

Effects of Elevated Atmospheric CO₂ and/or O₃ on Intra- and Interspecific Competitive Ability of Aspen

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Abstract: Three model communities of trembling aspen (monoculture, and mixed with either paper birch or sugar maple) were grown for seven years in elevated atmospheric CO₂ and O₃ using Free Air CO₂ Enrichment (FACE) technology. We utilized trends in species' importance, calculated as an index of volume growth and survival, as indications of shifting community composition. For the pure aspen communities, different clones emerged as having the highest change in relative importance values depending on the pollutant exposure. In the control and elevated CO₂ treatments, clone 42E was rapidly becoming the most successful clone while under elevated O₃, clone 8 L emerged as the dominant clone. In fact, growth of clone 8 L was greater in the elevated O₃ treatment compared to controls. For the mixed aspen-birch community, importance of aspen and birch changed by -16% and +62%, respectively, in the controls. In the treatments, however, importance of aspen and birch changed by -27% and +87%, respectively, in elevated O₃, and by -10% and +45%, respectively, in elevated CO₂. Thus, the presence of elevated O₃ hastened conversion of stands to paper birch, whereas the presence of elevated CO₂ delayed it. Relative importance of aspen and maple changed by -2% and +3%, respectively, after seven years in the control treatments. But in elevated O₃, relative importance of aspen and maple changed by -2% and +5%, respectively, and in elevated CO₂ by +9 and -20%, respectively. Thus, elevated O₃ slightly increases the rate of conversion of aspen stands to sugar maple, but maple is placed at a competitive disadvantage to aspen under elevated CO₂.

Key words: Sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), global change, growth.

Introduction

Global atmospheric CO₂ has increased by ~30% since the pre-industrial era primarily due to steadily increasing fossil fuel emissions (Keeling et al., 1995; IPCC, 2001; Stott and Kettleborough, 2002). Similarly, emissions of oxidized nitrogen (NO_x)

and volatile organic compounds (VOC) from fossil fuel combustion have increased background levels of tropospheric O₃ by 36–70% during the same time period (IPCC, 2001; Brasseur et al., 2001). While tropospheric O₃ is highly variable across the landscape, Fowler et al. (1999) suggest that nearly a quarter of the earth's forests are at risk from peak concentrations of 60 ppb O₃ or greater. They further predict nearly half of the earth's forests will be subjected to peak concentrations exceeding 60 ppb by the year 2100. There is little doubt, then, that large areas of the world's forests will soon be facing elevated levels of these two pollutants, which generally act in diametrically opposing manners with regard to plant growth (Karnosky et al., 2003 a).

The Aspen FACE experiment was established in northern Wisconsin in 1997 to examine the long-term interacting effects of these two greenhouse gases on ecosystem structure and function of northern hardwood model ecosystems consisting of multi-clonal monocultures of aspen (*Populus tremuloides* Michx.), mixed aspen-birch (*Betula papyrifera* Marsh.), or mixed aspen-maple (*Acer saccharum* Marsh.). Over the nearly decade-long study, we have reported on a number of ecosystem-level responses including net primary productivity (King et al., 2005), differences in clonal competitiveness (McDonald et al., 2002) and growth (Isebrands et al., 2001; Karnosky et al., 2005; Kubiske et al., 2006), and trophic interactions involving important saprophytic fungi (Karnosky et al., 2002) and herbivores (Percy et al., 2002; Holton et al., 2003). Furthermore, we have documented that the responses of elevated CO₂ and/or O₃ on dominant species cascade through the ecosystem as manifested by demonstrable changes in soil carbon accumulation (Loya et al., 2003) and soil microbial populations (Phillips et al., 2002). In this regard, forest ecosystem functioning is ultimately determined by the particular genetic composition of the dominant tree species present and the suite of physiological characteristics that each taxon possesses. In addition to the direct responses of individual taxa to increasing CO₂ and O₃, it is the potential changes in species composition, therefore, that will ultimately drive the most important changes in ecosystem functions (for example Schweitzer et al., 2004).

The impacts of CO₂ and/or O₃ on community-level processes remain elusive research needs (Karnosky, 2003) largely because the responses of individual plants to environmental stressors are poor predictors of their responses to those stressors in a competitive situation (Saxe et al., 1998; Poorter and

Navas, 2003; Laurence and Andersen, 2003). The model communities of the Aspen FACE experiment were designed to address three specific questions with respect to competitive interactions: 1) Will clones or species that display ozone sensitivity as individual plants be placed at a competitive disadvantage to those that are more ozone-tolerant as individuals? 2) Will clones or species that exhibit a strong growth response to elevated CO₂ as individual trees develop a competitive advantage over those that are less responsive as individuals? 3) In the presence of elevated O₃, will the competitive interactions between ozone-sensitive and ozone-tolerant clones or species be modified by elevated CO₂? In this paper, we evaluate how elevated CO₂ and/or O₃ affect the relative competitiveness of five clones in an aspen monoculture and aspen in mixed aspen-birch and aspen-maple communities after seven years of pollutant exposure.

Materials and 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 Oneida Co., Wisconsin, USA (45.6°N, 89.5°W). The soil is mixed, frigid, coarse loamy Alfic Haplorthod. A 30-cm clay loam plough layer grades into sandy loam above a stratified sand and gravel substratum. The site was cultivated for crops from the 1920s until 1972. From 1972 until 1996, the site served as a research facility for the U.S. Forest Service.

In 1996–1997, twelve 30-m diameter treatment rings were constructed to deliver elevated concentrations of atmospheric CO₂ and O₃ to the interior of the rings at canopy height (Hendrey et al., 1999). The design of the experiment was a full-factorial, randomized complete block design with three replicates. In 1997, the treatment rings were planted at 1 × 1 m spacing with rooted cuttings of five clones of trembling aspen, and open-pollinated seedlings of paper birch and sugar maple. The aspen monoculture consisted of five clones that have been studied previously for responses to elevated CO₂ and O₃ (Karnosky et al., 1996; Kubiske et al., 1998). In general, it was previously reported that aspen clones 271, 216, and 259 were relatively tolerant, intermediate, and sensitive in terms of O₃ sensitivity (Karnosky et al., 1996), and clones 42E and 8 L were relatively more and less responsive, respectively, to elevated CO₂ (Kubiske et al., 1998). Aspen in the mixed communities was comprised entirely of clone 216. The east half of each ring was aspen monoculture, northwest quarter of each ring was aspen-maple mixed (1 : 1) community, and the southwest quarter was aspen-birch (1 : 1) mixed community. Aspen clones were planted as pairs of ramets (i.e., *clone* refers to a population of identical genotypes, *ramet* refers to a single individual plant belonging to a clone) of each clone, randomly distributed throughout the 1 × 1 m grid. Aspen-birch and aspen-maple were planted in an alternating pattern throughout the 1 × 1 m grid.

The first full year of fumigation treatments occurred in 1998. Each year, CO₂ and O₃ fumigation began about mid-May with initiation of bud burst and continued through leaf senescence in mid- to late October. Target-elevated [CO₂] was 560 μl l⁻¹ and target-elevated [O₃] was 1.5 × that of ambient air. Carbon

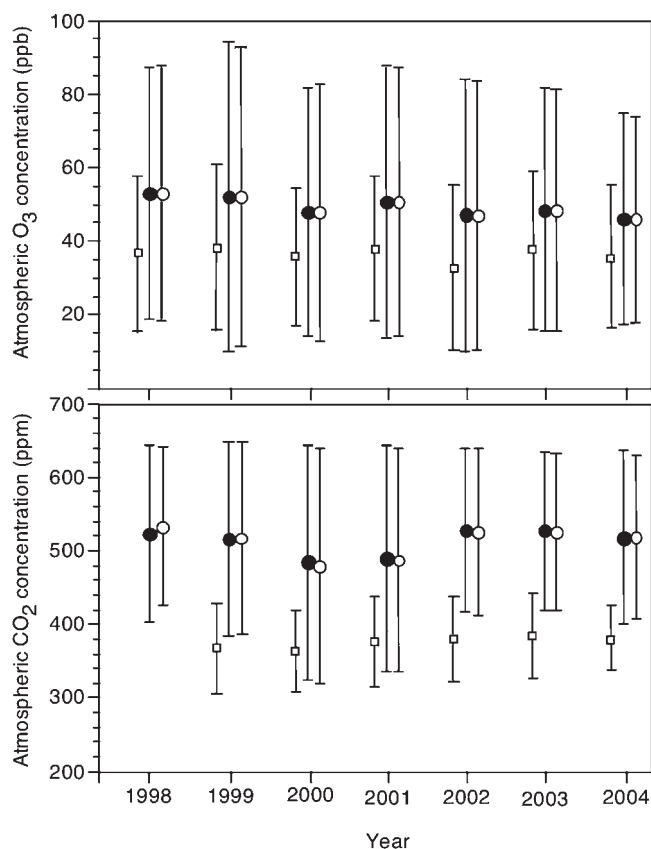


Fig. 1 Hourly mean atmospheric CO₂ and O₃ concentrations in the twelve treatment rings of the Aspen FACE experiment during daylight hours (8:00–20:00 h). Small squares are ambient CO₂ or O₃, filled circles are elevated CO₂ only or O₃ only treatments, and open circles are the CO₂ or O₃ concentrations in the elevated CO₂ + O₃ treatments. The vertical lines represent the 90% confidence intervals for 1-hour means.

dioxide and O₃ fumigations occurred only during daylight hours from bud burst until leaf senescence. Ozone fumigation occurred when conditions were appropriate for normal O₃ buildup in the troposphere. Ozone was not delivered when maximum temperatures were projected to be less than 15 °C or when plants were wet from fog, dew or rain events. The 90% confidence limits for hourly CO₂ and O₃ concentrations are shown in Fig. 1.

Annual growth measurements and importance value calculations

A central “core” area was identified in each ring where gas concentrations were the most stable. The core areas consisted of about 307 trees in each ring, and were encircled by 5–6 rows of trees. In September–October of each year, height (using height poles) and diameter (using diameter tape or digital calipers) were measured on every tree in the core area of each treatment ring. From 1997 to 2001, diameters were measured at 3 cm above the soil surface. Because of basal flare of the tree stems, diameters were measured at both 3 and 10 cm above the soil in 2001, and after 2001 they were measured only at 10 cm.

Table 1 Mean (\pm se) tree heights (cm) when planted in 1997 and after 7 years of growth in elevated CO₂ and O₃ treatments. There were no significant differences in heights among treatments in 1997. In 1997, aspen clone 271 was significantly taller ($p < 0.05$) than the other four clones, and aspen was significantly taller than maple ($p < 0.05$). 2004 means followed by the same letter in a row or column of a community are not significantly different ($p > 0.05$)

	Control		Elevated CO ₂		Elevated O ₃		Elevated CO ₂ + O ₃	
	1997	2004	1997	2004	1997	2004	1997	2004
Aspen clones								
Clone 8L	36 \pm 6	529 \pm 3 a	30 \pm 3	608 \pm 70 ac	42 \pm 5	610 \pm 62 ac	36 \pm 4	653 \pm 57 d
Clone 42E	40 \pm 7	765 \pm 33 b	48 \pm 1	817 \pm 39 bd	45 \pm 3	627 \pm 7 ac	49 \pm 2	774 \pm 56 b
Clone 216	49 \pm 1	629 \pm 7 c	50 \pm 4	629 \pm 25 c	47 \pm 2	535 \pm 20 a	52 \pm 2	659 \pm 31 cd
Clone 259	40 \pm 2	402 \pm 2 e	44 \pm 3	462 \pm 15 e	43 \pm 4	340 \pm 18 e	40 \pm 4	355 \pm 8 e
Clone 271	64 \pm 6	763 \pm 24 b	71 \pm 4	852 \pm 45 df	67 \pm 7	676 \pm 43 c	67 \pm 5	806 \pm 12 bf
Aspen-birch								
Aspen	46 \pm 5	558 \pm 10 ab	44 \pm 3	636 \pm 45 a	49 \pm 1	504 \pm 15 b	44 \pm 6	649 \pm 51 a
Birch	42 \pm 5	554 \pm 38 ab	41 \pm 2	676 \pm 58 b	41 \pm 1	551 \pm 25 a	40 \pm 1	623 \pm 98 ab
Aspen-maple								
Aspen	35 \pm 1	482 \pm 3 ab	42 \pm 4	573 \pm 22 a	36 \pm 3	461 \pm 50 b	37 \pm 3	536 \pm 66 ab
Maple	14 \pm 1	247 \pm 11 c	15 \pm 1	246 \pm 26 c	12 \pm 1	220 \pm 29 c	17 \pm 2	187 \pm 11 c

Height and diameter measurements were used to calculate tree stem volumes, assuming the main stem was shaped like a cone (see validation of this assumption in Kubiske et al., 2006). In 2001, the mean of the 3 and 10 cm above-soil diameter measurements was used to estimate tree stem volume. Stand volumes were calculated by summing tree stem volumes for each cohort (i.e., each species and aspen clone) and dividing by area occupied by each cohort. Area occupied by each cohort was determined from the number of trees planted in 1997, given that each tree occupied 1 m².

To evaluate the combined effects of growth and mortality, a relative importance (RI) index was calculated for each cohort and each year. RI was calculated from species- or clone-relative volume plus species- or clone-relative numbers:

$$RI = \frac{\text{volume of cohort at time } t}{\text{total volume of ring at time } t} + \frac{\text{number of trees of cohort at time } t}{\text{total number of trees in ring at time } t}$$

Mortality is included in annual changes of relative numbers, but the data were corrected for artificial tree removals such as partial harvests that occurred in 2000 and 2002. The maximum RI for any cohort is 2. To account for differences among clones and treatments in the numbers of ramets planted, RI values were standardized based on the 1997 value: $SRI = RI_t / RI_{1997}$; where RI_t = the RI of year t .

Statistical analyses

For all response variables, each community type was analyzed separately. Tree heights and diameters in 2004 were analyzed with a fixed effects, two-factor, split-plot ANOVA ($n = 3$) with clone or species as the split-plot factor. Tree volumes were analyzed for all years using orthogonal polynomials in repeated measures ANOVA for a fixed effects, two-factor, split-plot experiment with three replicate blocks and with clone or species as the split-plot factor (Steel and Torrie, 1980; Meredith and Stehman, 1991). Mortality functions were analyzed with a

Gehan-Wilcoxon non-parametrics test (Pyke and Thompson, 1986).

Relative importance values, and standardized RIs (SRIs), were analyzed using a split-plot repeated measures ANOVA with year as the split-plot factor (Moser et al., 1989). A separate model was run for each treatment to examine differences among clones. In cases where a clone had a significant year effect, another ANOVA model was used to compare treatments for that specific clone. This approach was more straightforward than the much more complicated repeated measures model that included all treatment, clone, and time factors. The RI and SRI data were transformed as $2\arcsin(\sqrt{|y|})$ (Steel and Torrie, 1980).

Results

Growth

There were no differences ($p > 0.05$) in height or diameter among treatments for any species or clone when the trees were planted in 1997 (Tables 1, 2). As of 2004, mean height and diameter of all aspen clones combined was significantly greater in +CO₂ (716 \pm 32 cm and 6.4 \pm 0.2 cm, respectively) compared to control (651 \pm 15 cm and 5.6 \pm 0.1 cm, respectively) ($p < 0.05$), but CO₂ effects on height and diameter of individual aspen clones were not statistically significant ($p > 0.05$). In contrast, after seven years of growth in +O₃, aspen clones 42E, 216, and 271 had decreased heights and diameters ($p < 0.05$) compared to controls. Aspen clone 8L, however, had increased height and diameter growth (by 15 and 25%, respectively) in +O₃ compared to control, but the differences were not statistically significant. 2004 heights and diameters of aspen clones in the combination treatment did not differ from those in control treatment except for clone 8L, which had 24% greater ($p < 0.05$) height. Ramets of aspen clone 259 were the smallest and those of clone 271, the largest trees in the aspen monoculture in every treatment.

Table 2 Mean (\pm se) tree diameters (cm) when planted in 1997 and after 7 years of growth in elevated CO₂ and O₃ treatments. There were no significant differences in diameters among treatments in 1997. In 1997, aspen clone 271 was significantly larger ($p < 0.05$) than the other four clones, and aspen was significantly larger than maple ($p < 0.05$). 2004 means followed by the same letter in a row or column of a community are not significantly different ($p > 0.05$)

	Control		Elevated CO ₂		Elevated O ₃		Elevated CO ₂ + O ₃	
	1997	2004	1997	2004	1997	2004	1997	2004
Aspen Clones								
Clone 8L	0.4 \pm 0.1	4.6 \pm 0.2 a	0.4 \pm 0.0	5.1 \pm 0.9 ac	0.5 \pm 0.1	5.5 \pm 0.5 af	0.4 \pm 0.0	5.2 \pm 0.5 ac
Clone 42E	0.5 \pm 0.1	6.1 \pm 0.4 cd	0.5 \pm 0.0	6.7 \pm 0.4 d	0.5 \pm 0.0	5.1 \pm 0.1 af	0.6 \pm 0.0	5.9 \pm 0.3 ade
Clone 216	0.6 \pm 0.0	5.6 \pm 0.1 c	0.7 \pm 0.0	5.8 \pm 0.2 c	0.6 \pm 0.0	4.8 \pm 0.2 a	0.7 \pm 0.0	5.6 \pm 0.4 cd
Clone 259	0.6 \pm 0.0	3.8 \pm 0.0 b	0.6 \pm 0.0	4.8 \pm 0.1 a	0.7 \pm 0.1	3.6 \pm 0.2 b	0.6 \pm 0.0	3.7 \pm 0.0 b
Clone 271	0.7 \pm 0.0	6.5 \pm 0.3 e	0.8 \pm 0.0	7.6 \pm 0.2 e	0.7 \pm 0.1	5.8 \pm 0.3 f	0.7 \pm 0.0	6.8 \pm 0.1 e
Aspen-birch								
Aspen	0.6 \pm 0.0	5.1 \pm 0.0 ab	0.5 \pm 0.0	6.2 \pm 0.2 ac	0.6 \pm 0.0	4.6 \pm 0.1 b	0.6 \pm 0.1	5.4 \pm 0.1 ab
Birch	0.5 \pm 0.1	5.6 \pm 0.3 a	0.6 \pm 0.0	7.0 \pm 0.9 c	0.5 \pm 0.0	5.8 \pm 0.3 abc	0.5 \pm 0.0	6.0 \pm 0.6 ac
Aspen-maple								
Aspen	0.5 \pm 0.0	5.2 \pm 0.0 ab	0.6 \pm 0.0	6.6 \pm 0.2 b	0.5 \pm 0.0	4.9 \pm 0.6 a	0.5 \pm 0.0	6.0 \pm 0.5 b
Maple	0.3 \pm 0.0	2.5 \pm 0.1 c	0.3 \pm 0.0	2.1 \pm 0.2 c	0.3 \pm 0.0	2.2 \pm 0.2 c	0.3 \pm 0.0	2.0 \pm 0.2 c

By 2004, both species in the aspen-birch community had greater height (by 14 and 22%, respectively) and diameter growth (22 and 25%, respectively) in +CO₂ compared to controls, but only birch diameter was statistically significant ($p < 0.05$). In the aspen-maple community, aspen had 19% greater height and 27% greater diameter in +CO₂ than in controls (not significantly different). There were no significant differences between height and diameter in +O₃ or CO₂+O₃ versus control for either of the mixed species communities.

Volume growth of the five aspen clones was significantly increased by elevated CO₂ (significant CO₂ main effect, Table 3 and Fig. 2). Elevated O₃ had differential effects on volume growth among the aspen clones (significant clone within O₃ treatment effects). This significant clone within O₃ treatment interaction was due to the response of clone 8L in +O₃. Whereas the other four clones each had decreased volume growth in +O₃ compared to control, clone 8L had no decrease in volume growth. In the control, +CO₂ and +CO₂+O₃ treatments, clones 42E and 271 had the greatest volume growth, followed by clones 8L and 216. Clone 259 had the least amount of volume growth in any treatment. However, in +O₃, clones 8L and 271 had the greatest volume growth, followed by clones 42E and 216 and then clone 259.

Volume growth in the aspen-birch community was the most responsive to elevated CO₂ (Table 3, Fig. 3). The species \times CO₂ interaction for volume growth was not significant; nonetheless, volume of birch trees in +CO₂ was 89% greater than in the control treatment, compared to 60% for the aspen trees in that community. In +O₃, aspen volume growth was 25% less compared to controls, whereas birch volume growth was only 5% less compared to controls.

In the aspen-maple community, volume growth of aspen trees was significantly greater than that of maple in all treatments (Table 3, Fig. 4). There was a significant species within CO₂ treatment effect because aspen had significantly greater vol-

ume growth in +CO₂ compared to controls ($p < 0.05$) whereas maple did not. Interestingly, while aspen clone 216 had decreased volume growth with +O₃ in the aspen monoculture and the aspen-birch community, it was not significantly affected by +O₃ in the aspen-maple community.

Mortality

In the aspen monoculture, aspen clone 271 had the lowest mortality ($p < 0.05$) of all treatments (Fig. 5). Clone 259 had the most mortality in all treatments, except for +CO₂+O₃, in which clone 259 mortality was the same as that for clones 8L and 42E ($p > 0.05$). Compared to the control, clone 42E had less ($p < 0.05$) mortality in +CO₂, and clone 259 had more ($p < 0.05$) mortality in +CO₂ and +O₃.

In the aspen-birch community, aspen had significantly more mortality than birch in all treatments (Fig. 6). Birch mortality was similar across all treatments, but aspen had greater mortality ($p < 0.05$) in +CO₂ compared to the control. In the aspen-maple community (Fig. 7), aspen had more mortality than maple in the control treatment, but maple had more than aspen in +CO₂. Aspen had significantly less mortality, and maple more mortality ($p < 0.05$) in +CO₂ than in the control treatment.

Importance values

Relative importance values of the five aspen clones did not change with time in the control or +CO₂ treatments (Figs. 8A, B). In those treatments, clones 271 and 216 had higher importance values than the other clones because of greater numbers of ramets planted. In +O₃, clone 259 had significantly decreasing RI (Fig. 8C, $p < 0.05$). Clone 259 exhibited downward trends in RI in the other treatments, but these were not statistically significant ($p > 0.05$). To account for different numbers of ramets planted for each clone and treatment, RI was standardized based on the initial RI in 1997 (Figs. 8E–H). In the control

Table 3 Repeated measures analyses of variance of volume growth of co-occurring trembling aspen clones (Cln), co-occurring trembling aspen and paper birch, and co-occurring trembling aspen and sugar maple grown in elevated CO₂, elevated O₃, and their combination. Volume growth curves are depicted in Figs. 2–4, respectively

	df	Mean MS	<i>p</i>	Linear MS	<i>p</i>	Quadratic MS	<i>p</i>
Aspen clones (Fig. 2)							
CO ₂	1	76064136	0.05	88978680	0.05	3210441	0.05
Error 1	2	4398346		4590438		173119	
O ₃	1	4918906	0.13	47463355	0.12	639358	0.10
Error 2	2	7724846		6829091		79671	
CO ₂ × O ₃	1	917612	0.79	400990	0.88	140963	0.77
Error 3		9880297		13065749		1241928	
Cln	24	135675449	0.00	140792277	0.00	7323199	0.00
Cln(CO ₂)	4	7702253	0.06	9170728	0.06	401538	0.19
Cln(O ₃)	4	9875592	0.03	10891819	0.03	1057460	0.01
Cln(CO ₂ × O ₃)	4	1226163	0.81	1348666	0.82	123969	0.74
Error 4	32	3060474		3577955		247912	
Aspen-birch (Fig. 3)							
CO ₂	1	62798617	0.01	73138274	0.01	3307493	0.00
Error 1	2	8490460		8697941		265316	
O ₃	1	21133030	0.26	17637394	0.23	45397	0.48
Error 2	2	8552411		6222447		61279	
CO ₂ × O ₃	1	10312267	0.03	7473486	0.10	145151	0.47
Error 3	2	353022		919139		182320	
Sp	1	36907990	0.10	30922560	0.14	42805	0.71
Sp(CO ₂)	1	404372	0.85	1000270	0.77	192915	0.44
Sp(O ₃)	1	400027	0.85	344693	0.87	16787	0.82
Sp(CO ₂ × O ₃)	1	4474500	0.54	4749859	0.54	32283	0.75
Error 4	8	10845696		11479126		286483	
Aspen-maple (Fig. 4)							
CO ₂	1	12391912	0.06	13807264	0.07	863822	0.15
Error 1	2	879463		1143575		168916	
O ₃	1	2377445	0.46	1719603	0.48	422	0.93
Error 2	2	2945683		2373506		49896	
CO ₂ × O ₃	1	634986	0.42	355337	0.59	25575	0.73
Error 3	2	613802		892155		162336	
Sp	1	210176470	0.00	213296572	0.00	8361304	0.00
Sp(CO ₂)	1	14176212	0.03	16578002	0.02	1174019	0.01
Sp(O ₃)	1	1373907	0.45	796830	0.54	10952	0.75
Sp(CO ₂ × O ₃)	1	819388	0.55	420420	0.66	46805	0.51
Error 4	8	2137548		1982773		97161	

and +CO₂ treatments, clone 42E had increasing ($p < 0.05$) and clone 259 decreasing ($p < 0.05$) SRIs (Figs. 8E, F). In +O₃, clone 42E had no changes in SRI, rather clone 8L had increasing SRI ($p < 0.05$) with time (Fig. 8G). Thus, clone 8L attained a competitive advantage over the other clones in +O₃. The decrease in SRI of clone 259 in +O₃ was larger than in the other three treatments, indicating that not only is clone 259 a poor competitor in all treatments, but it is particularly sensitive to +O₃. No clone had increasing SRI in the +CO₂+O₃ treatment.

The year within-species effect on RI and SRI was significant for all treatments in the aspen-birch and aspen-maple communities. At the time of planting in 1997, aspen cuttings were sig-

nificantly larger than birch or maple seedlings resulting in larger RIs for aspen in both of those communities (Figs. 9A–D, 10A–D). In all treatments, aspen (of the aspen-birch community) had significant decreases ($p < 0.05$) and birch significant increases ($p < 0.05$) in RI from 1998 to 1999 but with no further changes thereafter (Figs. 9A–D). After 1998, aspen RI was significantly different ($p < 0.05$) from birch RI in +CO₂ for 2004, and in +O₃ for all years except 1999. For SRI, aspen had significant decreases ($p < 0.05$) and birch significant increases ($p < 0.05$) in RI from 1998 to 1999 but with no further changes thereafter in the control, +O₃, and +CO₂+O₃ treatments. SRI of the +CO₂ treatment continued to increase for birch ($p < 0.05$) and decrease for aspen ($p < 0.05$) from 1998 onward.

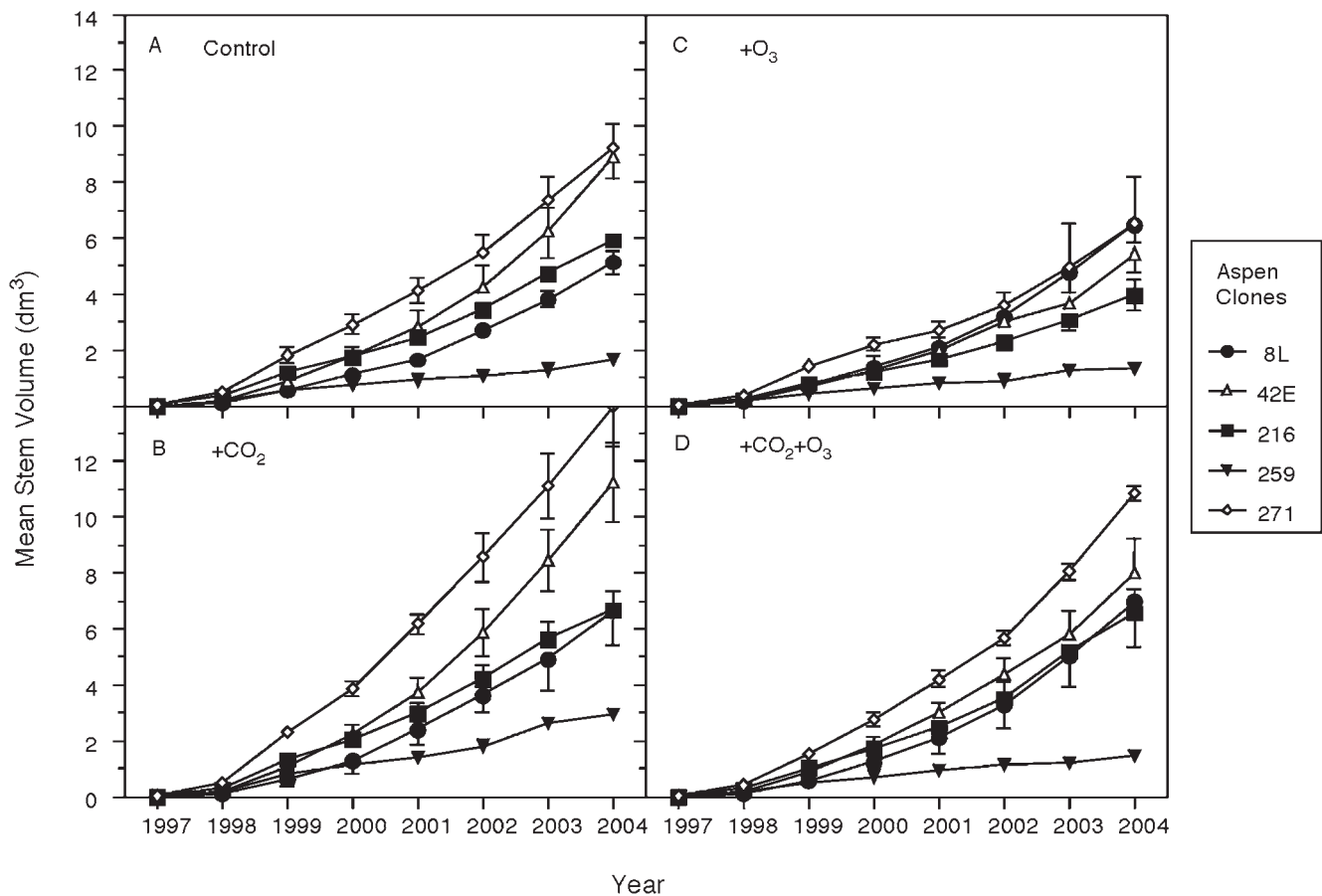


Fig. 2 Annual stem volume growth (mean \pm se) of five, co-occurring trembling aspen clones exposed to ambient air (A: control), elevated CO₂ (B: +CO₂), elevated O₃ (C: +O₃), and elevated CO₂+O₃ (D: +CO₂+O₃).

In the aspen-maple community, the rooted aspen cuttings were substantially larger than the maple seedlings, thus aspen began the experiment with a 2-fold higher RI (Figs. 10A–D). In the control and +O₃ treatments, aspen RI and SRI increased ($p < 0.05$) from 1997 to 1999, but then decreased again to the 1997 level (Fig. 10A). The response was similar for maple in the opposite direction. In +CO₂ and +CO₂+O₃, the importance of aspen increased ($p < 0.05$) and remained high while that of maple decreased ($p < 0.05$) and remained low through 2004.

Discussion

In order to understand and predict how plant community structure and function may be altered by global change, we need to understand how interactions among neighbouring plants within a community will alter the growth, survival, and reproductive fitness. Thus, we urgently need information about how elevated levels of greenhouse gases, such as CO₂ and O₃, influence stand formation and population dynamics, specifically with regard to the identities, numbers, sizes, and reproductive fitness of individuals within single and multiple species stands (Bazzaz and McConnaughay, 1992; McDonald et al., 2002; Kohut, 2003). In this paper, we showed that at the end of seven years of exposure to elevated CO₂ or O₃, the compositions of aspen 5-clone monocultures and of mixed aspen-birch or aspen-maple communities were becoming significantly different among the treatments.

Aspen monocultures

It is well known that growth responses to elevated CO₂ can be very different if the plants are grown in isolation than if they are grown in a monoculture (Poorter and Navas, 2003). In our aspen monoculture study, clone 42E increased in importance more under elevated CO₂ than in control treatments as this clone had increased growth under elevated CO₂. Clone 259 decreased in importance under elevated CO₂ more than in the control treatment because of its inability to compete under the dense canopies produced under elevated CO₂ (Karnosky et al., 2005). Differential growth responses of aspen clones to elevated CO₂ have previously been described in short-term greenhouse (Lindroth et al., 2001) and open-top chamber studies (Kubiske et al., 1998) but this report is the first documentation of increased mortality by a plant taxon under elevated CO₂ because of competition. Together, these studies documenting asymmetric effects of enriched CO₂ on the fitness and genetic structure of aspen populations suggest that rates of ecological succession may be altered (Lindroth et al., 2001) and biodiversity may be compromised under elevated CO₂.

The deleterious effects of elevated O₃ differed among the five aspen clones such that clone 8L competed better in elevated O₃ than it did in the control treatment, and clone 259 did not compete as well, as it had reduced growth and increased mortality. The high degree of O₃ tolerance of clone 8L and ex-

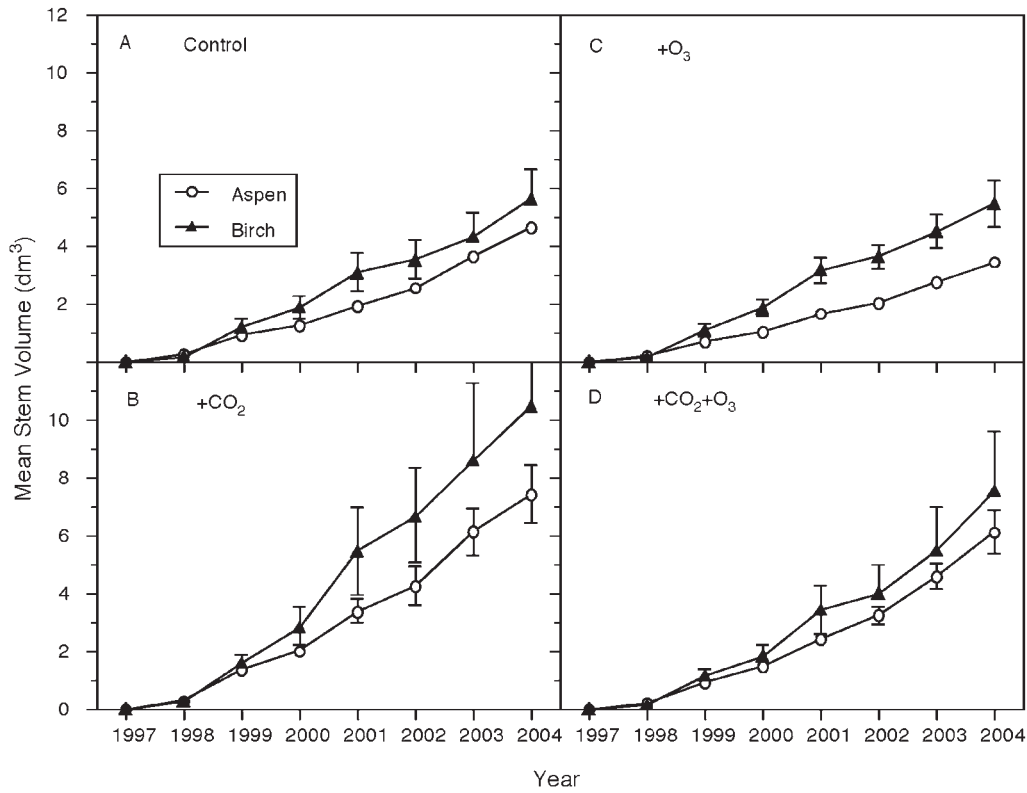


Fig. 3 Annual stem growth (mean \pm se) of co-occurring trembling aspen and paper birch trees exposed to ambient air (A: control), elevated CO₂ (B: +CO₂), elevated O₃ (C: +O₃), and elevated CO₂+O₃ (D: +CO₂+O₃).

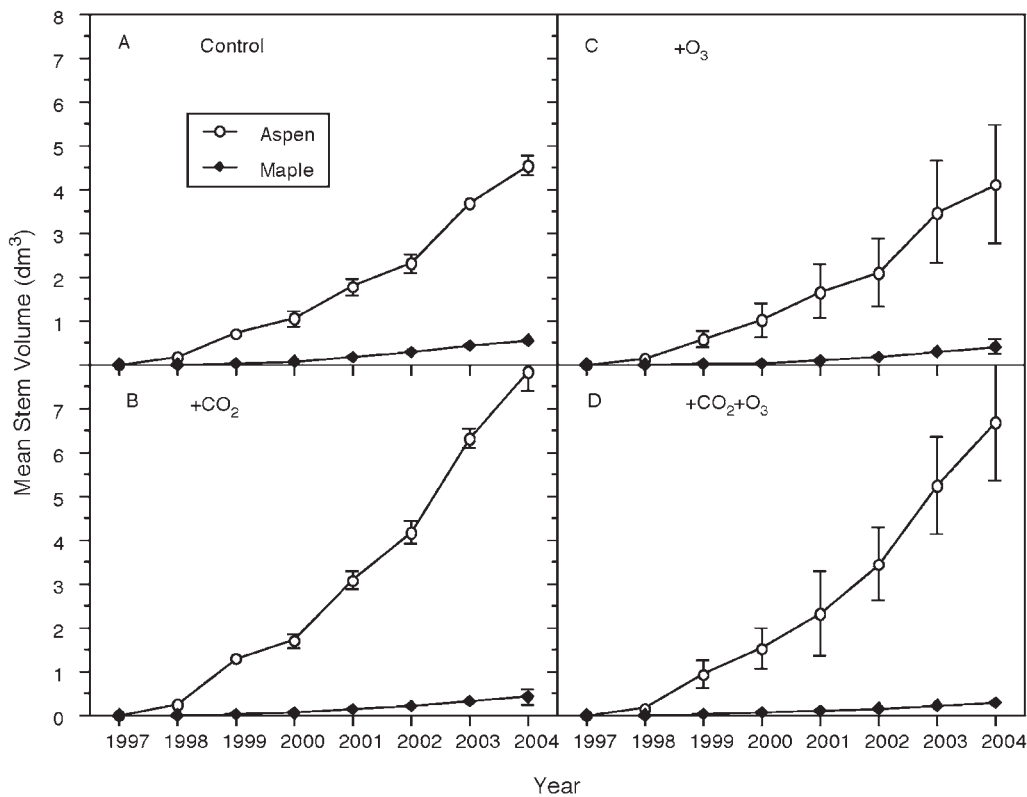


Fig. 4 Annual stem growth (mean \pm se) of co-occurring trembling aspen and sugar maple trees exposed to ambient air (A: control), elevated CO₂ (B: +CO₂), elevated O₃ (C: +O₃), and elevated CO₂+O₃ (D: +CO₂+O₃).

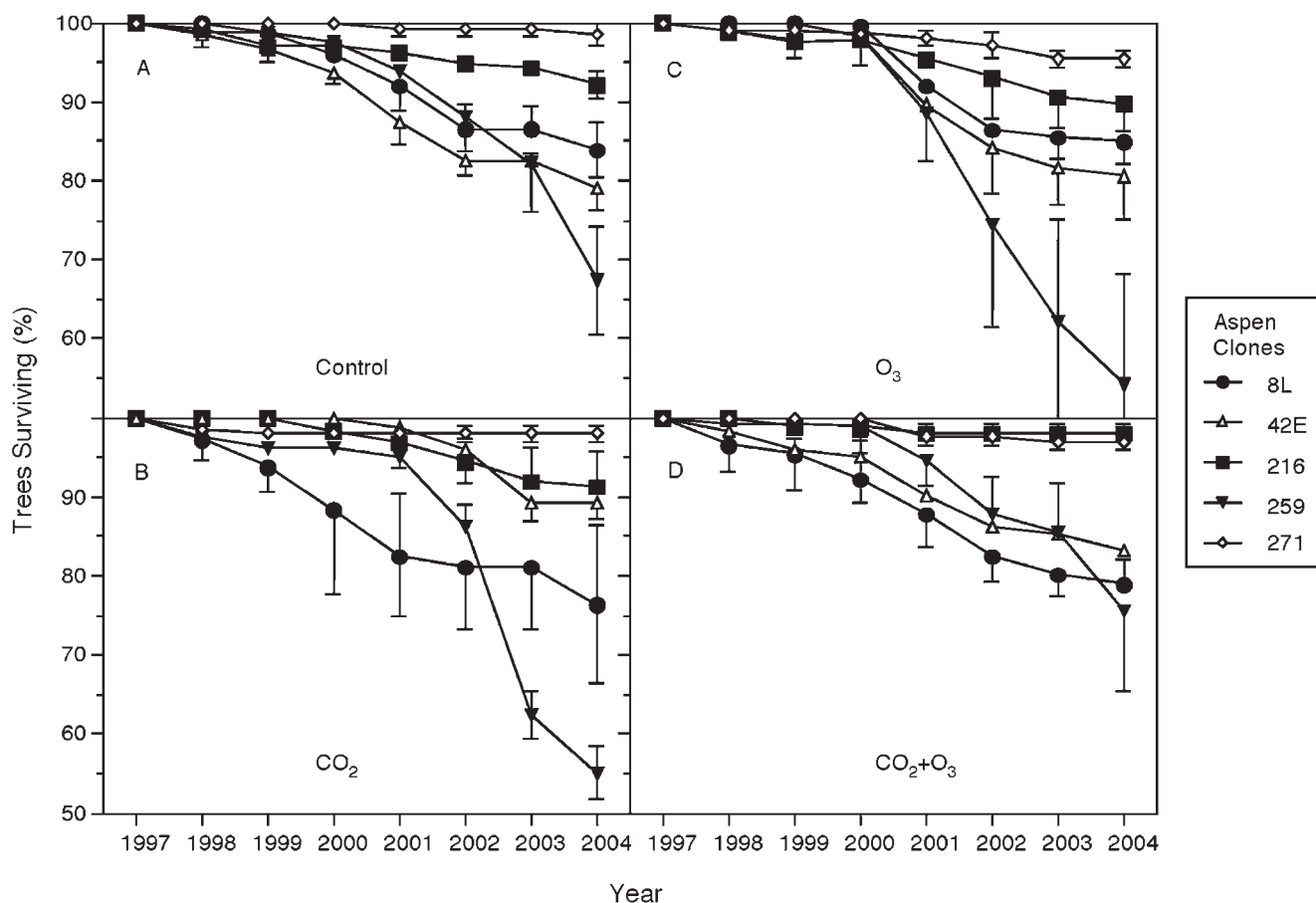


Fig. 5 Survival (mean \pm se) of five, co-occurring trembling aspen clones exposed to ambient air (A: control), elevated CO₂ (B: +CO₂), elevated O₃ (C: +O₃), and elevated CO₂+O₃ (D: +CO₂+O₃).

tre O₃ sensitivity of clone 259 have been previously reported by our group (Karnosky et al., 1996; Isebrands et al., 2001; Karnosky et al., 2005). Intraspecific changes in fitness caused by elevated O₃ have previously been reported for white pine (Karnosky, 1981) and aspen (Karnosky et al., 2003 b). Together, this research supports the hypothesis that elevated O₃ can influence the first stage of natural selection via elimination of sensitive genotypes, as previously suggested by Berrang et al. (1986, 1989, 1991).

Mixed communities

Elevated levels of CO₂ and O₃ can also influence community species composition (Miller, 1973; Arbaugh et al., 2003; Grams et al., 2002; Liu et al., 2004). In our study, competition with other species in elevated CO₂ influenced aspen growth more than the direct effects of elevated O₃. When aspen was grown with birch in elevated CO₂, it had increased mortality compared to the control; but when grown with maple in elevated CO₂, it had less mortality compared to the control. Aspen mortality in elevated O₃, as with birch and maple, did not differ from the control in either of those communities. Our results suggest that in elevated CO₂ aspen is competitively advantaged with both sugar maple and paper birch. However, under elevated O₃, aspen is competitively disadvantaged compared to these two species.

Conclusions

At the community level, previous studies suggest that good competitors may be afforded an added advantage in elevated CO₂, and poor competitors have an added disadvantage in elevated O₃. Whereas, in ordinary circumstances, spruce trees out-compete beech for N, elevated CO₂ stimulates the competitive ability of spruce while elevated O₃ inhibits the competitive ability of beech (Kozovits et al., 2005). Similarly, grass species with the greater propensity for light harvesting benefited more from elevated CO₂ than their competitors (Teyssonneyre et al., 2002). This idea was also identified by McDonald et al. (2002) who assessed CO₂ and O₃ effects on growth vis-à-vis competitive advantage or disadvantage of aspen trees. Aspen trees with a competitive advantage (identified as such by being larger) over their immediate neighbours benefited more from elevated CO₂ than their neighbours, whereas those with a competitive disadvantage were strongly affected by elevated O₃. Indeed, Poorter and Navas (2003) found that relative growth rate (RGR) in current ambient CO₂ was positively related to the RGR response to elevated CO₂ across 179 woody and herbaceous species. Our study is somewhat consistent with this idea. For example, the poorest competitor of the five aspen clones, clone 259, was more strongly inhibited in elevated O₃ than the other clones. A surprising result was the improved growth rate and competitiveness of clone 8L in elevated O₃ compared to the control.

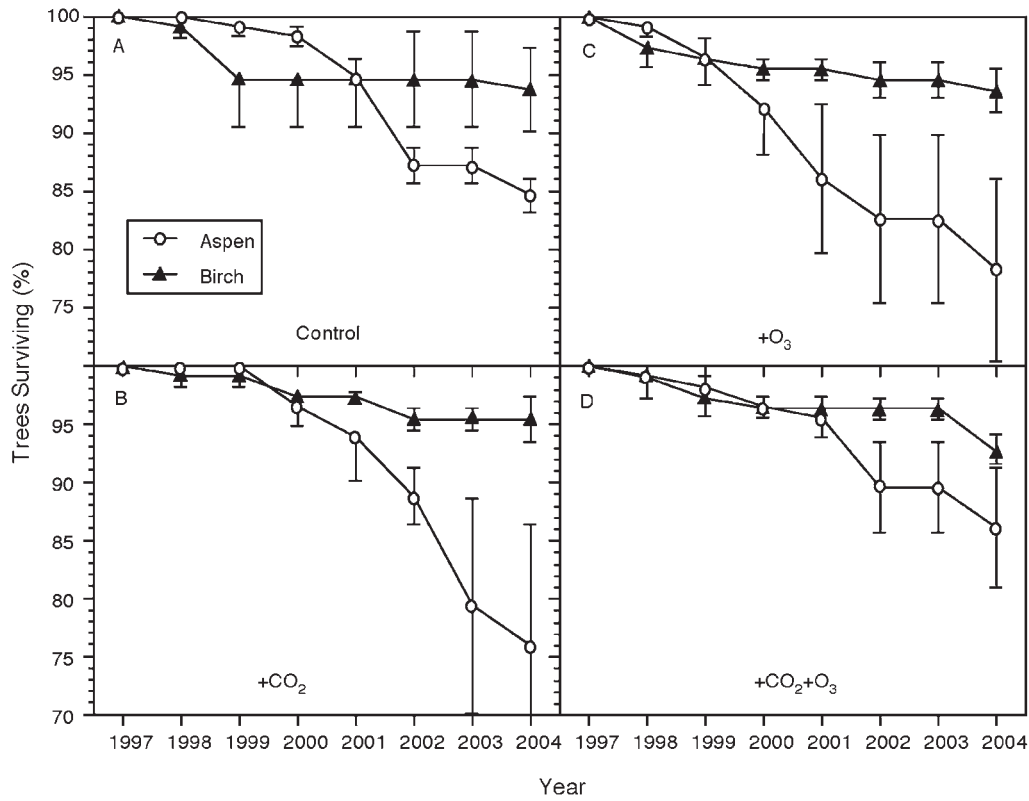


Fig. 6 Survival (mean \pm se) of co-occurring trembling aspen and paper birch trees exposed to ambient air (A: control), elevated CO₂ (B: +CO₂), elevated O₃ (C: +O₃), and elevated CO₂+O₃ (D: +CO₂+O₃).

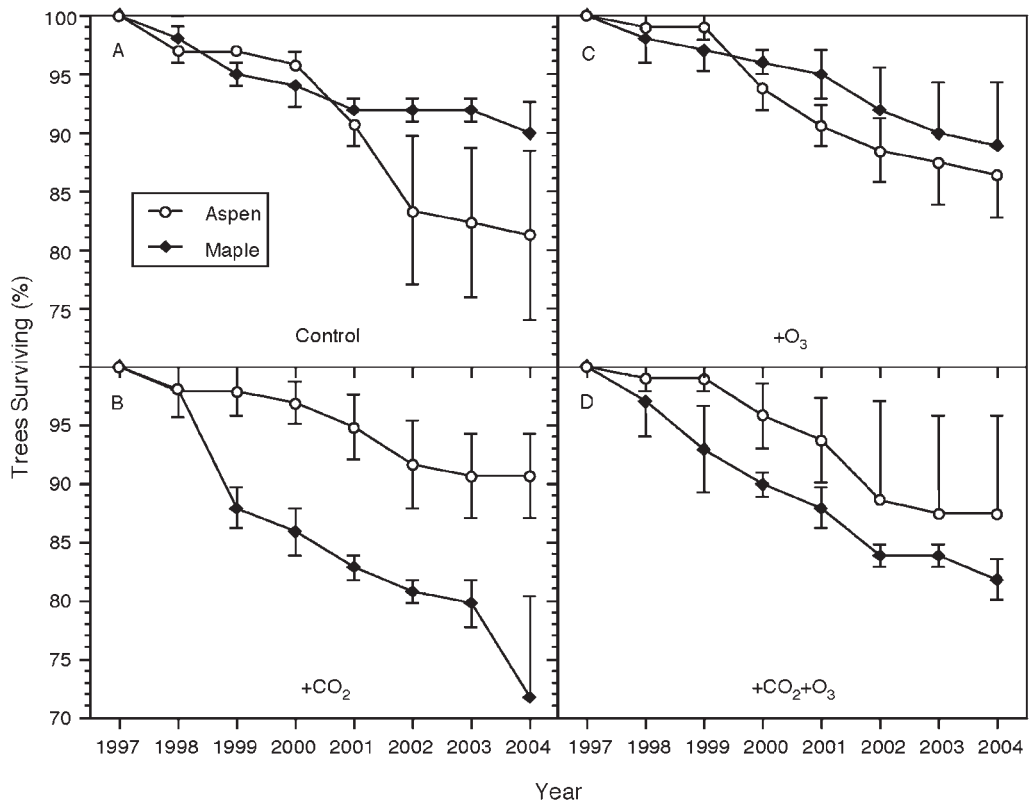


Fig. 7 Survival (mean \pm se) of co-occurring trembling aspen and sugar maple trees exposed to ambient air (A: control), elevated CO₂ (B: +CO₂), elevated O₃ (C: +O₃), and elevated CO₂+O₃ (D: +CO₂+O₃).

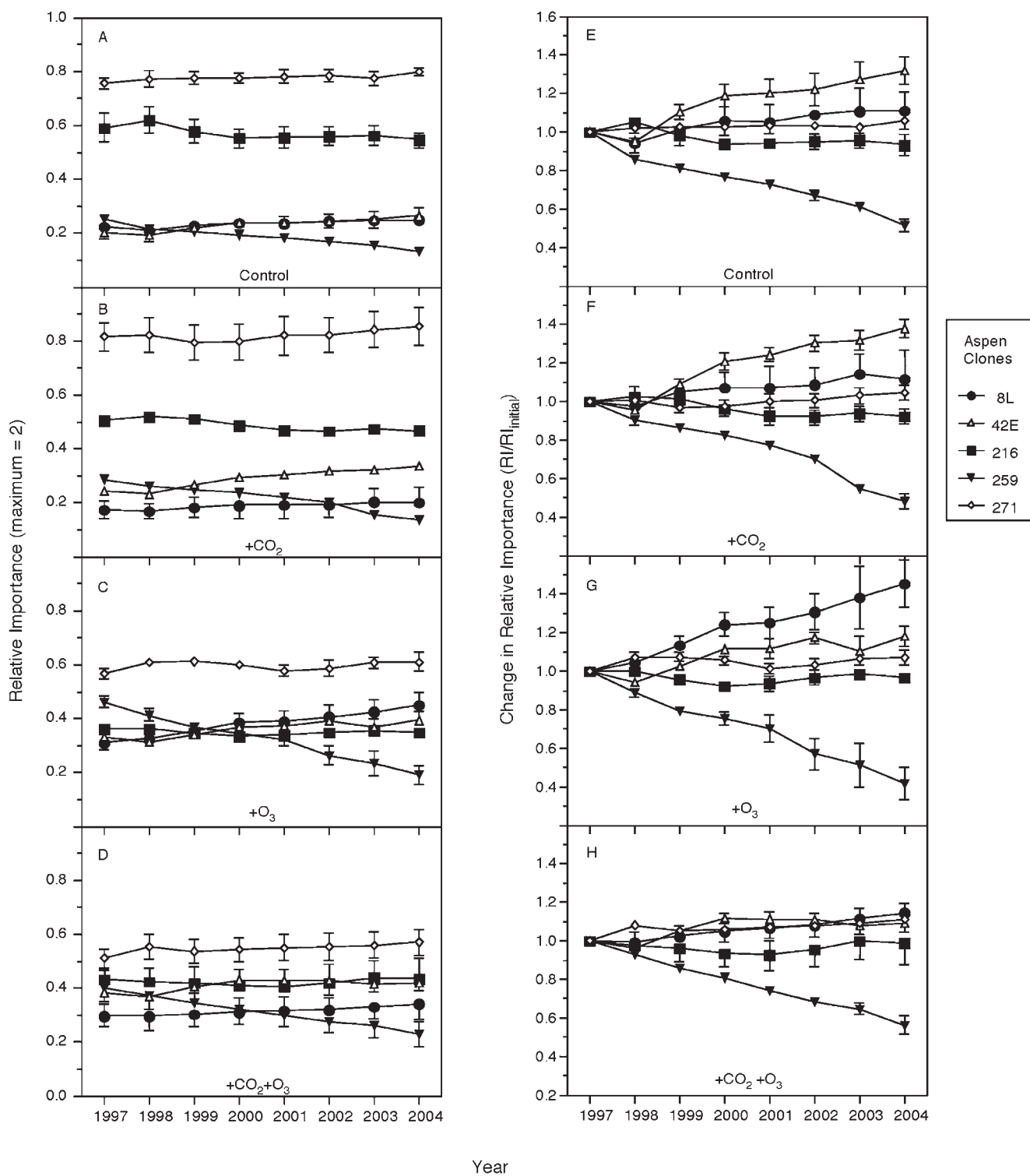


Fig. 8 Means ± se of relative importance (referred to as RI in the text; **A–D**) and changes in relative importance (referred to as SRI in the text; **E–H**) of five, co-occurring trembling aspen clones exposed to ambient air (**A, E**: control), elevated CO₂ (**B, F**: +CO₂), elevated O₃ (**C, G**: +O₃), and elevated CO₂+O₃ (**D, H**: +CO₂+O₃).

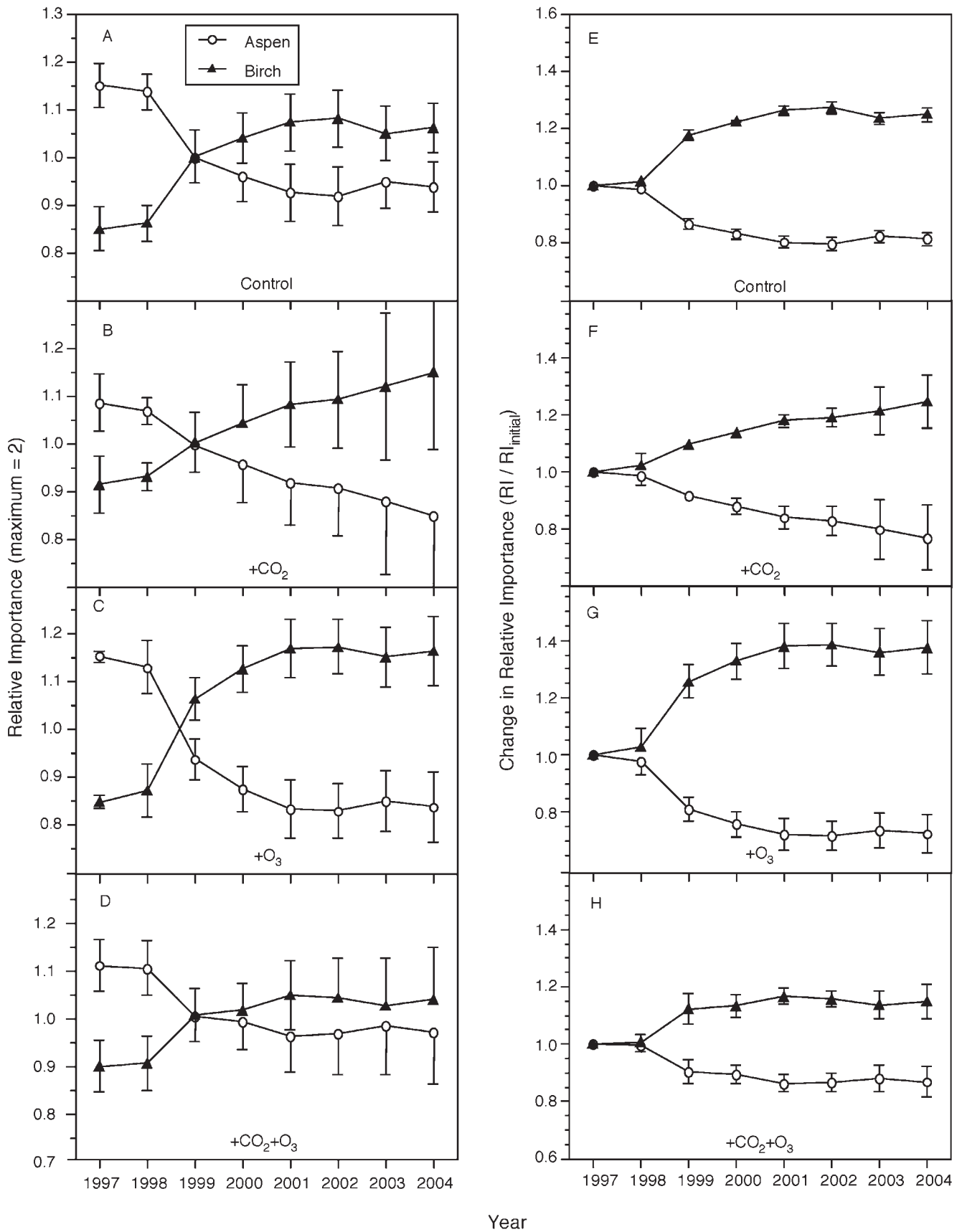


Fig. 9 Means \pm se of relative importance (referred to as RI in the text; **A–D**) and changes in relative importance (referred to as SRI in the text; **E–H**) of co-occurring trembling aspen and paper birch trees exposed to ambient air (**A, E**: control), elevated CO₂ (**B, F**: +CO₂), elevated O₃ (**C, G**: +O₃), and elevated CO₂+O₃ (**D, H**: +CO₂+O₃).

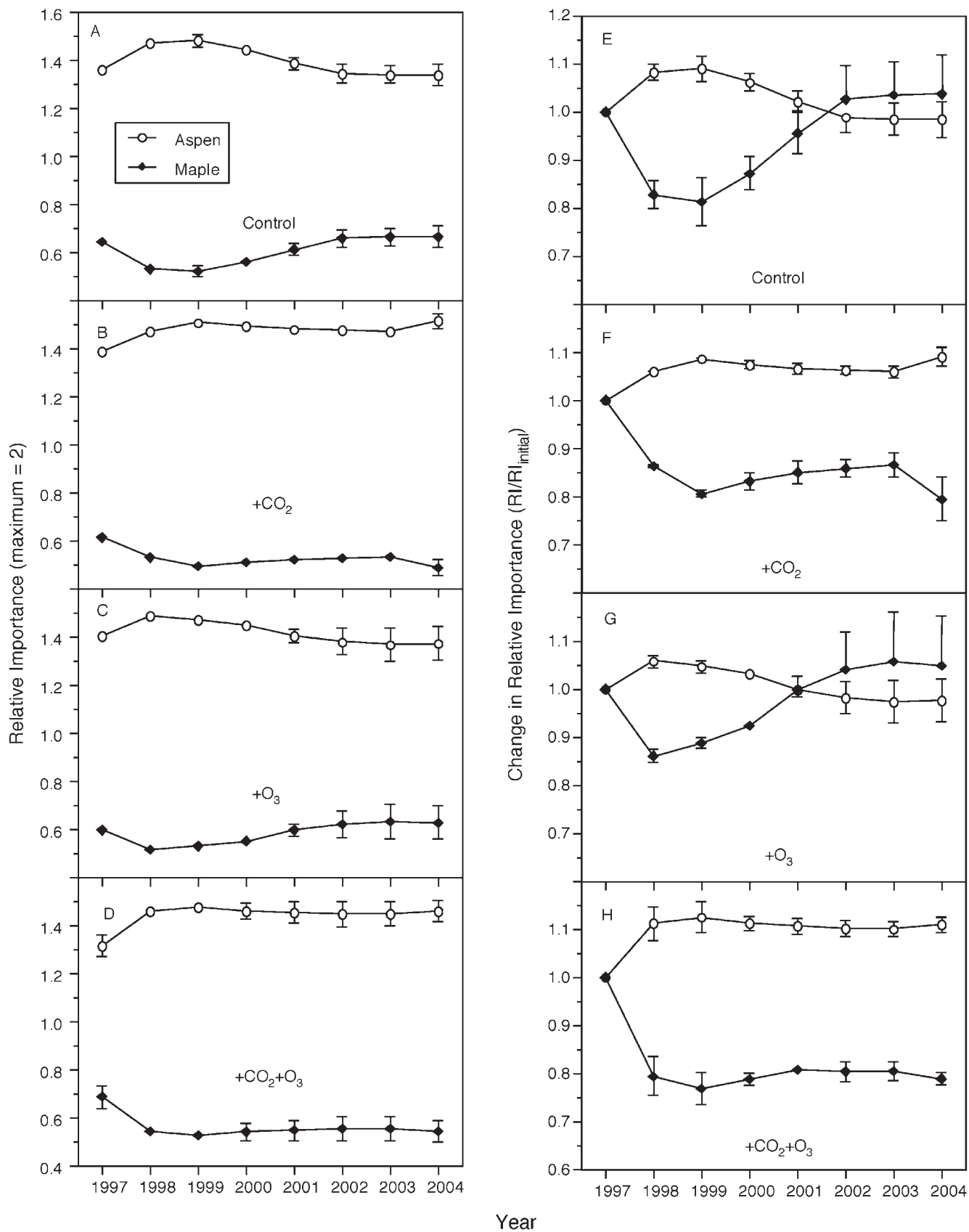


Fig. 10 Means \pm se of relative importance (referred to as RI in the text; **A–D**) and changes in relative importance (referred to as SRI in the text; **E–H**) of co-occurring trembling aspen and sugar maple trees exposed to ambient air (**A, E**: control), elevated CO₂ (**B, F**: +CO₂), elevated O₃ (**C, G**: +O₃), and elevated CO₂+O₃ (**D, H**: +CO₂+O₃).

Our work is consistent with other research suggesting that species composition of forest stands can be altered by elevated CO₂ (Catovsky and Bazzaz, 1999; Bauer et al., 2001; Dijkstra et al., 2002) or elevated O₃ (Miller, 1973; McBride and Laven, 1999; Grams et al., 2002; Arbaugh et al., 2003; Kozovits et al., 2005). It is also clear from this developing literature that knowledge about responses of plants to elevated CO₂ and/or O₃, acquired from plants growing in monoculture may not be transferred to plants grown under interspecific competition, as is typically found in forest situations (Kozovits et al., 2005).

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