$) them by 11.2%, 7.8%, and 28.7%, respectively, compared with the current ambient control (Fig. 1, Table 1). Effects of both $[CO_2]$ and $[O_3]$ were negated when present in combination. Likewise, stand BA and volume were significantly greater in elevated $[CO_2]$ and lower in

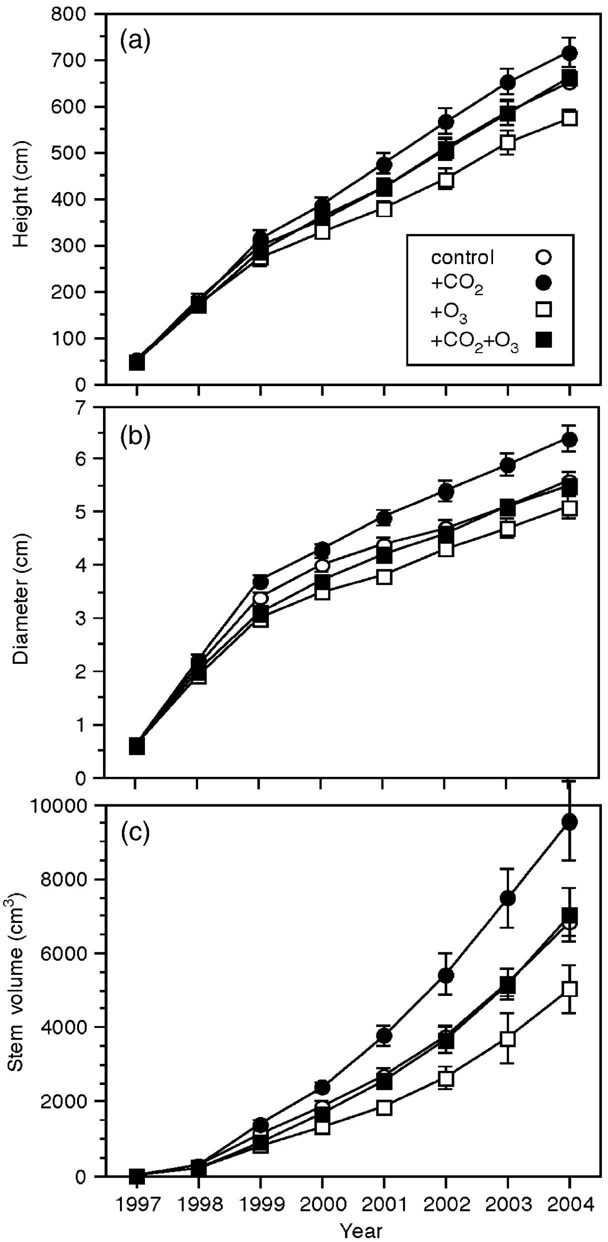

Fig. 1 Mean (± SE, $n = 3$) of accumulated stem height, diameter and volume per tree in the aspen free-air CO_2-enrichment experiment. Measurements were conducted at the end of each year; 1998 was the first full year of CO_2 and O_3 treatments. Treatments are: ○, current ambient atmosphere; •, elevated $[CO_2]$ atmosphere; □, elevated $[O_3]$ atmosphere; ■, elevated $[CO_2] + [O_3]$ atmosphere. Replicates averaged 164 trees in 1997 decreasing to 139 trees in 2004.

Table 1 Repeated measures analyses of variance using orthogonal polynomials of trembling aspen growth curves depicted in Figs 1 and 2

		Mean		Linear		Quadratic	
Source of variation	df	MS	*P*	MS	*P*	MS	*P*
Tree height							
Block	2	134	0.83	4278	0.54	6791	0.44
CO_2	1	16	0.66	25 656	0.08	31 492	0.15
Error 1	2	64		2412		5904	
O_3	1	138	0.69	19 629	0.07	35 250	0.11
Error 2	2	639		1501		4580	
$CO_2 \times O_3$	1	65	0.78	169	0.87	54	0.93
Error 3	2	652		4944		5250	
Tree diameter							
Block	2	0.315	0.39	0.142	0.52	0.010	0.68
CO_2	1	2.715	0.10	1.613	0.07	0.011	0.15
Error 1	2	0.335		0.122		0.002	
O_3	1	5.427	0.02	1.374	0.037	0.198	0.03
Error 2	2	0.134		0.053		0.006	
$CO_2 \times O_3$	1	0.215	0.41	0.131	0.45	0.000	0.98
Error 3	2	0.201		0.152		0.022	
Tree volume							
Block	2	2 087 014	0.49	5 432 303	0.54	253 641	0.62
CO_2	1	18 816 748	0.05	22 423 435	0.04	931 332	0.05
Error 1	2	2 026 184		1 064 491		48 332	
O_3	1	22 041 551	0.06	19 629 477	0.06	191 919	0.21
Error 2	2	1 345 667		1 363 940		56 728	
$CO_2 \times O_3$	1	790 173	0.60	742 365	0.68	1666	0.96
Error 3	2	2 031 537		3 194 030		416 646	
Stand basal area							
Block	2	1.07	0.90	1.28	0.86	0.51	0.31
CO_2	1	197.65	0.05	161.01	0.04	0.06	0.55
Error 1	2	11.53		6.38		0.11	
O_3	1	350.21	0.02	170.68	0.03	3.70	0.03
Error 2	2	5.85		4.72		0.10	
$CO_2 \times O_3$	1	7.15	0.49	1.65	0.69	5.66	0.14
Error 3	2	10.06		7.76		0.23	
Stand volume							
Block	2	57.8	0.68	69.7	0.70	7.6	0.63
CO_2	1	1723.6	0.04	1976.5	0.04	61.8	0.03
Error 1	2	80.37		79.1		2.2	
O_3	1	2226.9	0.04	1927.5	0.04	10.0	0.23
Error 2	2	93.2		88.8		3.4	
$CO_2 \times O_3$	1	30.1	0.67	9.4	0.83	7.4	0.53
Error 3	2	125.4		163.8		13.0	

elevated [O_3] compared with control ($P < 0.05$, Fig. 2, Table 1). There was no difference in stand BA or stand volume between the combination treatment and the current ambient control.

An important question is whether CO_2 fertilization or O_3 growth inhibition are sustained over time. We fit third-order polynomials to tree and stand volume growth of each treatment ring by least squares regression ($P < 0.001$, $R^2 > 0.95$) and calculated the first and second derivatives. First derivatives (dv/dt; slopes of the tangent lines representing growth velocity at each year) show that annual tree volume increment and stand volume increment increased for the duration of the experiment in all treatments ($P < 0.05$, Tables 2 and 3). Second derivatives (d^2v/dt^2; year-to-year changes in growth velocity, i.e., growth acceleration) show that annual growth velocity increased at an increasing rate for trees and stands in the current

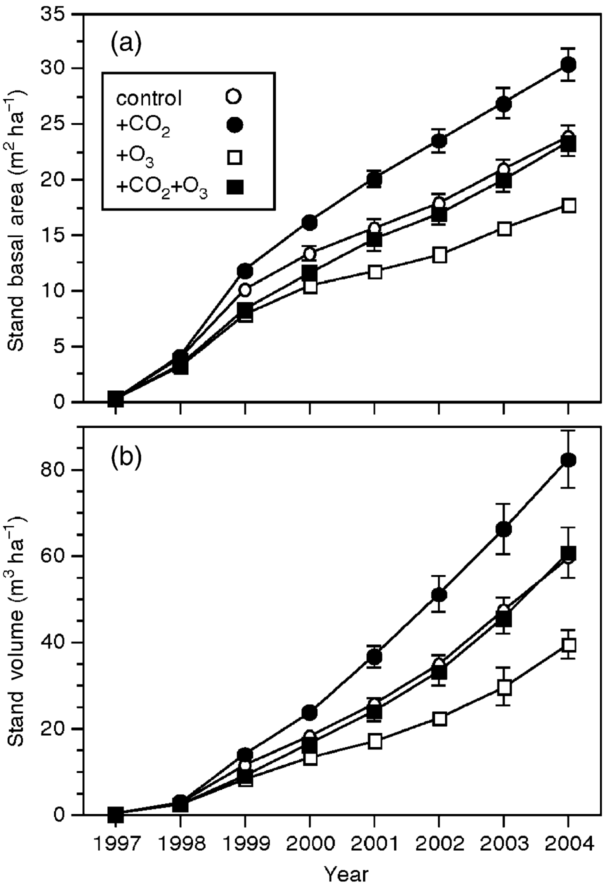

Fig. 2 Mean (± SE, $n = 3$) of accumulated stand basal area and volume in the aspen free-air CO$_2$-enrichment experiment. Treatments are: ○ , current ambient atmosphere; ● , elevated [CO$_2$] atmosphere; □, elevated [O$_3$] atmosphere; ■, elevated [CO$_2$] + [O$_3$] atmosphere. Replicate stands covered 164 m^2 and averaged 164 trees in 1997 decreasing to 139 trees in 2004.

ambient control, elevated [O$_3$], and elevated [CO$_2$] + [O$_3$] treatments. However, trees and stands in the elevated [CO$_2$] treatment had declining d^2v/dt^2. Thus, growth in elevated [CO$_2$] continued to increase each year but at a decreasing rate. We should point out that the second derivative of a third-order polynomial is always a straight line ($y = mx + b$). We used this approach because we favored simplicity for the sake of interpretation over a more complicated (and arbitrary) function. Consequently, the large annual fluctuations in relative growth rates described below do not appear in this part of the analysis.

Following the first full year of CO$_2$ fumigation (1998), annual RGI of trees and stands grown in elevated [CO$_2$] were consistently higher than RGI of trees and stands grown in current ambient conditions (control) through the 2001 growing season (Table 4). The RGI of trees and stands in elevated [O$_3$] were significantly lower than the RGI of control trees during 1998 and 1999. The similarity between RGI of trees and stands for each treatment × year combination indicates that tree removals had negligible impact on stand growth and development (mean mortality plus harvests per ring were: 20 trees in current ambient rings, 22 in elevated [CO$_2$], 34 in elevated [O$_3$], and 22 in elevated [CO$_2$] + [O$_3$]).

We could not compare absolute differences in tree and stand annual RGIs among years because they are confounded by large, age-related declines from 1998 to 2003. For example, the difference in RGI between the current ambient control and the elevated [CO$_2$] treatment in 1999 is 0.21 cm^3 cm^{-3} y^{-1}, compared with the difference of 0.02 cm^3 cm^{-3} yr^{-1} in 2002. We corrected for these age effects by calculating percent differences between the current ambient control and the elevated [CO$_2$], [O$_3$], and [CO$_2$] + [O$_3$] treatments for each year (%RGI$_{\mathrm{CO_2}}$, %RGI$_{\mathrm{O_3}}$, %RGI$_{\mathrm{CO_2+O_3}}$, respectively). Tree %RGI$_{\mathrm{CO_2}}$ and %RGI$_{\mathrm{O_3}}$ were close to zero in 2002 and 2003 indicating little or no difference in growth rate between trees in the treatments and current ambient control for those years. This suggests decline of the CO$_2$ fertilization effect and amelioration of O$_3$-induced growth inhibition, similar to the response of d^2v/dt^2 described above (Table 4). However, before 2001 tree and stand %RGI$_{\mathrm{CO_2}}$, %RGI$_{\mathrm{O_3}}$, and %RGI$_{\mathrm{CO_2+O_3}}$ all exhibited large year-to-year variability with no clear pattern suggesting that other factors were influencing the CO$_2$ and O$_3$ growth responses. We examined several possible explanations including N limitations, water limitations, and interannual variation in a number of climatological variables.

We regressed total foliar N contents of harvested trees against stem volume and found no significant differences ($P > 0.05$) among slopes of the regression lines (Fig. 3). This indicates that N limitations on growth did not differ among treatments.

We also examined daily soil moisture content at three depths. Very rarely did soil moisture in the upper 5 cm of the soil profile drop below field capacity (−0.03 MPa), and at no time did it drop below the permanent wilting point (−1.50 MPa). Also, we found no significant relationships between %RGI$_{\mathrm{CO_2}}$ or %RGI$_{\mathrm{O_3}}$ at the tree and stand levels vs. annual (Fig. 4) or monthly (not shown) rainfall. These results suggest that interannual variation in soil moisture did not modify the CO$_2$ or O$_3$ responses despite relatively low precipitation during the experiment (see below).

Climate variation

We began collecting meteorological data in 1999. July was the warmest month of the growing season each year of the experiment in terms of both air and soil temperature, with the exception of 2003 in which

Table 2 First ($\mathrm{d}v/\mathrm{d}t$) and second ($\mathrm{d}^2v/\mathrm{d}t^2$) derivatives of third-order polynomials fit to tree volume growth curves where v is mean tree stem volume (dm^3) per FACE ring and t is year.

	Current ambient		Elevated CO_2	
	$\mathrm{d}v/\mathrm{d}t$	$\mathrm{d}^2v/\mathrm{d}t^2$	$\mathrm{d}v/\mathrm{d}t$	$\mathrm{d}^2v/\mathrm{d}t^2$
1997	0.472 ± 0.037 a	0.063 ± 0.041 ab	0.319 ± 0.046 a	0.350 ± 0.056 c
1998	0.553 ± 0.043 a	0.099 ± 0.030 ad	0.659 ± 0.030 ab	0.329 ± 0.055 ch
1999	0.669 ± 0.060 abe	0.134 ± 0.020 df	0.978 ± 0.076 bc	0.309 ± 0.055 chi
2000	0.822 ± 0.071 ae	0.170 ± 0.009 cdfh	1.276 ± 0.128 cd	0.288 ± 0.054 chi
2001	1.010 ± 0.072 ef	0.206 ± 0.005 defhi	1.554 ± 0.180 di	0.267 ± 0.053 cehi
2002	1.233 ± 0.063 fh	0.242 ± 0.014 fhi	1.810 ± 0.232 il	0.247 ± 0.052 cfhi
2003	1.493 ± 0.044 hk	0.277 ± 0.025 hi	2.047 ± 0.283 ln	0.226 ± 0.051 hi
2004	1.788 ± 0.014 km	0.313 ± 0.036 ik	2.262 ± 0.333 n	0.205 ± 0.050 i
	Elevated O_3		Elevated $CO_2 + O_3$	
	$\mathrm{d}v/\mathrm{d}t$	$\mathrm{d}^2v/\mathrm{d}t^2$	$\mathrm{d}v/\mathrm{d}t$	$\mathrm{d}^2v/\mathrm{d}t^2$
1997	0.288 ± 0.074 a	−0.023 ± 0.064 a	0.348 ± 0.055 a	0.096 ± 0.035 b
1998	0.382 ± 0.024 a	0.027 ± 0.057 ad	0.464 ± 0.036 ab	0.136 ± 0.037 abd
1999	0.426 ± 0.032 a	0.077 ± 0.050 ade	0.620 ± 0.046 ab	0.175 ± 0.039 bde
2000	0.521 ± 0.069 ae	0.127 ± 0.043 def	0.815 ± 0.078 beh	0.215 ± 0.041 cde
2001	0.666 ± 0.100 ae	0.178 ± 0.036 efh	1.050 ± 0.116 eh	0.255 ± 0.043 ceh
2002	0.861 ± 0.125 ef	0.228 ± 0.030 fhk	1.325 ± 0.157 hk	0.294 ± 0.045 cfhk
2003	1.106 ± 0.143 fh	0.278 ± 0.025 hk	1.639 ± 0.201 km	0.334 ± 0.047 hk
2004	1.402 ± 0.154 hk	0.329 ± 0.020 k	1.993 ± 0.247 mn	0.374 ± 0.049 k

ANOVA indicated significant ($P<0.05$) year effects for $\mathrm{d}v/\mathrm{d}t$ in all treatments, and for $\mathrm{d}^2v/\mathrm{d}t^2$ only in the current ambient treatment. There were significant CO_2 and O_3 main effects for $\mathrm{d}v/\mathrm{d}t$, and the year by treatment interactions were significant for $\mathrm{d}^2v/\mathrm{d}t^2$ ($P<0.05$). Means followed by the same letter are not significantly different ($P>0.05$) for the following contrasts: among first or second derivatives within each year; among years within the first or second derivative of each treatment.
FACE, free-air CO_2-enrichment.

August was the warmest month (Fig. 5). Based on July temperature, the warmest years were 1999 and 2002. The coolest month of each growing season was October. Annual air temperature patterns and daytime temperatures were consistent with the 30-year monthly means.

Monthly rainfall was consistently below the 30-year monthly mean for the duration of the experiment, with the exceptions of May 1999, June and July 2000, and October 2004. 2001 had the greatest cumulative precipitation deficit (30-year mean growing season rainfall minus growing season rainfall) until October. 2003 had the greatest season-long precipitation deficit. The wettest year was 2000, which also had the lowest monthly PPF and net radiation for July and August. The lowest PPF for May, July and August occurred in 2004.

Growth–Climate Relationships

We found a number of significant relationships ($P<0.05$) between specific climatological variables and tree and stand $\%\mathrm{RGI}_{CO_2}$ and $\%\mathrm{RGI}_{O_3}$. Mean daily July PPF was positively related to annual variation in both tree $\%\mathrm{RGI}_{CO_2}$ ($f(x) = 0.075(x^2)-2.759(x)$, $r^2 = 0.56$, Fig. 6a) and stand $\%\mathrm{RGI}_{CO_2}$ ($f(x) = 0.087(x^2)-3.252(x)$, $r^2 = 0.56$, Fig. 7a), and was negatively related to tree $\%\mathrm{RGI}_{O_3}$ ($f(x) = -0.086(x^2) + 3.481(x)$, $r^2 = 0.33$, Fig. 6a) and stand $\%\mathrm{RGI}_{O_3}$ ($f(x) = -0.084(x^2) + 3.740(x)$, $r^2 = 0.29$, Fig. 7a). In addition to July PPF, mean daily temperature during October of the previous year was positively related to tree $\%\mathrm{RGI}_{CO_2}$ ($f(x) = 0.325(x^2)-1.109(x)$, $r^2 = 0.61$, Fig. 6b) and stand $\%\mathrm{RGI}_{CO_2}$ ($f(x) = 0.729(x^2)-4.565(x)$, $r^2 = 0.63$, Fig. 7b), and negatively related to tree $\%\mathrm{RGI}_{O_3}$ ($f(x) = -0.697(x^2) + 5.650(x)$, $r^2 = 0.34$, Fig. 6b) and stand $\%\mathrm{RGI}_{O_3}$ ($f(x) = -0.422(x^2) + 2.731(x)$, $r^2 = 0.20$, Fig. 7b). October 2003 temperature had strong influence on the shape of the regression functions and were not included in the regressions. October 2003 temperature was uncoupled from %RGIs in 2004 probably because the extremely low PPF during July 2004 dominated 2004 growth responses to elevated CO_2 and O_3.

Discussion

Growth responses of these aspen forests after 8 years of treatments were similar to those reported for the same

Table 3 First (dv/dt) and second (d^2v/dt^2) derivatives of third-order polynomials fit to stand volume growth curves (Table 2) where v is stand volume ($m^3\,ha^{-1}$) per FACE ring and t is year.

	Current ambient		Elevated CO_2	
	dv/dt	d^2v/dt^2	dv/dt	d^2v/dt^2
1997	4.54 ± 0.44 a	0.87 ± 0.10 a	3.28 ± 0.62 a	3.78 ± 0.80 b
1998	5.47 ± 0.45 ab	0.99 ± 0.07 a	6.77 ± 0.22 b	3.21 ± 0.65 bd
1999	6.52 ± 0.46 ab	1.12 ± 0.04 a	9.69 ± 0.72 d	2.63 ± 0.49 de
2000	7.70 ± 0.45 bc	1.24 ± 0.02 ah	12.03 ± 1.13 de	2.05 ± 0.34 efa
2001	9.01 ± 0.42 cd	1.37 ± 0.04 ai	13.79 ± 1.38 eh	1.48 ± 0.18 fi
2002	10.44 ± 0.39 de	1.50 ± 0.07 adi	14.98 ± 1.48 h	0.90 ± 0.03 ik
2003	12.00 ± 0.34 ek	1.62 ± 0.10 ad	15.60 ± 1.43 h	0.33 ± 0.13 km
2004	13.69 ± 0.31 k	1.75 ± 0.13 ao	15.63 ± 1.22 hk	−0.25 ± 0.29 m
	Elevated O_3		Elevated $CO_2 + O_3$	
	dv/dt	d^2v/dt^2	dv/dt	d^2v/dt^2
1997	4.60 ± 0.51 a	−0.64 ± 0.53 c	3.74 ± 0.77 a	0.81 ± 0.51 a
1998	4.16 ± 0.09 a	−0.23 ± 0.43 ch	4.68 ± 0.44 ab	1.07 ± 0.46 a
1999	4.13 ± 0.35 a	0.17 ± 0.33 chi	5.88 ± 0.49 bc	1.33 ± 0.40 ab
2000	4.51 ± 0.61 a	0.58 ± 0.24 hil	7.34 ± 0.77 cf	1.59 ± 0.35 abd
2001	5.30 ± 0.79 a	0.99 ± 0.18 ild	9.06 ± 1.06 fd	1.85 ± 0.29 bdio
2002	6.49 ± 0.89 ab	1.04 ± 0.19 ld	11.04 ± 1.32 de	2.12 ± 0.24 bdo
2003	8.10 ± 0.94 bc	1.81 ± 0.25 d	13.29 ± 1.53 e	2.38 ± 0.19 do
2004	10.11 ± 1.00 c	2.21 ± 0.34 do	15.80 ± 1.70 k	2.64 ± 0.14 o

ANOVA indicated significant ($P < 0.05$) year effects for dv/dt and d^2v/dt^2 in all treatments. The $CO_2 \times O_3 \times$ year interactions were significant for dv/dt and d^2v/dt^2. Means followed by the same letter are not significantly different ($P > 0.05$) for the following contrasts: among first or second derivatives within each year; among years within the first or second derivative of each treatment. FACE, free-air CO_2-enrichment.

Table 4 Mean (± SE; $n = 3$) tree and stand annual relative volume growth increment (RGI) calculated as $\ln(\text{vol}_{\text{year 2}}) - \ln(\text{vol}_{\text{year 1}})$ for trembling aspen trees grown under four treatments of atmospheric gasses

		Elevated	Elevated	Elevated
	Control	$[CO_2]$	$[O_3]$	$[CO_2] + [O_3]$
Tree volume RGI ($cm^3\,cm^{-3}\,yr^{-1}$)				
1998	3.82 ± 0.04	3.70 ± 0.19 (−3.1)	3.60 ± 0.11 (−5.8)	3.65 ± 0.11 (−4.6)
1999	1.38 ± 0.05	1.59 ± 0.09 (14.9)	1.32 ± 0.00 (−4.2)	1.38 ± 0.04 (0.2)
2000	0.48 ± 0.02	0.53 ± 0.03 (11.4)	0.49 ± 0.03 (2.1)	0.60 ± 0.06 (25.3)
2001	0.37 ± 0.03	0.45 ± 0.02 (24.6)	0.33 ± 0.03 (−7.0)	0.43 ± 0.02 (18.7)
2002	0.34 ± 0.01	0.36 ± 0.03 (4.7)	0.34 ± 0.04 (1.0)	0.35 ± 0.04 (2.8)
2003	0.32 ± 0.01	0.32 ± 0.01 (0.4)	0.32 ± 0.09 (0.2)	0.34 ± 0.02 (8.4)
2004	0.27 ± 0.02	0.24 ± 0.01 (−11.4)	0.32 ± 0.06 (16.9)	0.31 ± 0.02 (11.5)
Stand volume RGI ($m^3\,m^{-3}\,ha^{-1}\,yr^{-1}$)				
1998	3.83 ± 0.04	3.71 ± 0.18 (−3.0)	3.60 ± 0.12 (−6.0)	3.63 ± 0.12 (−5.1)
1999	1.37 ± 0.05	1.58 ± 0.08 (15.3)	1.32 ± 0.02 (−4.0)	1.38 ± 0.05 (0.7)
2000	0.46 ± 0.02	0.52 ± 0.02 (13.9)	0.47 ± 0.04 (3.0)	0.59 ± 0.05 (28.9)
2001	0.34 ± 0.02	0.43 ± 0.02 (27.5)	0.27 ± 0.02 (−22.0)	0.38 ± 0.03 (12.6)
2002	0.31 ± 0.03	0.33 ± 0.01 (5.1)	0.27 ± 0.03 (−11.9)	0.32 ± 0.04 (2.0)
2003	0.31 ± 0.01	0.26 ± 0.01 (−16.5)	0.25 ± 0.10 (−18.2)	0.32 ± 0.02 (3.9)
2004	0.23 ± 0.01	0.22 ± 0.01 (−3.3)	0.31 ± 0.09 (35.0)	0.29 ± 0.02 (25.7)

Values in parentheses are the % differences in RGI between current ambient control and the elevated $[CO_2]$, $[O_3]$ and $[CO_2] + [O_3]$ treatments calculated from three replicates (referred to as $\%RGI_{CO_2}$, $\%RGI_{O_3}$ and $\%RGI_{CO_2+O_3}$, respectively, in the text). Two-factor ANOVA on RGI following $\log(RGI + 1)$ transformation (Steel and Torrie 1980) with year as a co-variate indicated significant CO_2 main effects ($P = 0.04$).

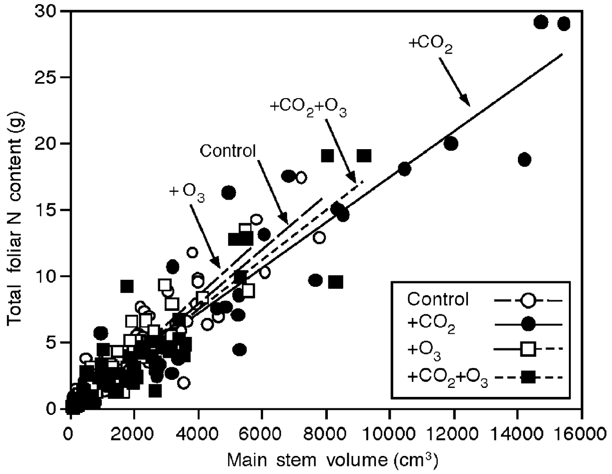

Fig. 3 Total foliage N content determined from destructive harvests of trees in the Aspen free-air CO_2-enrichment experiment. ○, Current ambient air; ●, elevated [CO_2] □, elevated [O_3]; ■, elevated [$CO_2 + O_3$]. There were no significant differences among slopes of the regression equations: Current ambient: $f(x) = 1.89(x) + 0.84$, $r^2 = 0.86$; $+CO_2$: $f(x) = 1.70(x) + 0.14$, $r^2 = 0.93$; $+O_3$: $f(x) = 2.36(x) + 0.12$, $r^2 = 0.90$; $+CO_2 + O_3$: $f(x) = 1.68(x) + 0.51$, $r^2 = 0.78$.

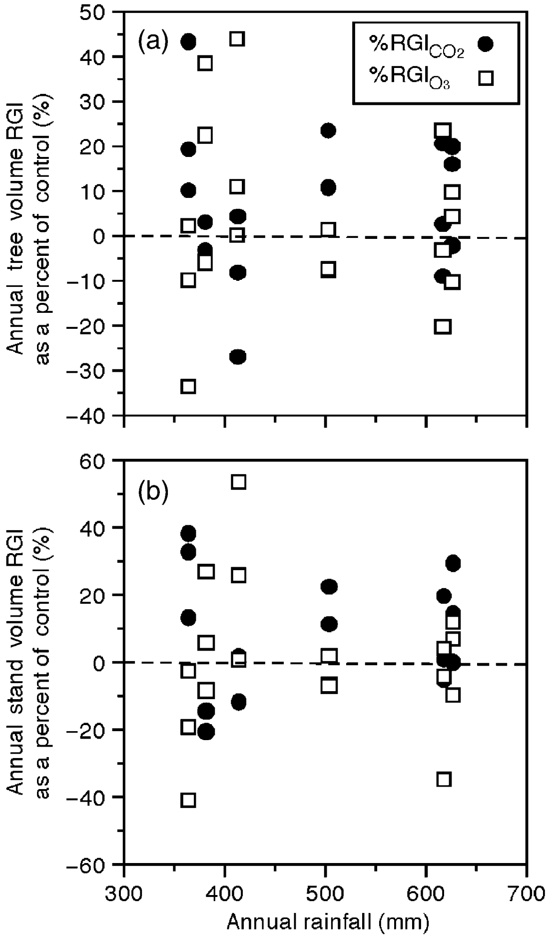

Fig. 4 Scatter plots of annual rainfall vs. the percent difference in annual relative tree volume growth increment (RGI) of aspen forests grown in atmospheres of elevated [CO_2] or [O_3] compared with those in current ambient (control) atmosphere ($n = 3$) at the tree (upper panel) and stand (lower panel) levels. ●, elevated [CO_2]; □, elevated [O_3].

experiment after 3 years of treatment: elevated CO_2 increased growth, and elevated O_3 decreased growth (Isebrands *et al.*, 2001). The combination treatment did not alter growth; the presence of O_3 negated the CO_2 fertilization effect, or the presence of elevated [CO_2] ameliorated the adverse effect of O_3 (Isebrands *et al.*, 2001). Moreover, we found evidence that the growth stimulation by elevated [CO_2] may be decreasing over time. Derivatives of the polynomial growth functions show that, while absolute growth rates continued to increase in all treatments, the annual growth increases under elevated [CO_2] became smaller with each successive year. Decreases in CO_2-induced growth stimulation over time are not uncommon (Tissue *et al.*, 1997; Oren *et al.*, 2001). We examined several possible explanations including treatment-related differences in N limitations, influences of rainfall patterns, and interannual variation in numerous other climatological variables.

Decreases in CO_2-induced growth stimulation are widely hypothesized to be caused by accelerated exploitation of soil resources, particularly N and water, by more rapidly growing plants, and by negative feedbacks on soil N processing (Oren *et al.*, 2001). Consensus from several forest FACE experiments, including the present one, indicates that elevated CO_2 does not decrease soil N mineralization (Zak *et al.*, 2003). This leaves the possibility of tissue N dilution caused by rapidly growing plants in elevated [CO_2]. In our study, relationships between total foliage N content and tree size did not differ among treatments indicating that N limitations on growth did not differ among treatments. Moreover, root-specific uptake of nitrate or ammonium was not affected by elevated [CO_2] or [O_3] (Johansen, 2004). We should point out, however, that differential N limitations among treatments may yet develop as trees continue to grow and affect biogeochemical processes (Luo *et al.*, 2004).

We also expected to find significant influences of soil water availability on both [CO_2] and [O_3] responses. Like soil N limitation, water limitations on atmospheric CO_2 responses are well documented (Schimel *et al.*, 2001), and rainfall was below the 30-year mean for much of the experiment. However, moisture of the upper soil horizon was consistently above field capacity

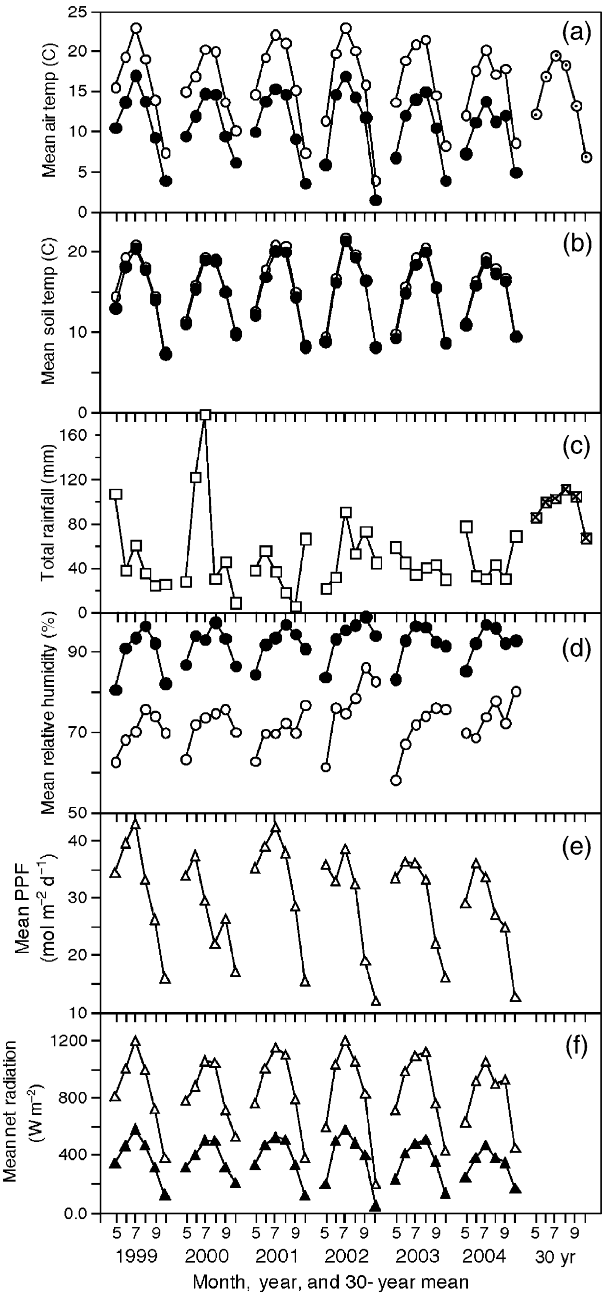

Fig. 5 Monthly climatological variables recorded at the aspen free-air CO_2-enrichment experiment from 1999 to 2004. (a and b) Open circles are mean daytime temperature, closed circles are mean nighttime temperature. Dotted circles are the 30-year daily high temperature means. (c) Monthly rainfall. Crossed symbols are the 30-year means. (d) Open circles are mean daytime relative humidity, closed symbols are mean nighttime relative humidity. (e and f). PPF is photosynthetic photon flux. Open symbols are mean daytime integrated values, closed symbols are mean nighttime integrated values.

(−0.03 MPa) and we found no relationships of growth responses to CO_2 or O_3 with rainfall or soil moisture at any depth.

Instead, we found strong correlation of interannual variability in $\%RGI_{CO_2}$ and $\%RGI_{O_3}$ with other key climatological variables. Specifically, Figs 6C and 7C show how the growth response to elevated [CO_2] and [O_3] paralleled decreasing July PPF from 2001 through 2004, and decreasing previous October temperature from 2001 to 2003. The importance of July PPF over that of rainfall was particularly evident in 1999, the wettest year of the experiment, in which the CO_2 growth response was inhibited by extreme cloudiness rather than stimulated by abundant rainfall. Thus, the trend of declining growth response to elevated [CO_2] (from derivative analysis) was influenced by interannual variability in climate. The relationships demonstrate interactions between interannual climatic variability and growth responses to elevated [CO_2] and [O_3] rather than simple influences of climate on tree or stand growth. These interactions represent a second, less-well-defined linkage between climate and the C cycle. The first linkage is the well-known contribution of atmospheric [CO_2] to the 'greenhouse effect' that makes Earth habitable and is implicated in global warming (Cicerone *et al*., 2001). The second, demonstrated here, is interannual variation in climatic variables interacting with atmospheric [CO_2] to affect growth.

Soil moisture, precipitation, temperature and PPF are all known drivers of ecosystem-atmosphere C exchange and growth. Interannual variability in climate can limit ecosystem C uptake below the potential of the total leaf area (Law *et al*., 2002; Paw U *et al*., 2004). Annual fluctuations in temperature were related to C exchange rates of trembling aspen forests in Canada (Arain *et al*., 2002). Annual growth from tree ring analyses has been correlated with growing season length, early spring temperature, and moisture availability (Peterson & Peterson, 1994; Little *et al*., 1995; Peterson *et al*., 2002). As in the present study, several unrelated climate variables may correlate well with annual growth. For example, annual growth of Douglas-fir (*Pseudotsuga menziesii*) was related to both monthly temperatures of the current year and precipitation during autumn of the previous year (Little *et al*., 1995). However, extremes in one climatic variable can uncouple growth responses from other variables. Growth of Englemann spruce (*Picea Engelmannii*) was positively correlated with summer temperature, but unusually warm July and August temperatures were associated with reduced growth the following year (Peterson & Peterson, 1994). Similarly, annual growth of subalpine fir (*Abies lasiocarpa*) was related to annual precipitation, but that response was limited by unusually high temperatures the previous year (Peterson *et al*., 2002). We found a similar phenomenon with growth response to elevated [CO_2] and [O_3] in which temperature of October 2003 was uncoupled

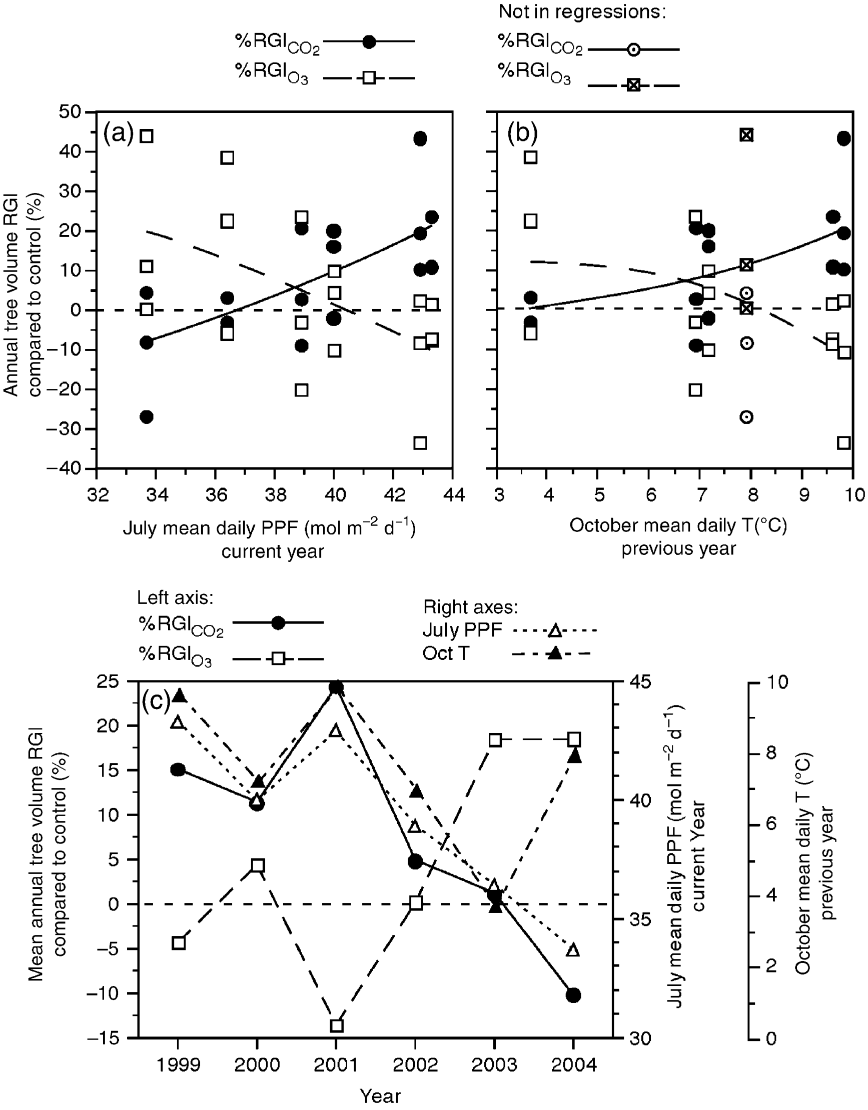

Fig. 6 Significant ($P<0.05$) relationships of specific climatological variables vs. the percent difference in annual relative tree volume growth increment (RGI) of aspen forests grown in atmospheres of elevated [CO_2] or [O_3] compared with those in current ambient atmosphere ($n = 3$, left vertical scale). ●, elevated [CO_2]; □, elevated [O_3]; ⊙, elevated [CO_2] in 2004; ⊠, elevated [O_3] in 2004. In every case, the combination treatment of both gases was not significant and is not shown. In panel c, △, July mean daily photosynthetic photon flux (PPF, right vertical scale); ▲, prior year October mean daily temperature (*T*, far right vertical scale). The apparent high correlation of PPF and *T* is, in part, a consequence of scaling; there is no meteorological explanation for high correlation between July PPF and previous October *T*.

from growth the following year by extremely cool and cloudy (low PPF) conditions during much of 2004.

In order for elevated [CO_2] or [O_3] to affect tree growth, they must directly or indirectly impact the utilization of either newly-fixed or stored C. Probably the most important effects of these gasses on tree growth are their direct action on photosynthetic fixation of CO_2. Instantaneous PPF of 800–1000 μmol photons m^{-2} s^{-1} is needed to saturate the photosynthetic apparatus of trembling aspen (Takeuchi *et al*., 2001). Support of high photosynthesis (and growth) rates requires high daily integrated PPF (Ceulemans & Impens, 1983). Interactive effects of PPF with [CO_2] on photosynthesis and growth have been clearly demonstrated (Takeuchi *et al*., 2001; Granados & Körner, 2002; Kubiske *et al*., 2002; Herrick & Thomas, 2003). There is also experimental evidence that high PPF interacts with O_3 exposure to negatively affect growth and physiology of

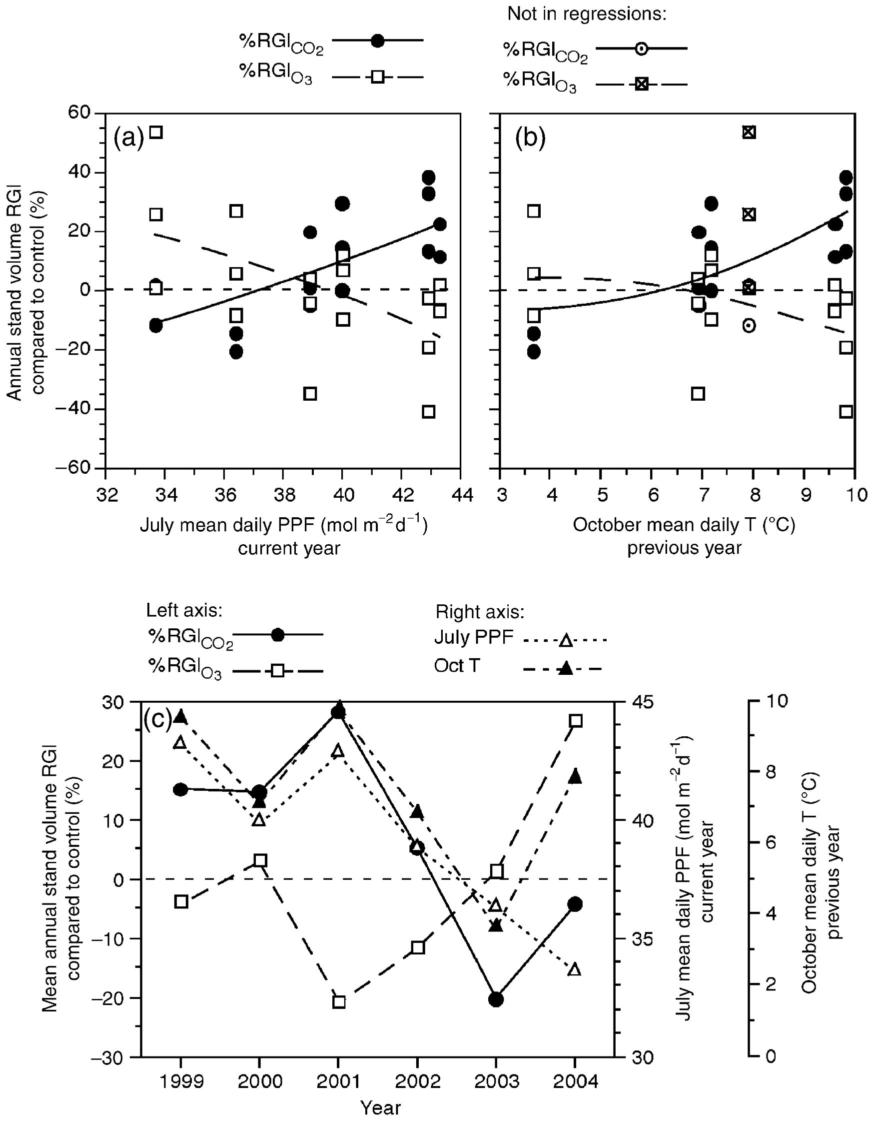

Fig. 7 Significant ($P<0.05$) relationships of specific climatological variables vs. the percent difference in annual relative stand volume growth increment (RGI) of aspen forests grown in atmospheres of elevated [CO_2] or [O_3] compared with those in current ambient atmosphere ($n=3$, left vertical scale). ●, elevated [CO_2]; □, elevated [O_3]; ⊙, elevated [CO_2] in 2004; ⊠, elevated [O_3] in 2004. In every case, the combination treatment of both gases was not significant and is not shown. In panel c, △, July mean daily photosynthetic photon flux (PPF, right vertical scale); ▲, prior year October mean daily temperature (*T*, far right vertical scale). The apparent high correlation of PPF and *T* is, in part, a consequence of scaling; there is no meteorological explanation for high correlation between July PPF and previous October *T*.

Populus spp. (Tjoelker *et al.*, 1993; Wustman *et al.*, 2001). Moreover, days of high PPF are days on which tropospheric O_3 concentration is normally high.

Photosynthesis provides C compounds for several processes that can roughly be grouped as growth, storage, and defense (Dickson, 1989; Herms & Mattson, 1992). Decreased allocation of C to storage can decrease growth the following season in some species (Waring, 1987). *Populus* spp. such as trembling aspen exhibit growth phenology commensurate with changes in utilization of stored and newly fixed C (Dickson & Nelson, 1982). Primary growth of these species begins with a determinate phase in which stored carbohydrates fixed the previous year are used for expansion of preformed, primordial tissues in over-wintering buds (Landhausser & Lieffers, 2003). Indeterminate primary growth often follows the determinate phase, particularly at the terminal shoot, using newly fixed carbohydrates from fully expanded leaves, and ceases by mid-to-late August in Wisconsin (Dickson, 1989). Secondary growth begins shortly after primary shoot extension and continues throughout most of the growing season even after the cessation of primary growth (Dickson, 1989; Landhausser & Lieffers, 2003). Although both indeterminate primary and secondary growth are supported by newly fixed carbohydrates, secondary growth accounts for the majority of volume growth in a given year. Thus, July PPF directly influences the amount of photosynthate available for stem volume growth.

Photosynthetic activity following cessation of growth is primarily allocated to storage (Horwath *et al*., 1994). Given a strong temperature dependence of photosynthesis on temperature (Medlyn *et al*., 2002; Bernacchi *et al*., 2003), it follows that October temperature in the north-temperate latitudes is of major importance in the photosynthetic activity of trees before leaf senescence. This is not a novel concept; Ceulemans & Impens (1983) found that net CO_2 exchange rate of twelve *Populus* clones in 1 year was significantly correlated with shoot growth the following year. We argue, therefore, that October temperature is important in limiting the amount of stored carbohydrate available to support the determinate growth phase the following year, giving rise to the relationships shown in Figs 6 and 7. In our experiment, leaves are photosynthetically active on the trees into October, with the average date of autumn leaf abscission being October 22 (D.F. Karnosky, unpublished data).

Conclusions

In this study, we demonstrated that growth responses of aspen forests to elevated [CO_2] and [O_3] varied considerably over 7 years in a manner that interacted with present-day interannual climate variation. We found no evidence that growth responses to [CO_2] declined systematically with increasing N or water limitations; although, in other circumstances either or both of those resources could influence growth response, as have been documented many times. The amount of photosynthetically active radiation during the current year, and temperature at the end of the previous year, explained 20–63% of the variation in growth responses to elevated [CO_2] and [O_3]. However, the impact of particular climate variables depended upon their association with the growth phenology of the species and would likely differ with species differing in growth phenology. Season-long indices of local climate introduce error into the climate $\times$ CO_2 or O_3 interactions by not focusing on seasonal growth phenology of individual species. Most importantly, our data indicate a feedback between forest C storage (i.e. growth) and atmospheric pollution that changes with climatic conditions. Some predictions of global atmospheric CO_2 build-up have begun to include the potential ameliorating effects of terrestrial ecosystem C storage. Predictions of forest ecosystem responses to increased atmospheric [CO_2] and [O_3] should also include the influence of interannual climatic variability on growth responses to CO_2 and O_3. Clearly more long-term work is needed to more fully understand the complexities of interannual climatic variability interactions with ecosystem responses to elevated [CO_2] and [O_3].

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