Tropospheric O_3 compromises net primary production in young stands of trembling aspen, paper birch and sugar maple in response to elevated atmospheric CO_2

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Summary

• Concentrations of atmospheric CO_2 and tropospheric ozone (O_3) are rising concurrently in the atmosphere, with potentially antagonistic effects on forest net primary production (NPP) and implications for terrestrial carbon sequestration.

• Using free-air CO_2 enrichment (FACE) technology, we exposed north-temperate forest communities to concentrations of CO_2 and O_3 predicted for the year 2050 for the first 7 yr of stand development. Site-specific allometric equations were applied to annual nondestructive growth measurements to estimate above- and below-ground biomass and NPP for each year of the experiment.

• Relative to the control, elevated CO_2 increased total biomass 25, 45 and 60% in the aspen, aspen–birch and aspen–maple communities, respectively. Tropospheric O_3 caused 23, 13 and 14% reductions in total biomass relative to the control in the respective communities. Combined fumigation resulted in total biomass response of –7.8, +8.4 and +24.3% relative to the control in the aspen, aspen–birch and aspen–sugar maple communities, respectively.

• These results indicate that exposure to even moderate levels of O_3 significantly reduce the capacity of NPP to respond to elevated CO_2 in some forests.

Key words: Aspen FACE (free-air CO_2 enrichment), elevated carbon dioxide, global change, net primary production (NPP), tropospheric ozone (O_3).

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Introduction

Land-based and remotely sensed data show a carbon sink in Northern Hemisphere forests of 0.30–0.68 petagrams (Pg = 10^{15} g) per year for the 1980s and 1990s, with 70% occurring in Eurasia (Myneni *et al.*, 2001; Pacala *et al.*, 2001). In the USA, the forest carbon sink was expanding because of forest recovery on former agricultural land and fire suppression, which offset 10–30% of USA fossil fuel emissions during the 1980s (Houghton *et al.*, 1999; Caspersen *et al.*, 2000; Birdsey & Lewis, 2002). Rising atmospheric CO_2 has received considerable attention as a possible stimulus to forest net primary production (NPP) that could further offset fossil fuel emissions (Ceulemans & Mousseau, 1994; Curtis & Wang, 1998; Houghton *et al.*, 2001). Less well recognized, however, is that tropospheric O_3 is also increasing globally (Fowler *et al.*, 1999), and is probably reducing the potential enhancement of forest NPP and terrestrial C sequestration caused by elevated atmospheric CO_2 (Karnosky *et al.*, 1999, 2003; Loya *et al.*, 2003; Felzer *et al.*, 2004).

Decades of experimental evidence show that small forest trees experience an average stimulation of 16–31% in biomass production under elevated atmospheric CO_2, but these responses can be constrained by soil nutrient availability or other environmental factors (Strain & Cure, 1994; McGuire *et al.*, 1995; Gebauer *et al.*, 1996; Curtis & Wang, 1998; Johnson, 1999; Zak *et al.*, 2000; Oren *et al.*, 2001). Evidence from long-term forest FACE (free-air CO_2 enrichment) experiments corroborates this finding at larger spatial and temporal scales. Net primary production of a 13-yr-old loblolly pine (*Pinus taeda*) ecosystem was stimulated 26% under CO_2 enrichment, and this response persisted for 4 yr (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002). A 10-yr-old sweetgum (*Liquidambar styraciflua*) ecosystem increased NPP an average 21% under CO_2 enrichment (Norby *et al.*, 2002). Three species of *Populus* grown in short rotation culture increased woody biomass by 15–27% under elevated CO_2 (Calfapietra *et al.*, 2003). Responses of mature forests to elevated atmospheric CO_2 are still poorly understood.

Most elevated CO_2 studies have not considered the phytotoxic effects of simultaneous exposure to elevated tropospheric O_3, which has been shown to decrease tree seedling growth from −2 to −69% (Pye, 1988). Pre-industrial concentrations of tropospheric O_3 are estimated to have been less than 10 nl l^{-1}, and have risen to 30–40 nl l^{-1} background levels today (Levy *et al.*, 1997). Tropospheric O_3 concentrations are expected to exceed 60 nl l^{-1} over large portions (50%) of the global forested land surface by the year 2100 (Felzer *et al.*, 2004). The decrease in agricultural productivity caused by ambient O_3 toxicity has been estimated at US$1.0–5.8 billion annually (1990 dollars) in the USA (Kopp *et al.*, 1985; Adams *et al.*, 1986; Murphy *et al.*, 1999), but economic losses to wood production are unknown (Krupa *et al.*, 2000). Biogeochemical modeling estimates of reductions in annual terrestrial C sequestration in the USA, caused by ambient O_3 pollution during the late 1980s to early 1990s, range from 18 to 38 Tg C yr^{-1}, which must be accounted for in future calculations of the global C budget (Felzer *et al.*, 2004). Therefore a key to understanding the role of forests in mitigating the build-up of atmospheric CO_2 is determining how NPP will respond to the interactive effects of elevated atmospheric CO_2 and tropospheric O_3.

Here we report on the NPP of intact experimental forest communities dominated by the most widespread tree taxa in North America, in response to the interactive effects of elevated atmospheric CO_2 and tropospheric O_3. The study was performed at the Aspen FACE project in Rhinelander, WI, USA (Dickson *et al.*, 2000). Communities of pure trembling aspen (*Populus tremuloides* Michx.), and competitive mixes of trembling aspen–paper birch (*Betula papyrifera* Marsh.) and trembling aspen–sugar maple (*Acer saccharum* Marsh.) were exposed for 7 yr to concentrations of atmospheric CO_2 and tropospheric O_3 predicted for the year 2050. Net primary production was estimated with species-specific allometric regressions developed at the site, applied to annual nondestructive measurements of all trees in the experimental plots. We hypothesized that (i) elevated atmospheric CO_2 would provide sustained enhancement of NPP in all three forest communities; and (ii) elevated tropospheric O_3 would decrease it. Because it has been postulated that elevated CO_2 may decrease O_3 uptake into the plant because of decreased stomatal conductance (Allen, 1990; Wustman *et al.*, 2003), our third hypothesis was that simultaneous exposure to both elevated CO_2 and elevated tropospheric O_3 would result in growth similar to the control.

Materials and Methods

Field experiment

The Aspen FACE project is a randomized complete block design of atmospheric CO_2 and tropospheric O_3 treatments, with species composition (aspen, aspen–birch, and aspen–maple) as a split-plot factor ($n = 3$). The 12 30-m-diameter plots are fumigated using free-air technology of the Brookhaven National Laboratory's design (Hendrey *et al.*, 1999) to maintain atmospheric targets of 560 ppm CO_2 and 1.5× ambient O_3 (Table 1). Fumigation is during daylight hours only, and begins at bud break in the spring and ends at

Table 1 Summary of Aspen FACE project control data for atmospheric fumigation treatments, 1998–2003. Values are mean daily concentrations or sums (O_3 exposure) for the entire growing season of each year

Treatment	1998	1999	2000	2001	2002	2003
Ambient CO_2 (control, +O_3) (ppm)	343	347	347	356	361	367
Elevated CO_2 (+CO_2, +CO_2 + O_3) (ppm)	530	548	547	528	537	535
Ambient O_3 (control, +CO_2) (ppb)	37.5	36.9	36.0	38.8	33.1	38.0
Elevated O_3 (+O_3, +CO_2 + O_3) (ppb)	54.5	51.9	49.3	52.6	49.5	51.0
Ambient O_3 exposure (control, +CO_2) (ppmh)	63.8	62.8	58.2	66.1	54.3	60.4
Elevated O_3 exposure (+O_3, +CO_2 + O_3) (ppmh)	97.4	88.8	81.6	90.0	81.4	81.1
Exposure duration (d)	166	143	139	143	138	145

leaf senescence in the fall, with an average growing season of 145 d (Table 1). Trees were planted at 1 × 1-m spacing, and fumigation began in 1997. Over the life of the experiment, system performance has been within 20% of the target 93% of the time for CO_2, and within 20% of the target 80% of the time for O_3 (www.aspenface.mtu.edu).

Tree growth is monitored by annual measurement of total height and diameter at 10 cm above-ground of all trees within the central core area of the plots (n = 3684). The core area in each plot measures 166, 76 and 65 m^2 for the aspen, aspen–birch and aspen–maple sections, respectively. The core area in which nondestructive studies are carried out is buffered from possible edge effects by five rows of trees on the outer edge of the plots. In 2000 and 2002, complete above- and below-ground harvests were performed on a total of 196 trees at the edge of the central core area to develop species-specific allometric biomass equations. Trees were harvested in midsummer at peak leaf area by severing the stem 3 cm above ground, separating foliage from wood (stem + branches). The tree heart root system was sampled by driving a 25.4-cm internal diameter corer to a depth of 25 cm centered on the severed tree stem. Between-tree coarse and fine (<1 mm diameter) root biomass was estimated with 10 randomly located cores, 15 cm diameter by 25 cm depth, within the subplots. All roots were removed from the soil by washing over a fine-mesh screen, and were sorted into coarse (heart + all roots >1 mm diameter) and fine (all roots <1 mm diameter). Only live root data are presented in the current study. All plant parts were dried to constant mass at 65°C and subsamples were combusted at 500°C for 7 h to correct for mineral content.

Estimating stand-level biomass and NPP

Allometric biomass equations (Table 2) were developed by regressing the logarithm of plant dry weight (g; foliage, wood, heart root system) against the logarithm of stem diameter (cm) of the harvested trees for each species (aspen, paper birch, sugar maple). Regressions were tested for significant effects of the experimental treatments on model intercept and slope, as well as for suitability of transformations and independent variables. Models of the form ln(dependent variable) = B_0 + B_1 ln(diameter) proved to explain most of the variation in the data, with statistically insignificant additional predictive power added by height. Allometric analyses of the biomass data from the two harvests (King *et al.*, 1996, 1999) indicated that biomass partitioning between foliage, wood and heart roots was unaffected by the treatments, allowing for use of a common model for each species. Model R^2 values ranged from 0.84 to 0.99, with seven of the nine models having $R^2 > 0.90$ (Table 2).

The species-specific regressions were applied to the annual diameter measurements of all trees in the core area of the plots for each year of the experiment, correcting for slight underestimation during back-transformation of biomass estimates using the method of Baskerville (1972). Biomass estimates of foliage, wood and heart roots of all trees in the subplots (g) were summed and divided by subplot area to arrive at stand-level estimates of tree biomass (g m^{-2}). Between-tree coarse and fine root biomass (g m^{-2}) for each year of the experiment was estimated by assuming that the partitioning of total root biomass to heart, coarse and fine root fractions determined by destructive harvest in 2000 and 2002 did not change over time. We then applied the respective root fractions to the allometrically determined estimates of heart root biomass for each year, to arrive at total root biomass. Annual fine root production cannot be determined by this method; however, a published record of annual peak fine root biomass will be useful when fine root turnover rates become available. Additionally, presentation of fine root biomass data allows comparison of the relative size of the fine root pool relative to other plant parts. Annual net wood and coarse root production was determined by subtracting previous year biomass from subsequent year biomass (g m^{-2} yr^{-1}). Tree mortality was not quantified explicitly in the current study; however, individual trees contributed to stand-level biomass and production estimates

Table 2 Allometric regressions used to predict tree component biomass of young aspen, paper birch and sugar maple at the Aspen FACE project in Rhinelander, WI, USA

Dependent variable	Intercept (P)	Parameter estimate (P)	MSE	R^2	n
Aspen foliage	1.48984 (<0.0001)	2.70111 (<0.0001)	0.14649	0.892	131
Aspen wood	1.48067 (<0.0001)	1.87997 (<0.0001)	0.04385	0.929	128
Aspen heart root	2.86029 (<0.0001)	1.87143 (<0.0001)	0.04421	0.929	128
Paper birch foliage	1.78036 (<0.0001)	2.38384 (<0.0001)	0.22940	0.836	37
Paper birch wood	3.19439 (<0.0001)	2.50650 (<0.0001)	0.06087	0.955	37
Paper birch heart root	2.48509 (<0.0001)	1.98989 (<0.0001)	0.05909	0.932	37
Sugar maple foliage	2.35586 (<0.0001)	2.29003 (<0.0001)	0.13239	0.906	25
Sugar maple wood	2.93748 (<0.0001)	2.88168 (<0.0001)	0.06722	0.968	25
Sugar maple heart root	3.03418 (<0.0001)	1.79167 (<0.0001)	0.10574	0.883	24

MSE, mean square error.
Models were developed from trees harvested destructively within FACE plots in 2000 and 2002. All models had the form $\log(y) = m \log(x) + b$, where y = biomass component (g) and x = diameter (cm). Baskerville's (1972) adjustment to the antilogarithm was applied when calculating absolute data from the log–log models.

only as long as they were alive. At the point when trees were recorded as 'dead' they were removed from subsequent allometric modeling, thereby implicitly accounting for mortality.

Stand-level estimates of total and component biomass and production were tested for main effects (CO_2, O_3) and split-plot effects (community, time) using split-plot ANOVA appropriate for the Aspen FACE experimental design (King *et al.*, 2001) using the STATISTICAL ANALYSIS SYSTEM software (SAS Institute, Cary, North Carolina, USA). Tree size in 1997 (diameter^2 × height) was used as a covariate in the ANOVA to account for initial differences in plant size.

Results

Annual biomass production

In 1997, the newly planted stands averaged 22, 15 and 11 g biomass m^{-2} in the aspen, aspen–birch and aspen–maple communities, respectively (Table 3; Fig. 1). Annual production of foliage, wood (stem + branches), and coarse roots in control plots increased from 1998 to 2003 in all communities (time $P < 0.000$). Over this time, annual foliage production averaged 250, 213 and 127 g m^{-2} in the aspen, aspen–birch and aspen–maple communities, respectively. Wood production averaged 372, 285 and 190 g m^{-2}, while coarse root production averaged 90, 76 and 52 g m^{-2} in the aspen, aspen–birch and aspen–maple communities, respectively. Annual fine root production was not quantified in the current study; however, July fine root biomass averaged 24, 20 and 24 g m^{-2} in the aspen, aspen–birch and aspen–maple control plots, respectively, from 1998 to 2003.

Annual biomass production of foliage, wood and coarse roots varied in response to the treatments over time, with significant CO_2 × time, O_3 × time and CO_2 × community × time interactions (Tables 3, 4). This variation in community responses to the treatments is not surprising given the

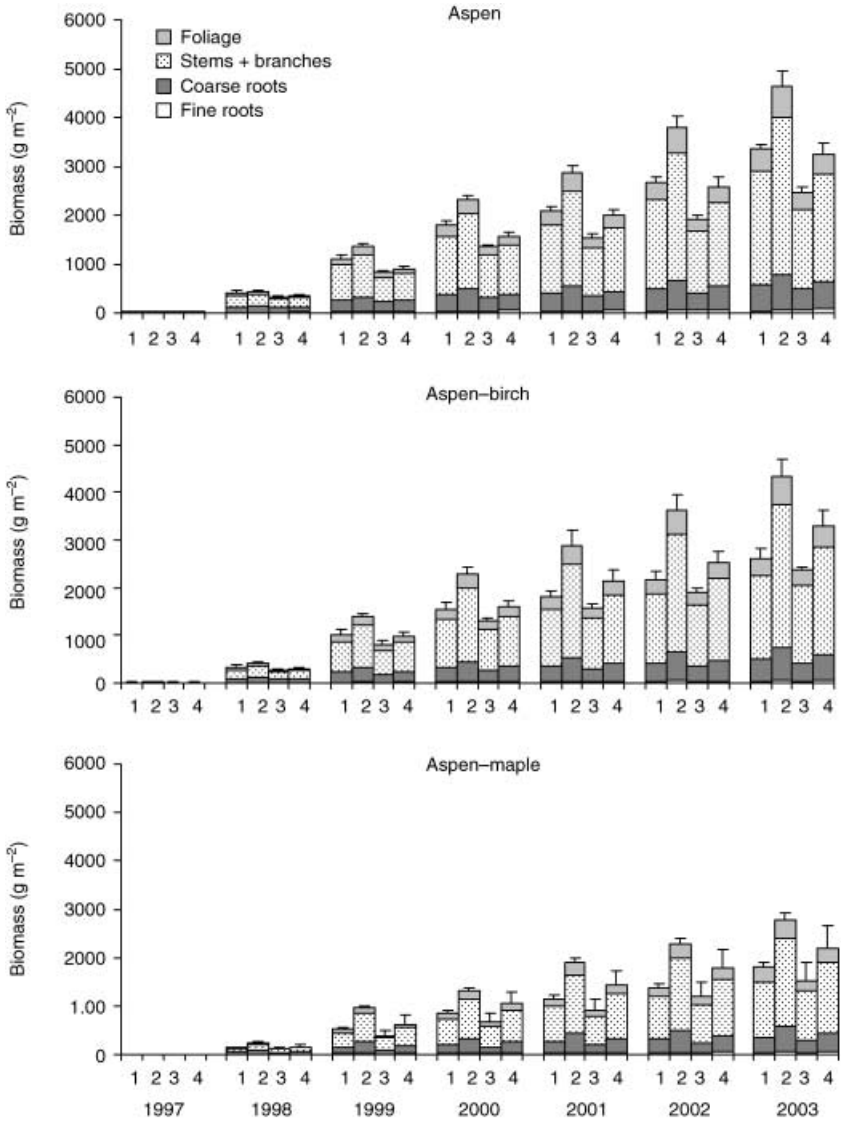

Fig. 1 Stand-level biomass of young forest stands exposed to a factorial arrangement of atmospheric CO_2 and tropospheric O_3 treatments for 7 yr at the Aspen FACE project in Rhinelander, WI, USA. Values are means (n = 3); bars are SEM total biomass. Treatment indicators: 1, control (ambient CO_2, ambient O_3); 2, elevated CO_2 (target 560 µl l^{-1}); 3, elevated O_3 (1.5× ambient); 4, combined (elevated CO_2 + O_3).

Table 3 Beginning (1997) and end (2003) biomass pools (g biomass m^{-2}) and yearly biomass production (g biomass m^{-2} yr^{-1}) by community and atmospheric treatment for foliage, wood (stems + branches), and coarse roots (tap root + all roots >1.0 mm diameter)

	Control			Elevated CO_2			Elevated O_3			+CO_2, +O_3		
Parameter	AA	AB	AM	AA	AB	AM	AA	AB	AM	AA	AB	AM
Pool size, 1997												
Foliage	1.5 (0.1)	1.4 (0.3)	0.9 (0.0)	1.6 (0.1)	1.5 (0.0)	1.0 (0.1)	1.5 (0.2)	1.4 (0.1)	0.8 (0.0)	1.5 (0.1)	1.4 (0.1)	1.0 (0.0)
Wood	7.6 (0.4)	5.7 (1.0)	2.5 (0.1)	8.0 (0.2)	6.1 (0.1)	3.2 (0.3)	7.3 (1.1)	6.0 (0.3)	2.5 (0.2)	7.2 (0.6)	5.7 (0.7)	2.8 (0.3)
Coarse roots	11.2 (0.3)	7.2 (0.8)	5.9 (0.1)	12.2 (0.2)	7.4 (0.2)	8.4 (0.5)	11.5 (1.2)	6.8 (0.2)	4.7 (0.3)	11.6 (0.7)	7.0 (0.9)	7.1 (0.4)
Fine roots	0.7 (0.0)	0.5 (0.0)	0.7 (0.0)	0.9 (0.0)	0.5 (0.0)	0.8 (0.0)	1.4 (0.1)	0.4 (0.0)	0.6 (0.0)	1.6 (0.1)	0.6 (0.1)	0.9 (0.0)
Foliage, wood and coarse root production, and fine root biomass, 1998												
Foliage	46.5 (5.8)	38.8 (8.4)	15.7 (1.0)	48.8 (5.0)	51.5 (3.9)	24.2 (3.1)	34.8 (2.6)	33.4 (3.2)	14.4 (1.4)	37.7 (4.1)	37.4 (2.3)	17.7 (5.4)
Wood	226.1 (29.3)	174.8 (38.1)	70.2 (4.7)	237.4 (25.2)	233.1 (18.9)	109.4 (15.0)	166.9 (12.7)	148.4 (13.6)	65.0 (7.8)	181.6 (21.0)	167.4 (9.9)	77.0 (24.7)
Coarse roots	105.0 (9.8)	79.8 (13.4)	41.2 (1.8)	112.7 (10.1)	100.9 (7.8)	71.3 (7.5)	87.9 (3.4)	64.0 (3.8)	31.7 (2.6)	95.1 (8.2)	77.2 (3.5)	46.9 (12.6)
Fine roots	7.8 (0.7)	5.7 (0.9)	5.7 (0.2)	9.5 (0.8)	8.1 (0.6)	7.4 (0.7)	11.9 (0.5)	4.7 (0.2)	4.9 (0.3)	15.2 (1.1)	7.4 (0.3)	7.3 (1.8)
Foliage, wood and coarse root production, and fine root biomass, 1999												
Foliage	139.2 (7.3)	132.1 (14.7)	65.0 (4.6)	169.5 (8.6)	187.8 (4.7)	116.7 (5.5)	99.5 (5.7)	108.5 (9.3)	49.6 (11.8)	107.7 (5.6)	130.2 (9.2)	77.3 (18.9)
Wood	471.6 (11.1)	452.2 (38.0)	236.4 (23.4)	614.7 (38.9)	667.4 (27.8)	465.4 (45.1)	327.1 (16.2)	358.6 (36.1)	173.9 (53.5)	356.1 (8.1)	449.3 (35.4)	297.4 (75.9)
Coarse roots	135.8 (3.0)	131.6 (7.4)	81.6 (6.9)	175.9 (10.7)	181.8 (7.7)	159.4 (14.2)	107.5 (2.2)	101.3 (8.0)	51.4 (10.7)	115.9 (1.4)	130.5 (9.0)	100.4 (18.3)
Fine roots	16.9 (0.6)	14.4 (1.3)	15.7 (0.8)	23.0 (1.0)	21.8 (0.6)	22.2 (0.6)	24.8 (0.8)	11.6 (0.6)	11.8 (1.8)	31.8 (1.2)	18.9 (1.0)	20.9 (4.1)
Foliage, wood and coarse root production, and fine root biomass, 2000												
Foliage	234.7 (11.5)	208.9 (21.3)	110.7 (7.8)	301.4 (12.0)	311.3 (21.0)	166.0 (5.9)	168.1 (6.0)	180.0 (9.5)	90.0 (23.7)	196.9 (9.8)	216.5 (14.9)	135.6 (29.3)
Wood	390.5 (24.4)	260.0 (13.4)	216.3 (21.0)	538.9 (34.9)	443.4 (71.7)	250.6 (38.9)	278.8 (12.4)	260.0 (22.3)	194.7 (62.2)	376.5 (45.1)	317.4 (54.1)	292.5 (70.0)
Coarse roots	106.2 (5.8)	90.3 (6.7)	60.6 (4.9)	144.8 (7.8)	134.5 (21.0)	67.9 (12.8)	88.3 (3.1)	79.3 (3.2)	45.7 (8.5)	112.1 (10.2)	100.0 (14.9)	75.2 (16.5)
Fine roots	24.1 (0.9)	20.4 (1.7)	23.1 (1.3)	34.0 (1.3)	31.9 (2.1)	28.5 (0.6)	35.4 (0.5)	16.9 (0.5)	18.0 (2.9)	47.8 (1.7)	27.7 (1.5)	31.1 (5.6)
Foliage, wood and coarse root production, and fine root biomass, 2001												
Foliage	271.3 (11.2)	244.5 (19.8)	152.0 (11.3)	376.9 (22.1)	393.7 (45.1)	244.1 (14.3)	194.2 (7.6)	217.9 (13.7)	125.0 (32.7)	252.6 (19.2)	289.1 (35.5)	188.5 (38.3)
Wood	209.0 (12.1)	191.7 (16.6)	193.9 (21.8)	404.1 (62.9)	450.0 (118.9)	386.0 (48.7)	167.9 (7.4)	207.3 (18.1)	167.9 (47.5)	306.9 (54.6)	372.1 (126.9)	264.4 (61.3)
Coarse roots	35.1 (2.0)	37.8 (2.2)	49.8 (3.2)	70.0 (12.1)	83.2 (24.5)	96.9 (6.3)	25.7 (1.3)	38.2 (4.2)	35.6 (6.3)	57.4 (9.5)	74.2 (24.7)	58.3 (10.6)
Fine roots	26.4 (0.8)	22.9 (1.6)	29.2 (1.6)	39.4 (2.0)	38.2 (3.9)	37.5 (1.2)	38.5 (0.7)	19.5 (0.8)	22.8 (3.7)	56.0 (2.9)	34.2 (3.2)	38.9 (6.4)
Foliage, wood and coarse root production, and fine root biomass, 2002												
Foliage	355.1 (15.8)	295.9 (24.8)	187.6 (10.9)	507.8 (32.9)	496.5 (45.7)	299.2 (16.2)	246.3 (12.5)	265.9 (10.6)	164.8 (44.2)	335.1 (27.7)	346.1 (32.7)	237.6 (49.6)
Wood	434.5 (28.6)	296.4 (7.4)	177.7 (17.0)	695.4 (73.2)	567.0 (55.6)	295.8 (37.3)	283.1 (30.3)	252.2 (29.2)	193.3 (59.5)	431.4 (61.3)	376.0 (47.8)	244.2 (54.4)
Coarse roots	77.8 (5.4)	52.5 (4.3)	38.8 (3.5)	113.4 (7.5)	93.7 (7.3)	64.4 (5.5)	51.0 (3.6)	46.9 (8.4)	36.6 (8.2)	80.9 (10.6)	55.1 (8.0)	50.7 (11.6)
Fine roots	31.7 (1.1)	26.4 (1.8)	34.0 (1.5)	48.1 (2.5)	45.3 (4.1)	43.5 (1.5)	44.6 (1.0)	22.6 (0.5)	27.8 (4.6)	67.6 (3.8)	39.1 (2.9)	45.8 (7.8)
Foliage, wood and coarse root production, and fine root biomass, 2003												
Foliage	450.8 (17.4)	360.2 (26.7)	232.7 (12.9)	627.8 (49.0)	600.5 (48.5)	365.1 (21.3)	320.8 (19.1)	329.8 (12.7)	213.5 (58.7)	428.5 (30.4)	452.9 (43.2)	295.2 (62.7)
Wood	500.1 (9.8)	333.0 (9.8)	244.6 (52.3)	642.7 (89.5)	568.9 (51.7)	352.2 (48.7)	405.9 (28.6)	325.7 (19.5)	242.7 (75.7)	484.9 (17.7)	534.6 (60.0)	295.4 (69.1)
Coarse roots	82.3 (1.6)	62.1 (2.6)	42.1 (3.7)	91.5 (10.5)	86.1 (12.9)	68.6 (5.3)	66.6 (5.3)	60.1 (3.3)	39.7 (8.9)	84.5 (1.7)	101.8 (9.1)	53.9 (13.3)
Fine roots	37.2 (1.2)	30.5 (1.9)	39.1 (1.7)	55.1 (3.3)	51.7 (4.1)	50.0 (1.8)	52.5 (1.6)	26.6 (0.6)	33.2 (5.7)	79.7 (3.8)	48.0 (3.6)	53.1 (9.5)
Pool size, 2003*												
Foliage	450.8 (17.4)	360.2 (26.7)	232.7 (12.9)	627.8 (49.0)	600.5 (48.5)	365.1 (21.3)	320.8 (19.1)	329.8 (12.7)	213.5 (58.7)	428.5 (30.4)	452.9 (43.2)	295.2 (62.7)
Wood	2307.3 (89.4)	1773.9 (132.1)	1125.2 (67.4)	3223.2 (253.4)	3003.4 (246.1)	1816.7 (108.4)	1638.8 (99.2)	1611.9 (63.4)	1026.2 (306.1)	2192.8 (157.3)	2246.4 (216.2)	1461.1 (323.6)
Coarse roots	553.5 (18.4)	461.3 (29.5)	320.1 (13.8)	720.6 (43.9)	687.7 (54.7)	537.1 (19.6)	438.6 (13.6)	396.6 (9.4)	245.6 (42.5)	557.4 (26.4)	545.9 (41.7)	392.6 (70.6)
Fine roots	37.2 (1.2)	30.5 (1.9)	39.1 (1.7)	55.1 (3.3)	51.7 (4.1)	50.0 (1.8)	52.5 (1.6)	26.6 (0.6)	33.2 (5.7)	79.7 (3.8)	48.0 (3.6)	53.1 (9.5)

Fine root (<1.0 mm diameter) data are standing crop at height of growing season (mid-July). Values are means (n = 3) with standard error in parentheses. Community indicators: AA, pure aspen; AB, aspen–birch mix; AM, aspen–maple mix.

*Wood and coarse root pool size estimates for 2003 were determined using allometric biomass equations and may differ slightly from estimates arrived at by summing annual production caused by rounding. Differences are generally <3% and within the standard error of the allometric estimates.

Table 4 Statistical significance of atmospheric CO_2 (CO_2), tropospheric O_3 (O_3) and community experimental factors on stand-level foliage, wood and coarse root production from 1998 to 2003 at the Aspen FACE project in Rhinelander, WI, USA

Source	Foliage	Wood	Coarse roots
Block	ns	ns	ns
CO_2	0.041	0.009	0.004
O_3	0.039	0.039	0.017
$CO_2 \times O_3$	ns	ns	ns
Community	0.001	ns	ns
$CO_2 \times$ community	ns	ns	ns
$O_3 \times$ community	ns	0.057	ns
$CO_2 \times O_3 \times$ community	ns	ns	ns
Time	<0.000	<0.000	<0.000
$CO_2 \times$ time	<0.000	<0.000	0.001
$O_3 \times$ time	0.001	0.002	<0.000
$CO_2 \times O_3 \times$ time	ns	ns	ns
Community × time	<0.000	<0.000	<0.000
$CO_2 \times$ community × time	ns	0.059	0.031
$O_3 \times$ community × time	ns	ns	ns
$CO_2 \times O_3 \times$ community × time	ns	ns	ns

Data were analyzed using a repeated-measures split-plot ANOVA after King *et al*. (2001).
Wood, stem + branches; coarse roots, roots >1 mm diameter; ns, not statistically significant ($P > 0.05$).
Fine root production was not determined in this study.

interannual variability of weather, host-specific pathogens, etc. in such a long-term experiment. On average, elevated CO_2 increased foliage, wood and coarse root production from 31 to 71% relative to the control, with the aspen–birch and aspen–maple communities showing larger relative responses than pure aspen (Table 5). Elevated O_3 decreased annual production of foliage, wood and coarse roots relative to the control by 9–29% on average, with the aspen community generally showing the largest decrease in growth. Concurrent exposure to elevated CO_2 and O_3 caused small reductions in aspen foliage, wood and coarse root annual production relative to the control, and 15–30% increases in the aspen–birch and aspen–maple communities (Tables 4, 5).

Relative to the control, average July fine root biomass increased 45, 64 and 29% under elevated CO_2 in the aspen, aspen–birch and aspen maple communities, respectively, Tables 3, 5, 6). Tropospheric ozone caused an average decrease in fine root biomass relative to the control of 15 and 19% in the aspen–birch and aspen–maple communities (Tables 3, 5, 6), respectively, but curiously increased it 44% in the aspen community. In the $+CO_2$, $+O_3$ treatment, mean July fine root biomass increased relative to the control 107, 46 and 34% in the aspen, aspen–birch and aspen–maple communities, respectively (Tables 3, 5, 6).

Biomass accumulation

Changes in annual production caused by the experimental treatments during the 7-yr experimental period had cumulative impacts on standing biomass in the aspen, aspen–birch and aspen–maple communities (Table 6; Fig. 1). By 2003, total tree biomass in control plots averaged 3349, 2626 and 1717 g m^{-2} in the aspen, aspen–birch and aspen–maple communities, respectively (Table 3; Fig. 1). Biomass was distributed on average as 13.8% foliage, 67.3% wood (stems + branches), 17.6% coarse roots, and 1.5% in fine roots, with minor variations between communities. Allometric analyses (King *et al*., 1996) showed that shifts between the major biomass fractions because of the treatments were statistically insignificant (data not shown).

Relative to the control, elevated CO_2 increased total biomass by 24.9, 45.6 and 60.3% averaged over all years in aspen, aspen–birch and aspen–maple communities, respectively (Fig. 2). The degree of stimulation increased over time, with a significant $CO_2 \times$ time interaction (Table 6; Fig. 2). Tropospheric O_3 decreased standing biomass relative to the control by an average 22, 13 and 14% in the aspen, aspen–birch and aspen–maple communities, respectively (Table 6; Fig. 2). The aspen community sustained the largest decline, whereas growth in the aspen–birch and aspen–maple communities became less sensitive to tropospheric O_3 over time (Table 6; Fig. 2). Concurrent exposure to elevated CO_2 provided some protection against the negative effects of O_3 (Figs 1, 2). Standing biomass in the aspen community under the combined treatment ($+CO_2$, $+O_3$) declined on average 8% relative to the control, but by the fourth year of treatment had recovered to near ambient levels. Biomass production in aspen–birch and aspen–maple communities under concurrent exposure was

Table 5 Average relative response (percentage change relative to control) of foliage, wood (stems + branches), and coarse root mean annual production, and mean fine root biomass from 1998 to 2003, to experimental treatments at the Aspen FACE project in Rhinelander, WI, USA

	$+CO_2$			$+O_3$			$+CO_2 + O_3$		
Parameter	AA	AB	AM	AA	AB	AM	AA	AB	AM
Foliage	35.7	59.4	59.1	–29.0	–11.3	–13.9	–9.3	15.0	24.6
Wood	40.4	71.5	63.2	–27.0	–9.1	–8.9	–4.2	29.8	29.1
Coarse roots	30.6	49.8	68.3	–21.2	–14.2	–23.4	0.7	18.7	22.7
Fine roots	45.1	63.8	28.8	44.1	–15.3	–19.3	106.9	45.7	34.3

Values calculated as (treatment mean – control mean)/control mean × 100.
Community indicators: AA, pure aspen; AB, aspen–birch mix; AM, aspen–maple mix.

Table 6 Statistical significance of atmospheric CO_2, tropospheric O_3 and community experimental factors on stand-level biomass from 1997 to 2003 at the Aspen FACE project in Rhinelander, WI, USA

Source	Foliage	Wood	Coarse roots	Fine roots	Total
Block	ns	ns	ns	ns	ns
CO_2	0.041	0.008	0.004	0.003	0.008
O_3	0.039	0.015	0.008	ns	0.016
$CO_2 \times O_3$	ns	ns	ns	ns	ns
Community	0.001	0.016	ns	<0.000	0.031
$CO_2 \times$ community	ns	ns	ns	0.031	ns
$O_3 \times$ community	ns	0.009	ns	<0.000	0.043
$CO_2 \times O_3 \times$ community	ns	ns	ns	ns	ns
Time	<0.000	<0.000	<0.000	<0.000	<0.000
$CO_2 \times$ time	<0.000	<0.000	<0.000	<0.000	<0.000
$O_3 \times$ time	0.001	<0.000	<0.000	ns	<0.000
$CO_2 \times O_3 \times$ time	ns	ns	ns	ns	ns
Community × time	<0.000	<0.000	<0.000	<0.000	<0.000
$CO_2 \times$ community × time	ns	ns	ns	0.011	ns
$O_3 \times$ community × time	ns	<0.000	ns	0.036	0.001
$CO_2 \times O_3 \times$ community × time	ns	ns	ns	ns	ns

Data were analyzed using a repeated-measures split-plot ANOVA after King *et al*. (2001). Wood, stems + branches; coarse roots, all roots >1 mm diameter; fine roots, roots <1 mm diameter; ns, not statistically significant ($P > 0.05$).

comparable with, or greater than, that in control plots, with a stimulation of 8 and 24%, respectively, averaged over the 7-yr period (Fig. 2).

Discussion

The Aspen FACE project has provided a unique experimental platform for investigating forest ecosystem responses to the rising concentrations of atmospheric CO_2 and tropospheric O_3. A hallmark of the experiment is the consistency of response of many ecosystem properties to the atmospheric treatments (Karnosky *et al*., 2003, 2005), including growth (Isebrands *et al*., 2001; Percy *et al*., 2002; Karnosky *et al*., 2005); leaf physiology (Noormets *et al*., 2001; Takeuchi *et al*., 2001); soil respiration and soil C cycling (King *et al*., 2001, 2004; Loya *et al*., 2003; Karberg *et al*., 2005); and soil N transformations and microbial dynamics (Larson *et al*., 2002; Holmes *et al*., 2003; Zak *et al*., 2003). The primary driver of many of these ecosystem-level responses to the experimental treatments is NPP. We hypothesized that NPP would be stimulated by elevated atmospheric CO_2 and decreased by tropospheric O_3. Combined fumigation was expected to result in NPP similar to that of the control. This analysis of 7 yr of NPP data largely supports these hypotheses.

Allometric modeling of biomass and NPP

Growth of the experimental forest communities of the Aspen FACE project compares well with growth of stands of similar age reported from sites in north-central Wisconsin, Minnesota and Alaska. After 7 yr growth, control stands of pure aspen at our site had total above-ground (wood + foliage) and below-ground (coarse + fine roots) biomass of 2758 and 591 g m^{-2}, respectively. Ruark & Bockheim (1988) reported above- and below-ground biomass in naturally regenerated 8-yr-old aspen stands in north-central Wisconsin of 2500 and 1380 g m^{-2}, respectively. The discrepancy in below-ground biomass was probably caused by residual root biomass from the previous stand in the study of Ruark & Bockheim (1988), whereas in our study cuttings were planted in root-free soil.

Alban & Perala (1990) reported average above-ground biomass of 2376 g m^{-2} from a series of sites 5 yr after harvest in northern Michigan and Minnesota. Paré & Van Cleve (1993) reported above-ground biomass of naturally regenerated aspen 14 yr after harvest near Fairbanks, Alaska of *c.* 5000 g m^{-2}, roughly twice the age and biomass of our study. The agreement between our study and these published reports gives confidence that the Aspen FACE stands are representative of natural forests, and supports our allometric approach to estimating biomass.

Applying species- and site-specific biomass regressions to annual nondestructive measurements of all trees in the experimental plots at Aspen FACE will be valid for estimating biomass and NPP of wood and coarse roots for some time to come (perhaps with some additional destructive harvesting). However, the utility of the allometric approach for fine roots may be limited. There has been difficulty in developing stand-level scaling relationships between above-ground plant parts and soil core estimates of fine root biomass (Kurz *et al*., 1996; King *et al*., 1999). This is because of high spatial variation in root distributions, and extremely plastic fine root responses to differences in environmental conditions (Nadelhoffer, 2000; King *et al*., 2002; Pregitzer, 2002). In the current study, we partitioned a fraction of heart root biomass (determined allometrically) to fine roots based on measured root biomass

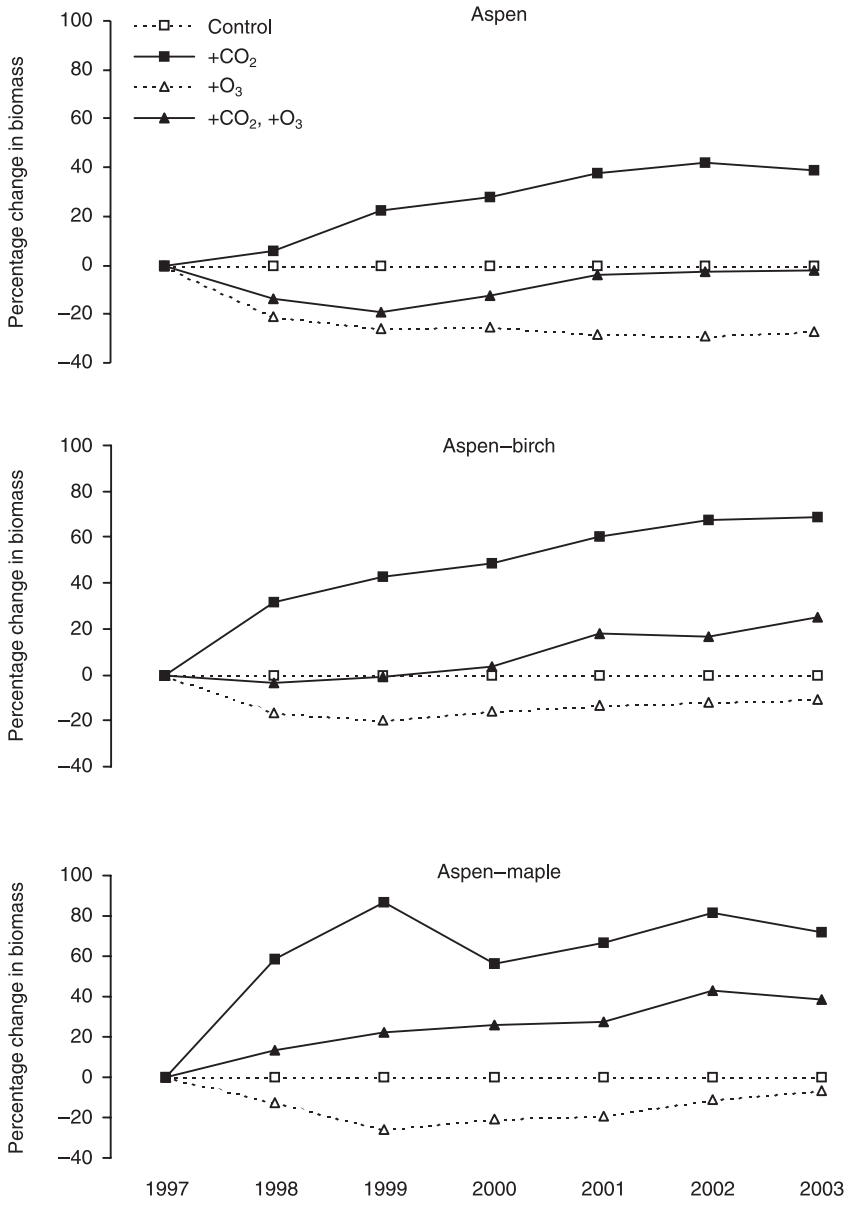

Fig. 2 Response of total biomass production of young forest stands exposed to a factorial arrangement of atmospheric CO_2 and tropospheric O_3 treatments for 7 yr at the Aspen FACE project in Rhinelander, WI, USA. Calculated as (treatment biomass – control biomass)/control biomass × 100.

partitioning from the destructive harvests in 2000 and 2002, of which the fine root sampling was much more rigorous in 2002. The fraction of total root biomass partitioned to fine roots varies with seasonal changes in fine root standing crop (Hendrick & Pregitzer, 1996; King *et al.*, 2002) and stage of stand development (King *et al.*, 1999). Hence, fine root biomass determined from our 'static' partitioning may or may not accurately reflect standing fine root biomass at a given point in time, and does not capture fine root production and turnover.

Similarly, allometric modeling of foliage biomass (NPP) at Aspen FACE has been valid for the early stage of stand development, but its utility will be limited in the future. Comparison of allometric estimates of stand-level foliage production (this study) with litter-trap estimates of litter production showed good agreement (R^2 = 0.89) for the years 2001–3 (C. P. Giardina, unpublished). However, foliage biomass becomes 'uncoupled' from stem growth after canopy closure in young stands, and is inversely related to it in older forests (Ovington, 1957; Ford, 1984; Cannell, 1985; Gower *et al.*, 1994; Miller, 1995). Collection of annual foliar litter production suggests the aspen and aspen–birch stands are approaching canopy closure; that is, the annual increment in litter production is decreasing (C.P.G., unpublished data). Therefore future stem growth may not be accompanied by proportional increments in foliage biomass, compromising the allometric approach.

Stimulation of NPP by elevated CO_2

This analysis of 7 yr of growth data supports our first hypothesis, that elevated atmospheric CO_2 (*c.* 550 ppm by

volume) will cause sustained enhancement of forest NPP and biomass accumulation. This is consistent with the thousands of studies conducted at smaller spatial and temporal scales and across a wide variety of plant species over the past several decades (Strain & Bazzaz, 1983; Eamus & Jarvis, 1989; Ceulemans & Mousseau, 1994; Strain & Cure, 1994; Amthor, 1995; Curtis & Wang, 1998; Norby *et al.*, 1999). Stimulation of total biomass accumulation by elevated atmospheric CO_2 at Aspen FACE averaged 43% for all communities, although this response developed over time (significant $CO_2 \times$ time interaction). This is higher than the average 25% growth enhancement reported for other forest FACE experiments (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002; Norby *et al.*, 2002; Calfapietra *et al.*, 2003), and the average 31% stimulation from a meta-analysis of the earlier elevated CO_2 literature (Curtis & Wang, 1998).

The large, sustained CO_2 enhancement of NPP at Aspen FACE could have several causes. Because of the relatively high latitude of the site (45°40′ N), the soil is of recent glacial origin, with good chemical and physical properties for forest growth (Dickson *et al.*, 2000). Analysis of soil N cycling from 1999 to 2003 (Holmes *et al.*, 2003, 2005) suggests that soil N availability is not constraining growth responses to elevated CO_2 at the Aspen FACE experiment. The north-temperate climate is mesic, with favorable site water balance for most of the year, because of low evaporative demand (calculated by King *et al.*, 2001). A large fraction of the global forest C sink occurs in recently glaciated north-temperate and boreal forest ecosystems, where long-term C storage in soils is especially important (Schlesinger, 1997; Myneni *et al.*, 2001). Therefore the nutrient limitation to sustained CO_2 enhancement of forest NPP, as reported from low-latitude forests on highly weathered soils (Oren *et al.*, 2001), may be less of a constraint at higher latitudes.

Additionally, the experimental stands at Aspen FACE are dominated by early successional species in the early stage of stand development, which confers greater growing space (less intertree competition) and greater productivity relative to older stands (Pregitzer & Euskirchen, 2004). This could provide the capacity for greater stimulation of NPP and other ecosystem properties in response to elevated CO_2 relative to older, closed-canopy forests (King *et al.*, 2004).

The stimulation of total biomass production at Aspen FACE was caused by proportional increases in all plant parts: roots, wood and foliage. Averaged across community type from 1997 to 2003, elevated CO_2 caused 42, 45 and 41% increases in foliage, wood and coarse root biomass, respectively. Allometric analyses on an individual tree basis, using the harvest data from 2000 and 2002 and at the stand level, showed that elevated CO_2 did not change biomass partitioning among plant parts (data not shown). This is consistent with our understanding of tree biomass partitioning responses to elevated atmospheric CO_2 (Gebauer *et al.*, 1996; King *et al.*, 1996; Norby *et al.*, 1999).

There were important differences in the magnitude of CO_2 enhancement of component and total plant biomass production between communities, however. The order of relative response was generally pure aspen < aspen–paper birch < aspen–sugar maple; however, the order of absolute stand-level biomass production has been pure aspen > aspen–paper birch > aspen–sugar maple. In the pure aspen community, it is possible that intraspecific competition has constrained the potential stand-level relative growth enhancement in response to elevated atmospheric CO_2. Interspecific competition in the aspen–birch community could possibly have allowed a greater overall growth response to elevated CO_2. The aspen–maple community started out with smaller trees and therefore less intertree competition (intra- and interspecific competition was reduced), hence there was a greater capacity to respond to elevated atmospheric CO_2.

McDonald *et al.* (2002) provide evidence that competitively advantaged trees in the pure aspen community at Aspen FACE show a greater relative growth response to elevated CO_2 compared with competitively disadvantaged trees in an autoregressive manner ('the big get bigger faster'). These results apparently scale to the level of the stand. It will be interesting to see how relative growth responses to the treatments change as the stands proceed through canopy closure, and intertree competition and mortality become more significant. More growing space in the young stands could contribute to the greater relative CO_2 growth enhancement at Aspen FACE compared with the Duke (DeLucia *et al.*, 1999; Hamilton *et al.*, 2002) and Oak Ridge National Laboratory (Norby *et al.*, 2002) experiments, which both have older, closed canopy forests. This is consistent with a recent synthesis of soil respiration results from the four forest FACE experiments, which found that the relative stimulation of soil respiration caused by elevated CO_2 was greater in young, open-canopy forests compared with older, closed-canopy forests (King *et al.*, 2004).

Decreased forest NPP from tropospheric O_3

Our second hypothesis was that elevated tropospheric O_3 (*c.* $1.5 \times$) would decrease forest NPP, which was again supported by this analysis of 7 yr of growth data from the Aspen FACE experiment. This result is largely consistent with the literature but, importantly, we feel provides realistic quantification of the magnitude of the response for an important forest type in north-temperate and boreal forest ecosystems. Our understanding of O_3 effects on vegetation is largely based on studies of crops or small trees grown in highly controlled environments for short periods (reviewed by Heck *et al.*, 1984; Pye, 1988; Samuelson & Kelly, 2001; Andersen, 2003). These studies show that, in a wide range of plant species, tropospheric O_3 causes almost universal reductions in crop yield or biomass production, but the magnitude of response has been highly dependent on experimental conditions. High

variation in experimental results and uncertain correlation between visible foliar injury and yield reduction have led to considerable efforts to compare seedling responses with those of mature trees to determine appropriate factors for scaling O_3 responses to the landscape (Chappelka & Samuelson, 1998; Matyssek & Innes, 1999; Samuelson & Kelly, 2001).

At Aspen FACE, chronic exposure to moderately elevated tropospheric O_3 (*c.* 1.5×) has resulted in an average reduction in biomass production of 22, 12 and 16% in the pure aspen, aspen–birch and aspen–maple communities, respectively. These results are comparable with the average 23% decrease in tree seedling growth reported in the review of Pye (1988), but higher than the 2.6–6.8% decrease in annual NPP in the USA during the late 1980s to early 1990s from the modeling study of Felzer *et al.* (2004). Importantly, the response to O_3 was modified by both community composition and time (significant $O_3 \times$ community $\times$ time interaction). The pure aspen community was the most sensitive to O_3 and maintained this sensitivity over time. The aspen–birch and aspen maple communities, however, appear to be losing sensitivity to O_3 relative to the control.

Differences in community response could be caused by compensatory growth of less-O_3-sensitive species (Pye, 1988; Broadmeadow & Jackson, 2000) in the mixed communities, or changes in O_3 responsiveness induced by competition (McDonald *et al.*, 2002; Liu *et al.*, 2004). In the aspen–maple community, sugar maple comprises *c.* 9% of wood biomass, whereas in the aspen–birch community the two species are more evenly represented with no clear dominance of one over the other (data not shown). Hence compensatory growth of less-O_3-sensitive species is unlikely to be the cause of the increased productivity over time. In a 2-yr phytotron study, Liu *et al.* (2004) observed that European beech experienced no reduction in total biomass production caused by elevated O_3 when grown in monoculture. However, when grown in mixed culture with Norway spruce O_3 caused a 32% reduction in beech biomass, and the spruce benefited (+13%) from the weak performance of its competitor. These results underscore the important fact that monospecific responses to O_3 are not simply additive, and more realistic experimental designs are required to determine long-term ecosystem responses to the changing atmosphere. An important aspect of the Aspen FACE experiment will be to see if the mixed communities fully regain productive capacity under elevated O_3.

As with elevated CO_2, growth under tropospheric O_3 does not appear to have altered biomass partitioning among the major plant parts, as there were no statistically significant shifts in root : shoot, foliage : branch or wood : coarse root ratios (data not shown). This finding apparently contradicts many earlier studies that show relative decreases in root growth under O_3, which is thought to aid in the repair of damaged photosynthetic structures by increased C allocation above ground (Karnosky *et al.*, 1996; Andersen, 2003). In our study, all plant parts became proportionally smaller under elevated O_3. The exception to this is fine roots in the pure aspen section, which showed an average 44% stimulation in biomass. Possible causes include (i) spurious values among the three replicates for each treatment; (ii) confounding by abundant fine roots from herbaceous species that proliferated under the open canopies of the elevated O_3 treatment; or (iii) it is a real effect. Fine root (<1-mm-diameter) biomass values for each replicate of the 2002 harvest upon which the static partitioning was based were 50.4, 48.1 and 34.0 g m^{-2}, compared with an average 31.7 g m^{-2} for control plots at that time. If herbaceous roots were accidentally included in our estimates, the static partitioning used here would propagate the error through each year of biomass estimation. This is unlikely as all communities were harvested and processed at the same time using the same method. Sampling error could also have biased towards high root biomass estimates, but this is unlikely as 10 cores of 15 cm diameter × 25 cm deep were used in each split-plot FACE ring section. The only other fine root harvest at the site performed in 1999 did not detect significant effects of O_3 on fine root biomass (King *et al.*, 2001). In any case, this finding is highly counterintuitive, and requires further study before we can conclude that elevated O_3 increases fine root biomass in young aspen ecosystems.

Tropospheric O_3 compromises stimulation of NPP caused by elevated CO_2

Our final hypothesis was that chronic exposure to elevated CO_2 and elevated tropospheric O_3 ($+CO_2$, $+O_3$) would result in forest NPP similar to that of the control. A putative 'protective effect' of elevated CO_2 has been discussed (Allen, 1990; Wustman *et al.*, 2003), in that decreased stomatal conductance under elevated CO_2 might decrease the flux of O_3 into the plant; there may be other protective mechanisms, such as responses of antioxidant enzymes (Rao *et al.*, 1995). Our analysis partially supports this hypothesis. For total and component biomass production, the interaction between CO_2 and O_3 was never statistically significant. Thus elevated CO_2 provided comparable stimulation to NPP at both levels of the O_3 treatment in all communities over time. Because of the sensitivity of the aspen community to O_3, however, total biomass production in this community was depressed for the first 3 yr of growth, after which it did not differ from the control. The aspen–birch and aspen–maple communities exhibited an average stimulation of total biomass production of 8 and 24%, respectively, under combined fumigation. Thus the large stimulation in biomass production all three communities experienced in response to elevated CO_2 was completely annulled or greatly reduced by concurrent exposure to moderate levels of tropospheric O_3.

Experiments using long-term exposure of trees to combined CO_2 and O_3 fumigation are beginning to show that responses to both gases are variable, depending on species/clone and

provenance. However, the antagonistic effects on growth of elevated CO_2 and tropospheric O_3 have generally been observed in these experiments. Dickson *et al.* (1998) exposed five hybrid poplar genotypes to factorial treatments of CO_2 and O_3 in open-top chambers (OTC) for 1 yr, and found that plants exposed to combined fumigation ($+CO_2$, $+O_3$) had biomass similar to the control. Broadmeadow & Jackson (2000) grew seedlings of oak, ash and pine under factorial CO_2 and O_3 treatments in OTC for 3 yr. Elevated CO_2 enhanced growth; O_3 decreased it; and combined fumigation provided some protection from O_3 in the order of species responsiveness: oak > pine > ash. In a 5-yr OTC experiment, Rebbeck & Scherzer (2002) found that yellow poplar growth was insensitive to O_3 alone, but increased 60% with combined fumigation ($+CO_2$, $+O_3$) relative to the control, but not until the fifth season. Similarly, Riikonen *et al.* (2004) found that growth of two clones of silver birch responded negatively to O_3, but only at ambient CO_2. Tree growth increased under elevated CO_2 and combined fumigation ($+CO_2$, $+O_3$) treatments. Together with our results these studies show that, in the long run, elevated CO_2 provides some protection from exposure to phytotoxic concentrations of tropospheric O_3 for a variety of forest tree species. However, this also means that gains in NPP that could be achieved under elevated CO_2 are being compromised by tropospheric O_3 pollution, and this has had continent-scale implications for C sequestration for some time (Felzer *et al.*, 2004).

Because CO_2 is chemically inert in the atmosphere, and human population growth and fossil energy consumption continue to increase, the concentration of atmospheric CO_2 will continue to rise for the foreseeable future. Tropospheric O_3 is highly reactive and was historically considered a regional pollutant. However, it is becoming apparent that the cumulative impact of industrialization around the globe is also raising the background concentration of this pollutant along with CO_2. Our analysis of 7 yr of growth data at the Aspen FACE project, and decades of earlier research, indicate that the concentration of atmospheric CO_2 expected for the year 2050 has the capacity to stimulate forest NPP. At least for young northern forests on glacial soils, this response does not appear to be constrained by nutrient or water limitations. However, the concurrent global rise in tropospheric O_3 is damaging forest physiology and growth to the point that potential gains in terrestrial C sequestration caused by rising CO_2 are partially or completely annulled. We conclude, therefore, that global monitoring of ambient O_3 exposure of vegetation should become an important part of government environmental protection programs. Moving forward with technologies that remove important anthropogenic precursors to photochemical O_3 formation (mainly oxidized forms of nitrogen) from automobile and industrial emissions would help to decrease concentrations of tropospheric O_3 because of its short half-life in the atmosphere, decreasing at least one constraint on the capacity of forest ecosystems to sequester atmospheric C.

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