Effects of Elevated Atmospheric CO_2 and/or O_3 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 CO_2 and O_3 using Free Air CO_2 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 CO_2 treatments, clone 42E was rapidly becoming the most successful clone while under elevated O_3, clone 8 L emerged as the dominant clone. In fact, growth of clone 8 L was greater in the elevated O_3 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 O_3, and by – 10% and + 45%, respectively, in elevated CO_2. Thus, the presence of elevated O_3 hastened conversion of stands to paper birch, whereas the presence of elevated CO_2 delayed it. Relative importance of aspen and maple changed by – 2% and + 3%, respectively, after seven years in the control treatments. But in elevated O_3, relative importance of aspen and maple changed by – 2% and + 5%, respectively, and in elevated CO_2 by + 9 and – 20%, respectively. Thus, elevated O_3 slightly increases the rate of conversion of aspen stands to sugar maple, but maple is placed at a competitive disadvantage to aspen under elevated CO_2.**

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

Introduction

Global atmospheric CO_2 has increased by ~ 30% since the preindustrial 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 O_3 by 36 – 70% during the same time period (IPCC, 2001; Brasseur et al., 2001). While tropospheric O_3 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 O_3 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 CO_2 and/or O_3 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 CO_2 and O_3, 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 CO_2 and/or O_3 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

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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 CO_2 as individual trees develop a competitive advantage over those that are less responsive as individuals? 3) In the presence of elevated O_3, will the competitive interactions between ozone-sensitive and ozone-tolerant clones or species be modified by elevated CO_2? In this paper, we evaluate how elevated CO_2 and/or O_3 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 CO_2 and O_3 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 CO_2 and O_3 (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 O_3 sensitivity (Karnosky et al., 1996), and clones 42E and 8 L were relatively more and less responsive, respectively, to elevated CO_2 (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, 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. Target-elevated [CO_2] was 560 µl l^{-1} and target-elevated [O_3] was 1.5 × that of ambient air. Carbon dioxide and O_3 fumigations occurred only during daylight hours from bud burst until leaf senescence. Ozone fumigation occurred when conditions were appropriate for normal O_3 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 CO_2 and O_3 concentrations are shown in Fig. **1**.

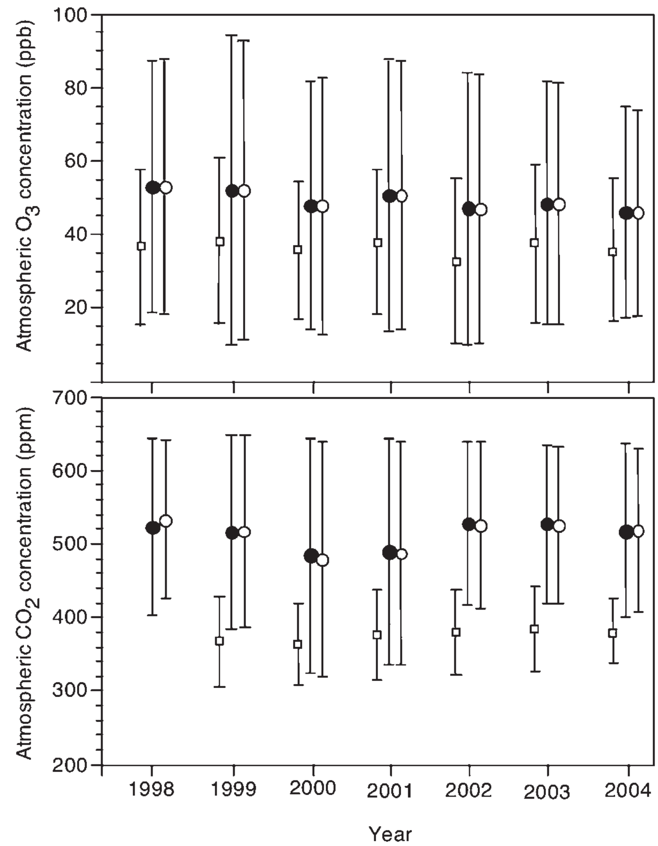

Fig. 1 Hourly mean atmospheric CO_2 and O_3 concentrations in the twelve treatment rings of the Aspen FACE experiment during daylight hours (8:00 – 20:00 h). Small squares are ambient CO_2 or O_3, filled circles are elevated CO_2 only or O_3 only treatments, and open circles are the CO_2 or O_3 concentrations in the elevated CO_2 + O_3 treatments. The vertical lines represent the 90% confidence intervals for 1-hour means.

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 (± se) tree heights (cm) when planted in 1997 and after 7 years of growth in elevated CO_2 and O_3 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 ± 6	529 ± 3 a	30 ± 3	608 ± 70 ac	42 ± 5	610 ± 62 ac	36 ± 4	653 ± 57 d
Clone 42E	40 ± 7	765 ± 33 b	48 ± 1	817 ± 39 bd	45 ± 3	627 ± 7 ac	49 ± 2	774 ± 56 b
Clone 216	49 ± 1	629 ± 7 c	50 ± 4	629 ± 25 c	47 ± 2	535 ± 20 a	52 ± 2	659 ± 31 cd
Clone 259	40 ± 2	402 ± 2 e	44 ± 3	462 ± 15 e	43 ± 4	340 ± 18 e	40 ± 4	355 ± 8 e
Clone 271	64 + 6	763 ± 24 b	71 ± 4	852 ± 45 df	67 ± 7	676 ± 43 c	67 ± 5	806 ± 12 bf
Aspen-birch								
Aspen	46 ± 5	558 ± 10 ab	44 ± 3	636 ± 45 a	49 ± 1	504 ± 15 b	44 ± 6	649 ± 51 a
Birch	42 ± 5	554 ± 38 ab	41 ± 2	676 ± 58 b	41 ± 1	551 ± 25 a	40 ± 1	623 ± 98 ab
Aspen-maple								
Aspen	35 ± 1	482 ± 3 ab	42 ± 4	573 ± 22 a	36 ± 3	461 ± 50 b	37 ± 3	536 ± 66 ab
Maple	14 ± 1	247 ± 11 c	15 ± 1	246 ± 26 c	12 ± 1	220 ± 29 c	17 ± 2	187 ± 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 $1 m^2$.

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 2arcsin(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 $+CO_2$ (716 ± 32 cm and 6.4 ± 0.2 cm, respectively) compared to control (651 ± 15 cm and 5.6 ± 0.1 cm, respectively) ($p < 0.05$), but CO_2 effects on height and diameter of individual aspen clones were not statistically significant ($p > 0.05$). In contrast, after seven years of growth in $+O_3$, 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 $+O_3$ 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 (± se) tree diameters (cm) when planted in 1997 and after 7 years of growth in elevated CO_2 and O_3 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 ± 0.1	4.6 ± 0.2 a	0.4 ± 0.0	5.1 ± 0.9 ac	0.5 ± 0.1	5.5 ± 0.5 af	0.4 ± 0.0	5.2 ± 0.5 ac
Clone 42E	0.5 ± 0.1	6.1 ± 0.4 cd	0.5 ± 0.0	6.7 ± 0.4 d	0.5 ± 0.0	5.1 ± 0.1 af	0.6 ± 0.0	5.9 ± 0.3 ade
Clone 216	0.6 ± 0.0	5.6 ± 0.1 c	0.7 ± 0.0	5.8 ± 0.2 c	0.6 ± 0.0	4.8 ± 0.2 a	0.7 ± 0.0	5.6 ± 0.4 cd
Clone 259	0.6 ± 0.0	3.8 ± 0.0 b	0.6 ± 0.0	4.8 ± 0.1 a	0.7 ± 0.1	3.6 ± 0.2 b	0.6 ± 0.0	3.7 ± 0.0 b
Clone 271	0.7 ± 0.0	6.5 ± 0.3 e	0.8 ± 0.0	7.6 ± 0.2 e	0.7 ± 0.1	5.8 ± 0.3 f	0.7 ± 0.0	6.8 ± 0.1 e
Aspen-birch								
Aspen	0.6 ± 0.0	5.1 ± 0.0 ab	0.5 ± 0.0	6.2 ± 0.2 ac	0.6 ± 0.0	4.6 ± 0.1 b	0.6 ± 0.1	5.4 ± 0.1 ab
Birch	0.5 ± 0.1	5.6 ± 0.3 a	0.6 ± 0.0	7.0 ± 0.9 c	0.5 ± 0.0	5.8 ± 0.3 abc	0.5 ± 0.0	6.0 ± 0.6 ac
Aspen-maple								
Aspen	0.5 ± 0.0	5.2 ± 0.0 ab	0.6 ± 0.0	6.6 ± 0.2 b	0.5 ± 0.0	4.9 ± 0.6 a	0.5 ± 0.0	6.0 ± 0.5 b
Maple	0.3 ± 0.0	2.5 ± 0.1 c	0.3 ± 0.0	2.1 ± 0.2 c	0.3 ± 0.0	2.2 ± 0.2 c	0.3 ± 0.0	2.0 ± 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 $+CO_2$ 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 $+CO_2$ than in controls (not significantly different). There were no significant differences between height and diameter in $+O_3$ or CO_2+O_3 versus control for either of the mixed species communities.

Volume growth of the five aspen clones was significantly increased by elevated CO_2 (significant CO_2 main effect, Table **3** and Fig. **2**). Elevated O_3 had differential effects on volume growth among the aspen clones (significant clone within O_3 treatment effects). This significant clone within O_3 treatment interaction was due to the response of clone 8L in $+O_3$. Whereas the other four clones each had decreased volume growth in $+O_3$ compared to control, clone 8L had no decrease in volume growth. In the control, $+CO_2$ and $+CO_2+O_3$ 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 $+O_3$, 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 CO_2 (Table **3**, Fig. **3**). The species × CO_2 interaction for volume growth was not significant; nonetheless, volume of birch trees in $+CO_2$ was 89% greater than in the control treatment, compared to 60% for the aspen trees in that community. In $+O_3$, 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 CO_2 treatment effect because aspen had significantly greater volume growth in $+CO_2$ compared to controls ($p < 0.05$) whereas maple did not. Interestingly, while aspen clone 216 had decreased volume growth with $+O_3$ in the aspen monoculture and the aspen-birch community, it was not significantly affected by $+O_3$ 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 $+CO_2+O_3$, 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 $+CO_2$, and clone 259 had more ($p < 0.05$) mortality in $+CO_2$ and $+O_3$.

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 $+CO_2$ 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 $+CO_2$. Aspen had significantly less mortality, and maple more mortality ($p < 0.05$) in $+CO_2$ than in the control treatment.

Importance values

Relative importance values of the five aspen clones did not change with time in the control or $+CO_2$ 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 $+O_3$, 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 CO_2, elevated O_3, and their combination. Volume growth curves are depicted in Figs. **2–4**, respectively

	df	Mean MS	*p*	Linear MS	*p*	Quadratic MS	*p*
Aspen clones (Fig. **2**)							
CO_2	1	76 064 136	0.05	88 978 680	0.05	3 210 441	0.05
Error 1	2	4 398 346		4 590 438		173 119	
O_3	1	4 918 906	0.13	47 463 355	0.12	639 358	0.10
Error 2	2	7 724 846		6 829 091		79 671	
$CO_2 \times O_3$	1	917 612	0.79	400 990	0.88	140 963	0.77
Error 3		9 880 297		13 065 749		1 241 928	
Cln	24	135 675 449	0.00	140 792 277	0.00	7 323 199	0.00
Cln(CO_2)	4	7 702 253	0.06	9 170 728	0.06	401 538	0.19
Cln(O_3)	4	9 875 592	0.03	10 891 819	0.03	1 057 460	0.01
Cln($CO_2 \times O_3$)	4	1 226 163	0.81	1 348 666	0.82	123 969	0.74
Error 4	32	3 060 474		3 577 955		247 912	
Aspen-birch (Fig. **3**)							
CO_2	1	62 798 617	0.01	73 138 274	0.01	3 307 493	0.00
Error 1	2	8 490 460		8 697 941		265 316	
O_3	1	21 133 030	0.26	17 637 394	0.23	45 397	0.48
Error 2	2	8 552 411		6 222 447		61 279	
$CO_2 \times O_3$	1	10 312 267	0.03	7 473 486	0.10	145 151	0.47
Error 3	2	353 022		919 139		182 320	
Sp	1	36 907 990	0.10	30 922 560	0.14	42 805	0.71
Sp(CO_2)	1	404 372	0.85	1 000 270	0.77	192 915	0.44
Sp(O_3)	1	400 027	0.85	344 693	0.87	16 787	0.82
Sp($CO_2 \times O_3$)	1	4 474 500	0.54	4 749 859	0.54	32 283	0.75
Error 4	8	10 845 696		11 479 126		286 483	
Aspen-maple (Fig. **4**)							
CO_2	1	12 391 912	0.06	13 807 264	0.07	863 822	0.15
Error 1	2	879 463		1 143 575		168 916	
O_3	1	2 377 445	0.46	1 719 603	0.48	422	0.93
Error 2	2	2 945 683		2 373 506		49 896	
$CO_2 \times O_3$	1	634 986	0.42	355 337	0.59	25 575	0.73
Error 3	2	613 802		892 155		162 336	
Sp	1	210 176 470	0.00	213 296 572	0.00	8 361 304	0.00
Sp(CO_2)	1	14 176 212	0.03	16 578 002	0.02	1 174 019	0.01
Sp(O_3)	1	1 373 907	0.45	796 830	0.54	10 952	0.75
Sp($CO_2 \times O_3$)	1	819 388	0.55	420 420	0.66	46 805	0.51
Error 4	8	2 137 548		1 982 773		97 161	

and $+CO_2$ treatments, clone 42E had increasing ($p < 0.05$) and clone 259 decreasing ($p < 0.05$) SRIs (Figs. **8E, F**). In $+O_3$, 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 $+O_3$. The decrease in SRI of clone 259 in $+O_3$ 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 $+O_3$. No clone had increasing SRI in the $+CO_2+O_3$ 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 significantly 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 $+CO_2$ for 2004, and in $+O_3$ 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, $+O_3$, and $+CO_2+O_3$ treatments. SRI of the $+CO_2$ treatment continued to increase for birch ($p < 0.05$) and decrease for aspen ($p < 0.05$) from 1998 onward.

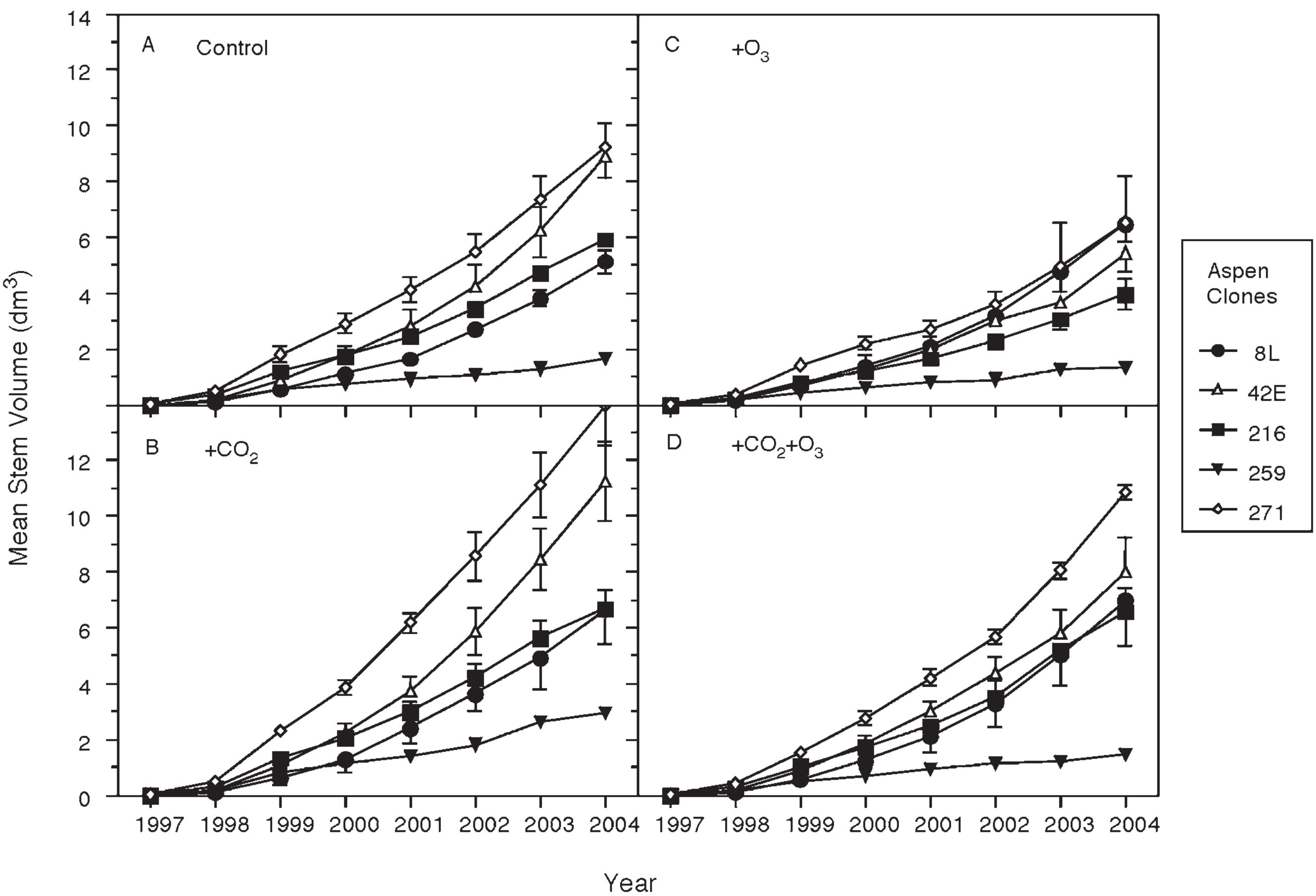

Fig. 2 Annual stem volume growth (mean ± se) of five, co-occurring trembling aspen clones exposed to ambient air (**A**: control), elevated CO_2 (**B**: $+CO_2$), elevated O_3 (**C**: $+O_3$), and elevated CO_2+O_3 (**D**: $+CO_2+O_3$).

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 $+O_3$ 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 $+CO_2$ and $+CO_2+O_3$, 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 CO_2 and O_3, 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 CO_2 or O_3, 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 CO_2 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 CO_2 than in control treatments as this clone had increased growth under elevated CO_2. Clone 259 decreased in importance under elevated CO_2 more than in the control treatment because of its inability to compete under the dense canopies produced under elevated CO_2 (Karnosky et al., 2005). Differential growth responses of aspen clones to elevated CO_2 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 CO_2 because of competition. Together, these studies documenting asymmetric effects of enriched CO_2 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 CO_2.

The deleterious effects of elevated O_3 differed among the five aspen clones such that clone 8L competed better in elevated O_3 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 O_3 tolerance of clone 8L and ex-

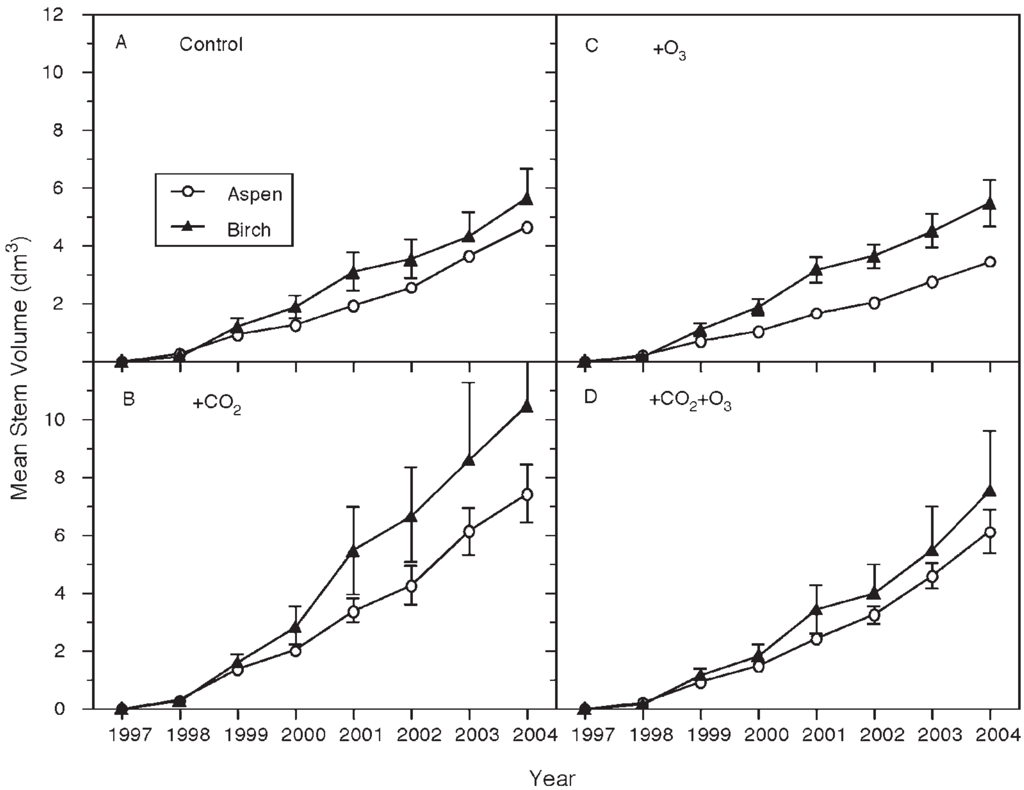

Fig. 3 Annual stem growth (mean ± se) of co-occurring trembling aspen and paper birch trees exposed to ambient air (**A**: control), elevated CO_2 (**B**: $+CO_2$), elevated O_3 (**C**: $+O_3$), and elevated CO_2+O_3 (**D**: $+CO_2+O_3$).

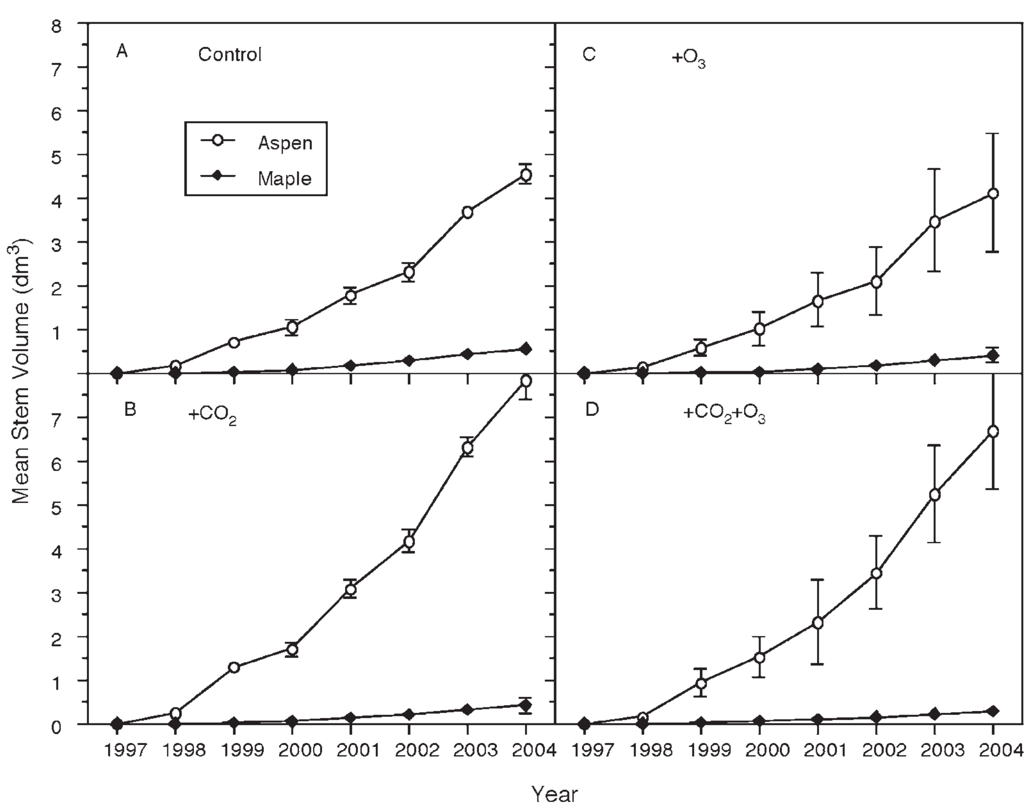

Fig. 4 Annual stem growth (mean ± se) of co-occurring trembling aspen and sugar maple trees exposed to ambient air (**A**: control), elevated CO_2 (**B**: $+CO_2$), elevated O_3 (**C**: $+O_3$), and elevated CO_2+O_3 (**D**: $+CO_2+O_3$).

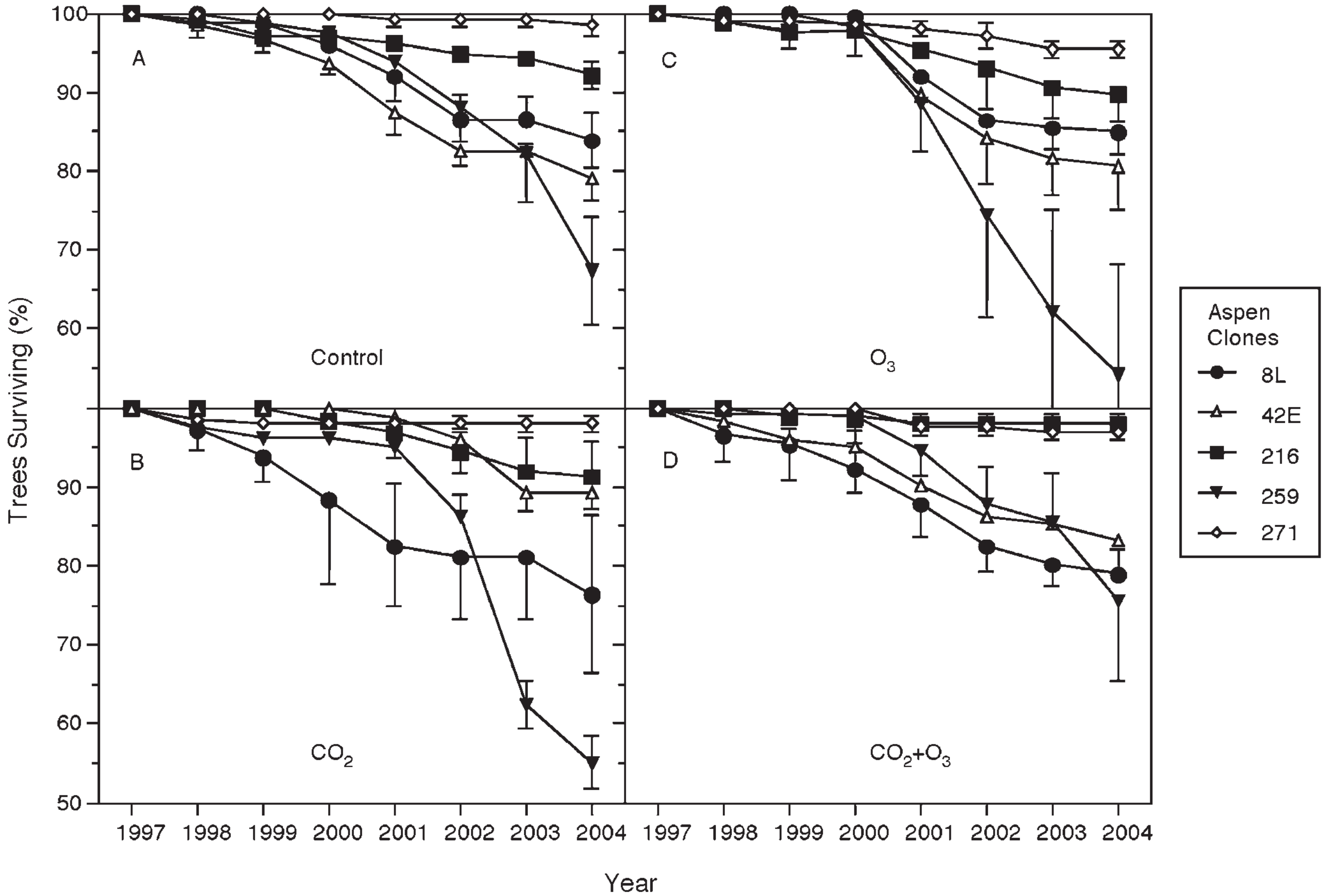

Fig. 5 Survival (mean ± se) of five, co-occurring trembling aspen clones exposed to ambient air (**A**: control), elevated CO_2 (B: +CO_2), elevated O_3 (**C**: +O_3), and elevated CO_2 + O_3 (**D**: +CO_2 + O_3).

treme O_3 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 O_3 have previously been reported for white pine (Karnosky, 1981) and aspen (Karnosky et al., 2003 b). Together, this research supports the hypothesis that elevated O_3 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 CO_2 and O_3 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 CO_2 influenced aspen growth more than the direct effects of elevated O_3. When aspen was grown with birch in elevated CO_2, it had increased mortality compared to the control; but when grown with maple in elevated CO_2, it had less mortality compared to the control. Aspen mortality in elevated O_3, as with birch and maple, did not differ from the control in either of those communities. Our results suggest that in elevated CO_2 aspen is competitively advantaged with both sugar maple and paper birch. However, under elevated O_3, 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 CO_2, and poor competitors have an added disadvantage in elevated O_3. Whereas, in ordinary circumstances, spruce trees out-compete beech for N, elevated CO_2 stimulates the competitive ability of spruce while elevated O_3 inhibits the competitive ability of beech (Kozovits et al., 2005). Similarly, grass species with the greater propensity for light harvesting benefited more from elevated CO_2 than their competitors (Teyssonneyre et al., 2002). This idea was also identified by McDonald et al. (2002) who assessed CO_2 and O_3 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 CO_2 than their neighbours, whereas those with a competitive disadvantage were strongly affected by elevated O_3, although that effect was strongly controlled by clonal effects. Indeed, Poorter and Navas (2003) found that relative growth rate (RGR) in current ambient CO_2 was positively related to the RGR response to elevated CO_2 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 O_3 than the other clones. A surprising result was the improved growth rate and competitiveness of clone 8L in elevated O_3 compared to the control.

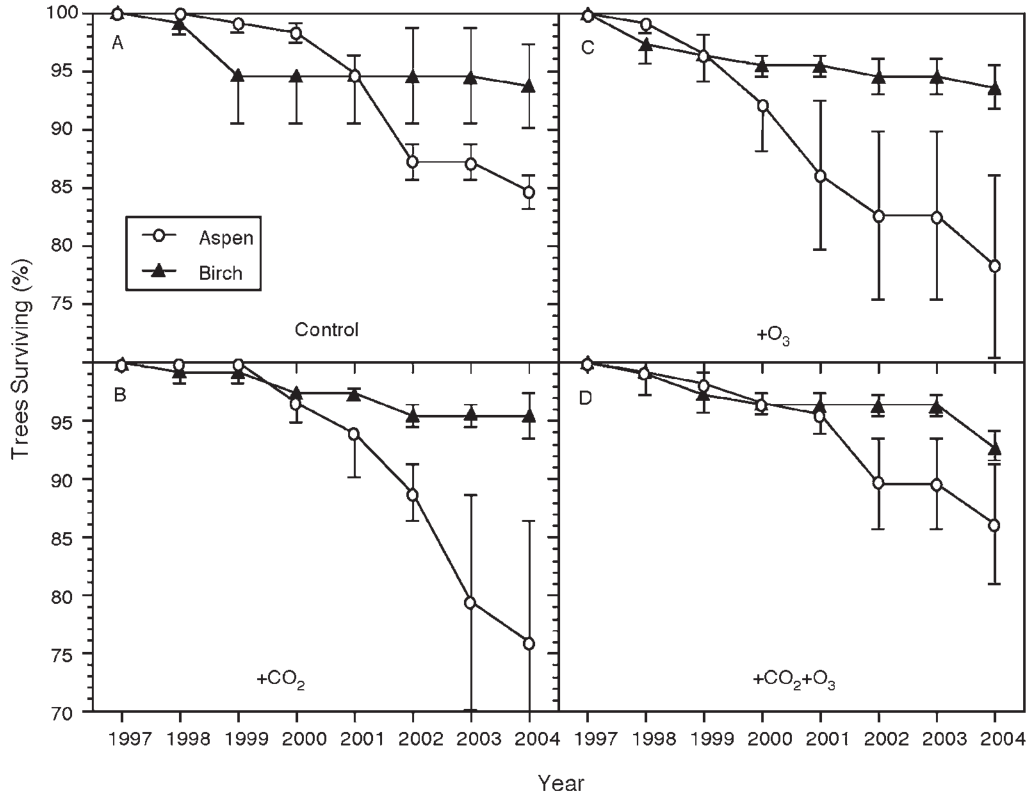

Fig. 6 Survival (mean ± se) of co-occurring trembling aspen and paper birch trees exposed to ambient air (**A**: control), elevated CO_2 (**B**: $+CO_2$), elevated O_3 (**C**: $+O_3$), and elevated CO_2+O_3 (**D**: $+CO_2+O_3$).

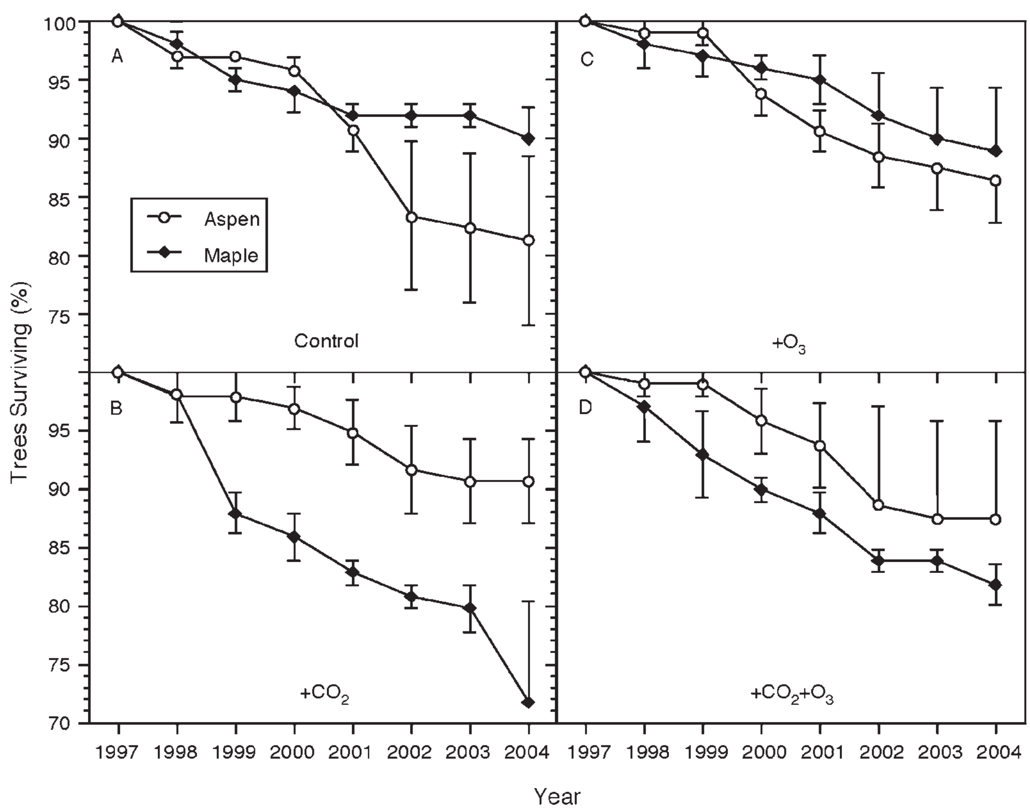

Fig. 7 Survival (mean ± se) of co-occurring trembling aspen and sugar maple trees exposed to ambient air (**A**: control), elevated CO_2 (**B**: $+CO_2$), elevated O_3 (**C**: $+O_3$), and elevated CO_2+O_3 (**D**: $+CO_2+O_3$).

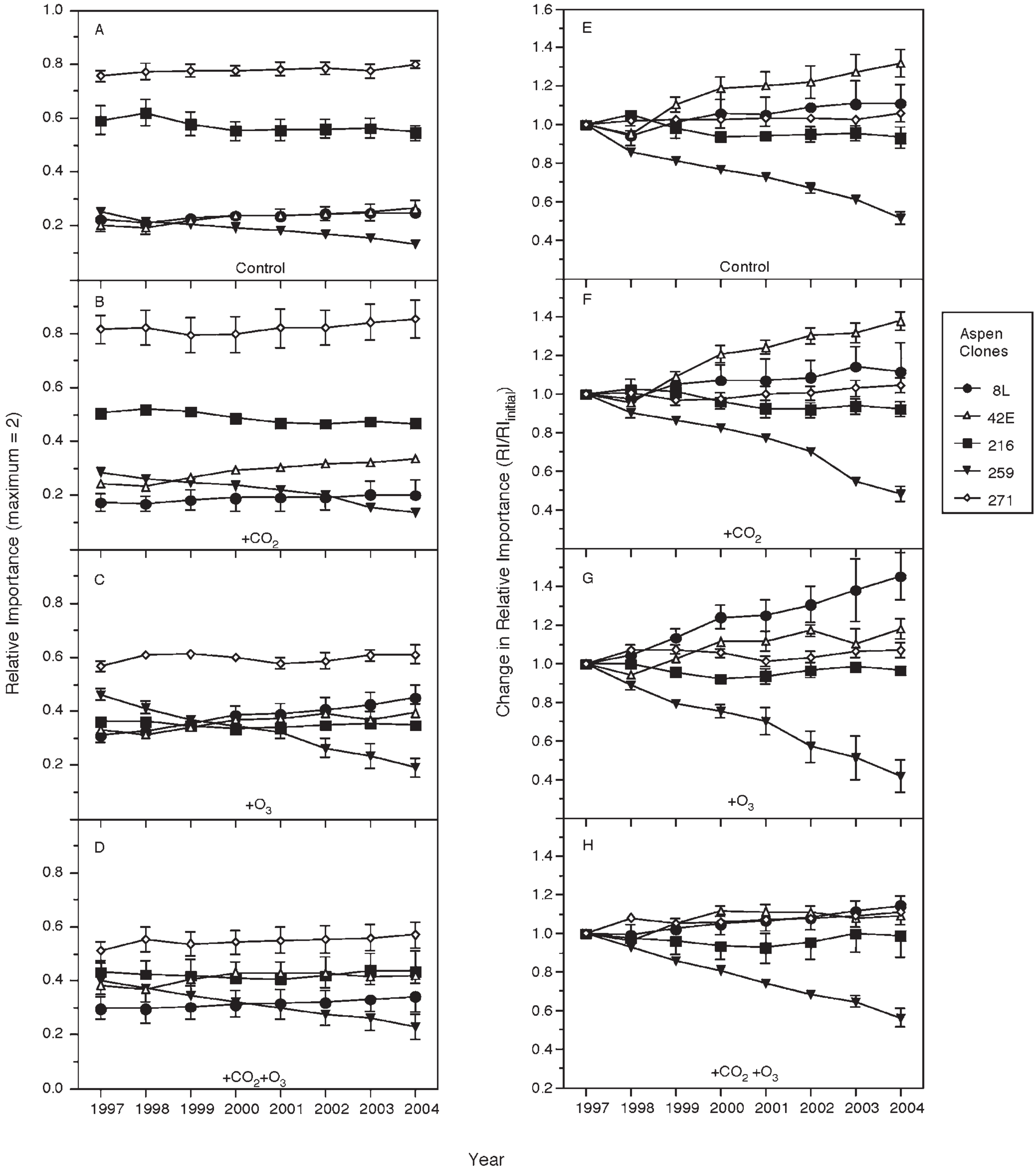

Fig. 8 Means ± se of relative importance (referred to as RI in the text; **A – D**) and changes in relative importance (referred to as SRI in the text; **E – H**) of five, co-occurring trembling aspen clones exposed to ambient air (**A, E**: control), elevated CO_2 (**B, F**: $+CO_2$), elevated O_3 (**C, G**: $+O_3$), and elevated CO_2+O_3 (**D, H**: $+CO_2+O_3$).

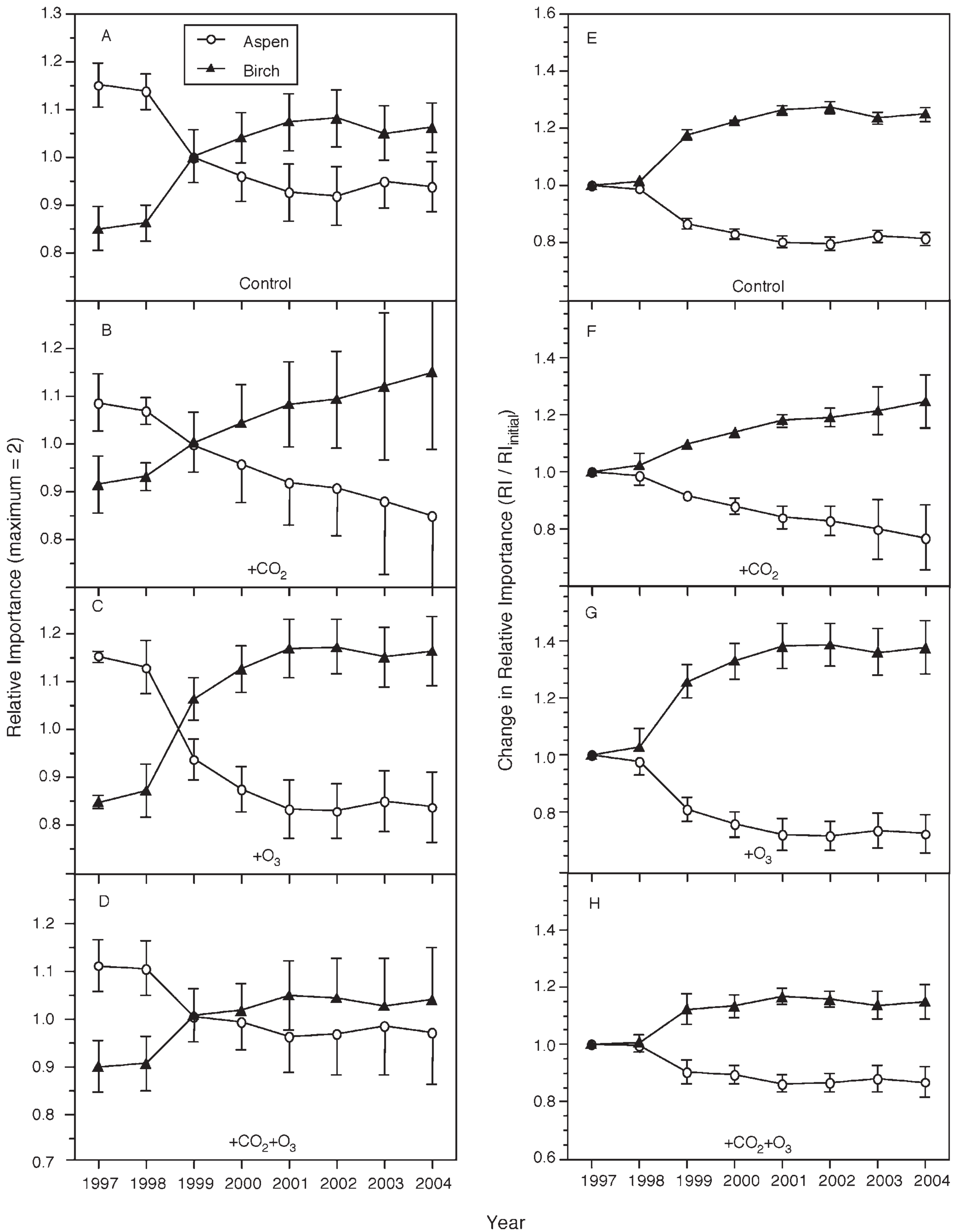

Fig. 9 Means ± se of relative importance (referred to as RI in the text; **A–D**) and changes in relative importance (referred to as SRI in the text; **E–H**) of co-occurring trembling aspen and paper birch trees exposed to ambient air (**A, E**: control), elevated CO_2 (**B, F**: +CO_2), elevated O_3 (**C, G**: +O_3), and elevated CO_2+O_3 (**D, H**: +CO_2+O_3).

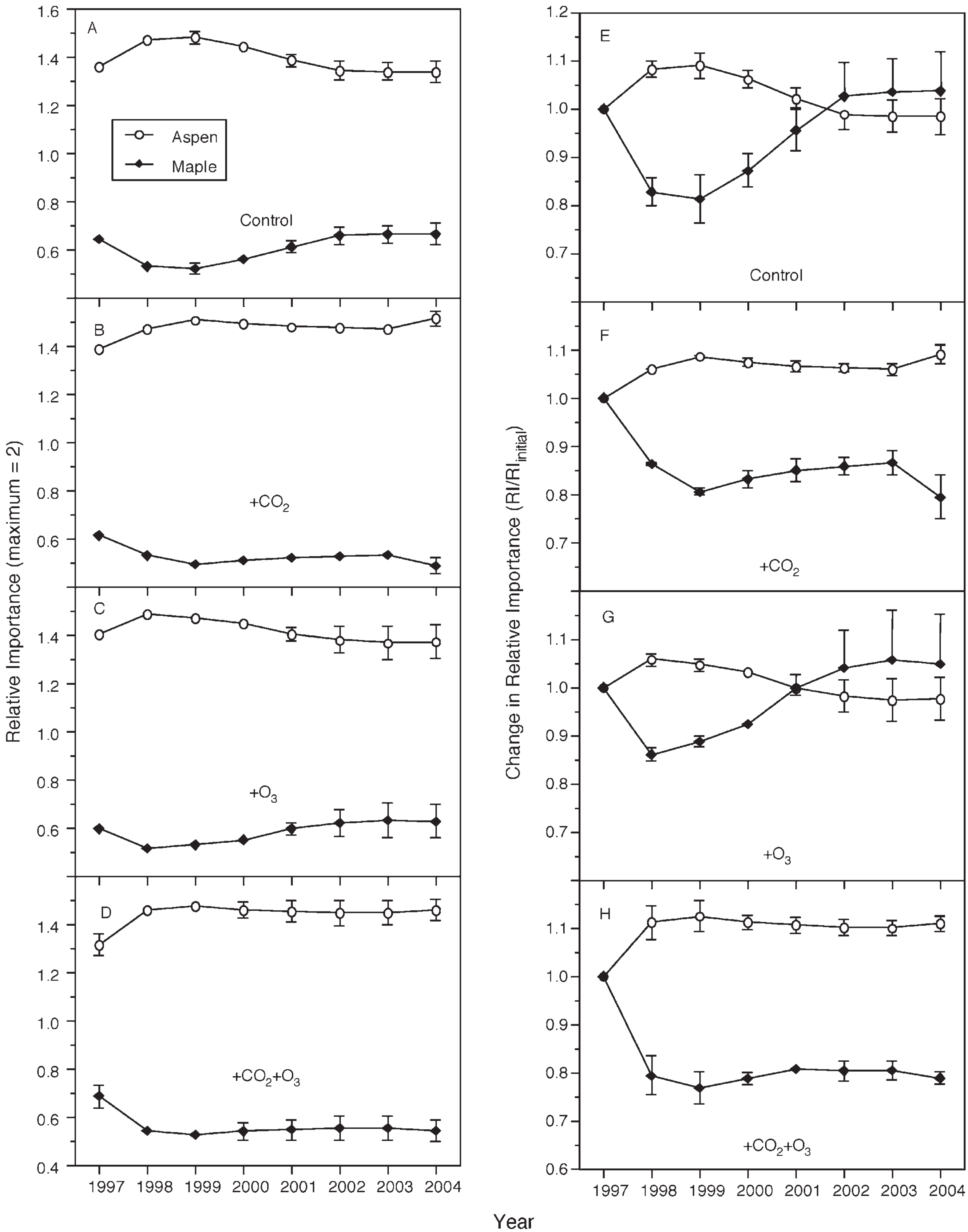

Fig. 10 Means ± se of relative importance (referred to as RI in the text; **A–D**) and changes in relative importance (referred to as SRI in the text; **E–H**) of co-occurring trembling aspen and sugar maple trees exposed to ambient air (**A, E**: control), elevated CO_2 (**B, F**: $+CO_2$), elevated O_3 (**C, G**: $+O_3$), and elevated CO_2+O_3 (**D, H**: $+CO_2+O_3$).

Our work is consistent with other research suggesting that species composition of forest stands can be altered by elevated CO_2 (Catovsky and Bazzaz, 1999; Bauer et al., 2001; Dijkstra et al., 2002) or elevated O_3 (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 CO_2 and/or O_3, 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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