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ESSAY REVIEW

Tropospheric O_3 moderates responses of temperate hardwood forests to elevated CO_2: a synthesis of molecular to ecosystem results from the Aspen FACE project

D. F. KARNOSKY,[1]† D. R. ZAK,[2] K. S. PREGITZER,[1,5] C. S. AWMACK,[3] J. G. BOCKHEIM,[4] R. E. DICKSON,[5] G. R. HENDREY,[6] G. E. HOST,[7] J. S. KING,[1] B. J. KOPPER,[3] E. L. KRUGER,[3] M. E. KUBISKE,[5] R. L. LINDROTH,[3] W. J. MATTSON,[5] E. P. MCDONALD,[5] A. NOORMETS,[8] E. OKSANEN,[9] W. F. J. PARSONS,[3] K. E. PERCY,[10] G. K. PODILA,[11] D. E. RIEMENSCHNEIDER,[5] P. SHARMA,[1] R. THAKUR,[1] A. SÔBER,[12] J. SÔBER,[1] W. S. JONES,[1] S. ANTTONEN,[13] E. VAPAAVUORI,[13] B. MANKOVSKA,[14] W. HEILMAN[15] and J. G. ISEBRANDS[16]

[1]*School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, Michigan 49931, USA;* [2]*University of Michigan, 430 E. University, Ann Arbor, Michigan 48109, USA;* [3]*University of Wisconsin, 1630 Linden Drive, Madison, Wisconsin 53706, USA;* [4]*University of Wisconsin, 1525 Observatory Drive, Madison, Wisconsin 53706, USA;* [5]*USDA Forest Service, North Central Research Station, Forestry Sciences Laboratory, 5985 Highway K, Rhinelander, Wisconsin 54501, USA;* [6]*Brookhaven National Laboratory, 1 South Technology Street, Upton, New York 11973, USA;* [7]*University of Minnesota-Duluth, Natural Resources Research Institute, 5013 Miller Trunk Highway, Duluth, MN 55811, USA;* [8]*University of Toledo, Department EEES, LEES Laboratory, Mail Stop 604, Toledo, Ohio 43606, USA;* [9]*University of Kuopio, PO Box 1627, 70211 Kuopio, Finland;* [10]*Natural Resources Canada, Canadian Forest Service, PO Box 4000, Fredericton, New Brunswick, Canada E3B 5P7;* [11]*Biological Sciences Department, University of Alabama-Huntsville, 301 Sparkman Drive, WH14Z, Huntsville, Alabama 35899, USA;* [12]*Estonian Institute of Ecology, 181 Rua Str, EE2400 Tartu, Estonia;* [13]*Suonenjoki Research Station, FIN-77600 Suonenjoki, Finland;* [14]*Forest Research Institute, T.G. Masarykova Street 2195, 960 92 Zvolen, Slovakia;* [15]*USDA Forest Service, 1407 S. Harrison Road, East Lansing, Michigan 48823, USA;* [16]*Environmental Forestry Consultants, LLC, PO Box 54, E7323 Hwy 54, New London, Wisconsin 54961, USA*

Summary

1. The impacts of elevated atmospheric CO_2 and/or O_3 have been examined over 4 years using an open-air exposure system in an aggrading northern temperate forest containing two different functional groups (the indeterminate, pioneer, O_3-sensitive species Trembling Aspen, *Populus tremuloides* and Paper Birch, *Betula papyrifera*, and the determinate, late successional, O_3-tolerant species Sugar Maple, *Acer saccharum*).
2. The responses to these interacting greenhouse gases have been remarkably consistent in pure Aspen stands and in mixed Aspen/Birch and Aspen/Maple stands, from leaf to ecosystem level, for O_3-tolerant as well as O_3-sensitive genotypes and across various trophic levels. These two gases act in opposing ways, and even at low concentrations ($1{\cdot}5\times$ ambient, with ambient averaging 34–36 nL L^{-1} during the summer daylight hours), O_3 offsets or moderates the responses induced by elevated CO_2.
3. After 3 years of exposure to 560 μmol mol^{-1} CO_2, the above-ground volume of Aspen stands was 40% above those grown at ambient CO_2, and there was no indication of a diminishing growth trend. In contrast, O_3 at $1{\cdot}5\times$ ambient completely offset the growth enhancement by CO_2, both for O_3-sensitive and O_3-tolerant clones. Implications of this finding for carbon sequestration, plantations to reduce excess CO_2, and global models of forest productivity and climate change are presented.

Key-words: Aggrading aspen forest, carbon budgets, carbon sequestration, interacting pollutants

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†Author to whom correspondence should be addressed. E-mail: karnosky@mtu.edu

Introduction

Global atmospheric CO_2 concentrations have risen by nearly 30% since pre-industrial times (Barnola *et al*. 1995; Stott *et al*. 2000; IPCC 2001). These increases are primarily due to fossil fuel emissions (Keeling *et al*. 1995). Similarly, emissions of oxidized nitrogen (NO_x) and volatile organic compounds from fossil fuel combustion have increased background concentrations of O_3 (Finlayson-Pitts & Pitts 1997; Fowler *et al*. 1998; Stevenson *et al*. 1998; Ryerson *et al*. 2001), which have risen some 36% over the same period (IPCC 2001). Fowler *et al*. (1999a, 1999b) suggest that nearly a quarter of the Earth's forests are currently at risk from tropospheric O_3 where peak concentrations exceed 60 nL L^{-1}. They further predict that half of the Earth's forests will be subjected to peak concentrations exceeding 60 nL L^{-1}.

Thousands of studies have been conducted to examine the impacts of elevated CO_2 (Ceulemans & Mousseau 1994; Saxe, Ellsworth & Heath 1998; Norby *et al*. 1999; Körner 2000) and O_3 (Chappelka & Samuelson 1998; Matyssek & Innes 1999; Bortier, Ceulemans & Temmerman 2000) on plant growth and biomass accrual. Many of these studies have been confounded by the artificial greenhouse conditions inside the exposure chambers (Olszyk, Tibbitts & Hertzberg 1980; McLeod, Fackrell & Alexander 1985). They have been limited by the available space to include only single trees or a few young, immature trees. Thus there is a need for larger-scale and longer-term studies to examine the impact of these gases on ecosystem structure and function (Heck *et al*. 1998).

Elevated CO_2 and O_3 affect trees in opposite ways. Elevated CO_2 stimulates photosynthesis (Tjoelker, Oleksyn & Reich 1998; Noormets *et al*. 2001a, 2001b) and growth above ground (Norby *et al*. 1999) and below ground (King *et al*. 2001; Kubiske & Godbold 2001), and delays autumnal foliar senescence (J.G. Isebrands, unpublished results). Trees grown under elevated CO_2 generally have lower nitrogen concentrations in their foliage (Cotrufo, Ineson & Scott 1998), lower Rubisco concentrations (Moore *et al*. 1999), and altered concentrations of defence compounds (Lindroth, Kinney & Platz 1993; Lindroth *et al*. 1997) and of antioxidants and other secondary metabolites (Norby *et al*. 2001a; Wustman *et al*. 2001).

In contrast to the largely beneficial effects of CO_2, O_3 is generally detrimental to tree growth and forest productivity. Ozone induces foliar injury (Karnosky 1976), decreases foliar chlorophyll content (Gagnon *et al*. 1992), accelerates leaf senescence (Karnosky *et al*. 1996), decreases photosynthesis (Coleman *et al*. 1995a), alters carbon allocation (Coleman *et al*. 1995b) and epicuticular wax composition (Mankovska, Percy & Karnosky 1998; Karnosky *et al*. 1999, 2002a), predisposes trees to attack by pests (Stark *et al*. 1968; Karnosky *et al*. 2002a) and decreases growth (Wang, Karnosky & Borman 1986; Karnosky *et al*. 1992, 1996, 1998). Extrapolation of open-top chamber O_3 exposures of Aspen to native Aspen stands suggests that 14–33% growth decreases could occur over 50% of its range in the eastern USA (Hogsett *et al*. 1997).

Current climate change scenarios predict further increases in atmospheric CO_2 (Stott *et al*. 2000) and O_3 concentrations (Stevenson *et al*. 1998; Fowler *et al*. 1999a, 1999b) over the next century. Little research has been done on the interactive impacts of these pollutants. Furthermore, conflicting results have been reported, even for a given species. For example, Volin & Reich (1996) and Volin, Reich & Givnish (1998) suggest that CO_2 ameliorates the effects of O_3 on trembling Aspen (*Populus tremuloides* Michx.) while Kull *et al*. (1996), McDonald *et al*. (2000, 2002), Sôber *et al*. (2002), Isebrands *et al*. (2001) and Wustman *et al*. (2001) suggest that CO_2 does not ameliorate, but sometimes exacerbates the negative impacts of O_3. Thus we do not fully understand how forest tree growth, or the composition and functioning of forests, will be influenced by interacting CO_2 and O_3.

The FACTS II (Aspen FACE) project was established in 1997 as the first open-air facility to examine the responses of forest trees to interacting CO_2 and O_3 (Dickson *et al*. 2000). Our objective was to examine how elevated atmospheric CO_2 and O_3 will affect the carbon and nitrogen cycles and ecological interactions of forests. Specifically, we are studying the impacts of these co-occurring greenhouse gases on aggrading northern forests in terms of carbon sequestration, physiological processes, growth and productivity, competitive interactions and stand dynamics, interactions with pests, and ecosystem processes such as foliar decomposition, mineral weathering and nutrient cycling.

This review (1) summarizes early results from Aspen FACE which show remarkable consistency from molecular through to ecosystem levels, in that relatively low O_3 concentrations offset the responses of Aspen and Birch to elevated CO_2; (2) places our findings in regard to forest productivity in the context of other CO_2/O_3 interaction studies; (3) draws implications in terms of global modelling; (4) summarizes effects on higher trophic levels; and (5) addresses research gaps and opportunities to better understand ecosystem responses to long-term exposures to interacting CO_2 and O_3.

SUMMARY OF EXPOSURE METHODS AND PLANT MATERIALS

The Aspen FACE project is a full factorial experiment with three replicate 30 m diameter rings of four treatments: control (ambient CO_2, ambient O_3); elevated CO_2 (560 μmol mol^{-1} CO_2 vs. ambient CO_2 of ≈360 μmol mol^{-1}; elevated O_3 (1·5 × ambient); and elevated CO_2 plus O_3 (Fig. 1). The experiment was planted in July 1997. The two gases have been administered during daylight hours from budbreak to budset during 1998–2001 for total growing seasons of 166,

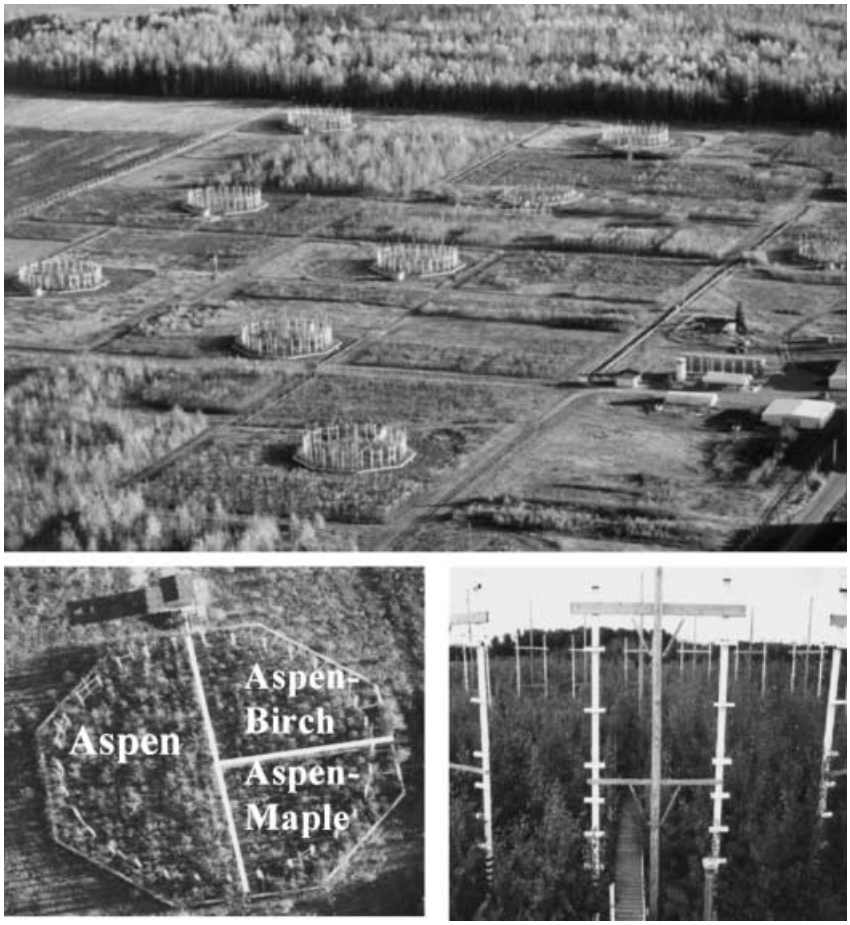

Fig. 1. Aerial view of the Aspen FACE project showing eight of 12 30 m diameter exposure rings (top). Each ring is divided into three sections as shown (bottom left). The gases are released through slots in the vertical vent pipes as shown in the bottom right photo.

143, 139 and 143 days, respectively. Daytime CO_2 concentrations in elevated CO_2 treatments averaged 530, 548, 548 and 541 μmol mol^{-1} for the four growing seasons. The respective 1 min average CO_2 concentrations were within 10% of the target for 78·5, 74·0, 67·3 and 71·2% of the time, and within 20% of the target for 94·0, 93·0, 91·9 and 92·7% of the time. O_3 exposures, which are summarized in Figs 2 and 3, averaged 54·5, 51·1, 48·9 and 52·8 nL L^{-1} (12 h daytime mean during the growing season) compared to control ring O_3, which averaged 34·6, 36·9, 36·0 and 36·6 nL L^{-1} for the same period. The growing season doses (SUM 00) for daylight hours were 97 900, 87 900, 78 800 and 90 700 nL L^{-1} h for O_3 treatments, compared with control values at 59 100, 62 800, 58 200 and 66 100 nL L^{-1} h. The CO_2 and O_3 concentrations were chosen to represent the predicted atmospheric concentrations of these gases in the northern Great Lakes Region in the year 2050.

The rings were planted using 3–6-month-old potted plants in midsummer 1997. The eastern half of each ring was randomly planted at 1 × 1 m spacing in two tree plots of five Aspen clones differing in O_3 tolerance (8L, 216 and 271 = relatively tolerant; 42E and 259 = relatively sensitive). The remaining half of each ring was further subdivided with a quarter ring being planted with alternating Aspen clone 216 and Birch (*Betula papyrifera*) and a quarter ring being planted with alternating Aspen clone 216 and Sugar Maple (*Acer saccharum*). Trembling Aspen is the most widely distributed tree species in North America. Aspen and Birch are the most important pulpwood species of the Great Lakes region, comprising over 70% of the round wood harvest (Piva 1996). According to the International Poplar Commission, the Aspen forest types make up more than 8·8 million ha in the USA and 17·8 million ha in Canada (Isebrands *et al.* 2001). Aspen–Birch–Maple stands are also important aesthetic components of northern forests. More details regarding the plant material, planting design, and the generation, dispensing and monitoring of CO_2 and O_3 are presented by Karnosky *et al.* (1999) and Dickson *et al.* (2000).

Synthesis of results

A summary of key results from the Aspen FACE project's establishment years, from time of plantation establishment in 1997 to crown closure in 2000, is shown in Table 1. The results are consistent across functional groups, from leaf biochemistry, gene

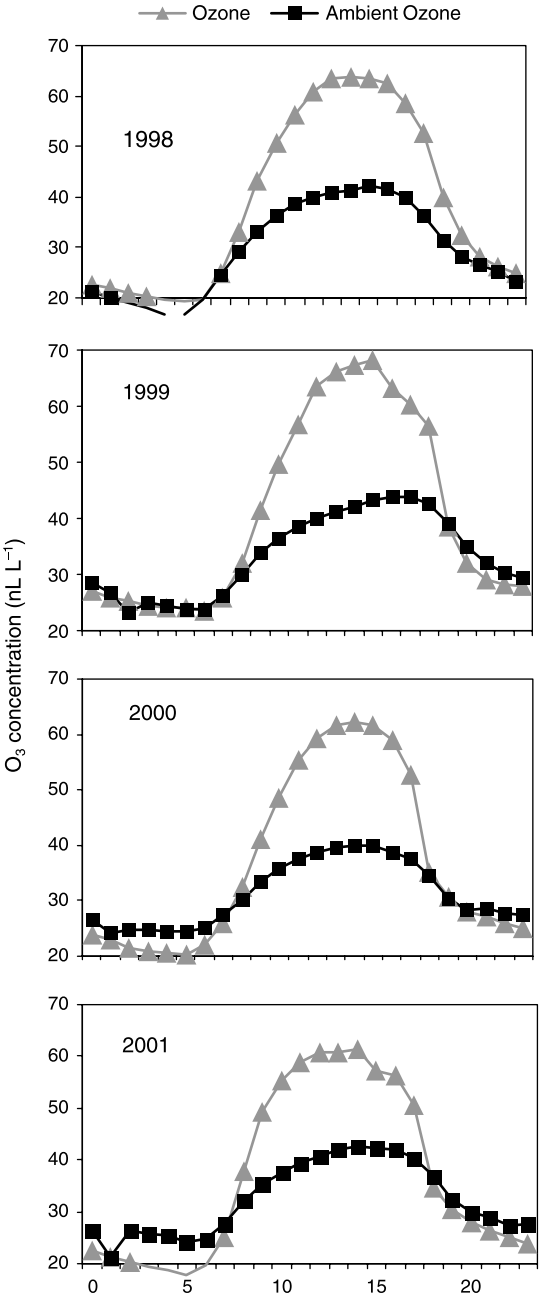

Fig. 2. Seasonal mean O_3 concentrations for ambient air (▲) and one elevated O_3 ring (■) in the Aspen FACE project.

expression and gas exchange through to ecosystem level, and across trophic levels in that elevated CO_2 and O_3 frequently exert opposite effects. When the two gases co-occur, low concentrations of ambient O_3 offset or substantially moderate the responses attributable to elevated CO_2.

GENE EXPRESSION AND BIOCHEMISTRY

Plants largely respond to stress by changes in assimilation of carbon and in the repartitioning of other resources. Elevated CO_2 and O_3 are sensed primarily by leaves (Dickson & Isebrands 1991) and result in dynamic and rapid changes in gene expression (Noormets, Podila & Karnosky 2000) and gas exchange (Hendrey *et al.* 1997). We have documented O_3-induced stimulations of transcript production of several antioxidants, including ascorbate peroxidase, catalase and glutathione reductase (Wustman *et al.* 2001). Interestingly, these same antioxidants appear to be downregulated under elevated CO_2, regardless of O_3 exposure, as was phenylalanine ammonia-lyase (PAL), a key enzyme in the shikimic acid pathway. CO_2- and O_3-induced decreases in transcripts of the small subunit of Rubisco were closely linked to independently measured decreases in Rubisco concentrations (Noormets *et al.* 2001a). Decreases in chlorophyll content, as measured by Wustman *et al.* (2001), were consistent with the degradation of chloroplasts (Oksanen, Sober & Karnosky 2001) under elevated O_3.

GAS EXCHANGE

The three tree species that we examined have differing photosynthetic responses to CO_2, O_3 and $CO_2 + O_3$. In the response of the upper crown to elevated CO_2, the rapid-growing, early successional species showed significant increases in light-saturated CO_2 assimilation rate (A_{max}): 20–33% for Aspen (Noormets *et al.* 2001a, 2001b; Sôber *et al.* 2003), and 50–72% for Birch (Takeuchi *et al.* 2001). These values were seen consistently from year 1, and no acclimation to CO_2 has yet been seen in sun leaves of Aspen and Birch. The relative limitation imposed by stomatal conductance on A_{max} in Aspen declined under elevated CO_2, indicating that upper canopy leaves operated closer to their CO_2-saturated rate (Noormets *et al.* 2001a). Improvements in shade photosynthesis of Aspen and Birch under elevated CO_2 were small, so that net gains in daily canopy C fixation were largely realized at the top of the canopy and were driven by increases in A_{max} (Takeuchi *et al.* 2001). We found minimal effects of CO_2 or O_3 on leaf dark respiration, with significant late-season increases in respiration only under elevated O_3 (Noormets 2001). Thus elevated CO_2 increased upper canopy A_{max} in Aspen by 33% and in Birch by 64% (Fig. 4), but not in Sugar Maple. Moreover, we found that O_3 and $CO_2 + O_3$ reduced the carboxylation efficiency of Aspen and Birch, but did not reduce A_{max} (Sôber *et al.* 2003). The declines in capacity were sufficient to eliminate any increase in A_{max} due to elevated CO_2 in Aspen and Birch (compare CO_2 and $CO_2 + O_3$ treatments in Fig. 4). Elevated O_3 did not reduce photosynthetic capacity or A_{max} in Sugar Maple.

In addition to species-specific responses, we also observed substantial variation in photosynthetic assimilation among Aspen genotypes. Elevated CO_2 stimulated A_{max} to a similar degree in two Aspen genotypes of contrasting sensitivity to O_3. However, elevated O_3 reduced A_{max} slightly in an O_3-tolerant genotype (clone 216) and more so in an O_3-sensitive genotype (clone 259). Elevated CO_2 counteracted this reduction

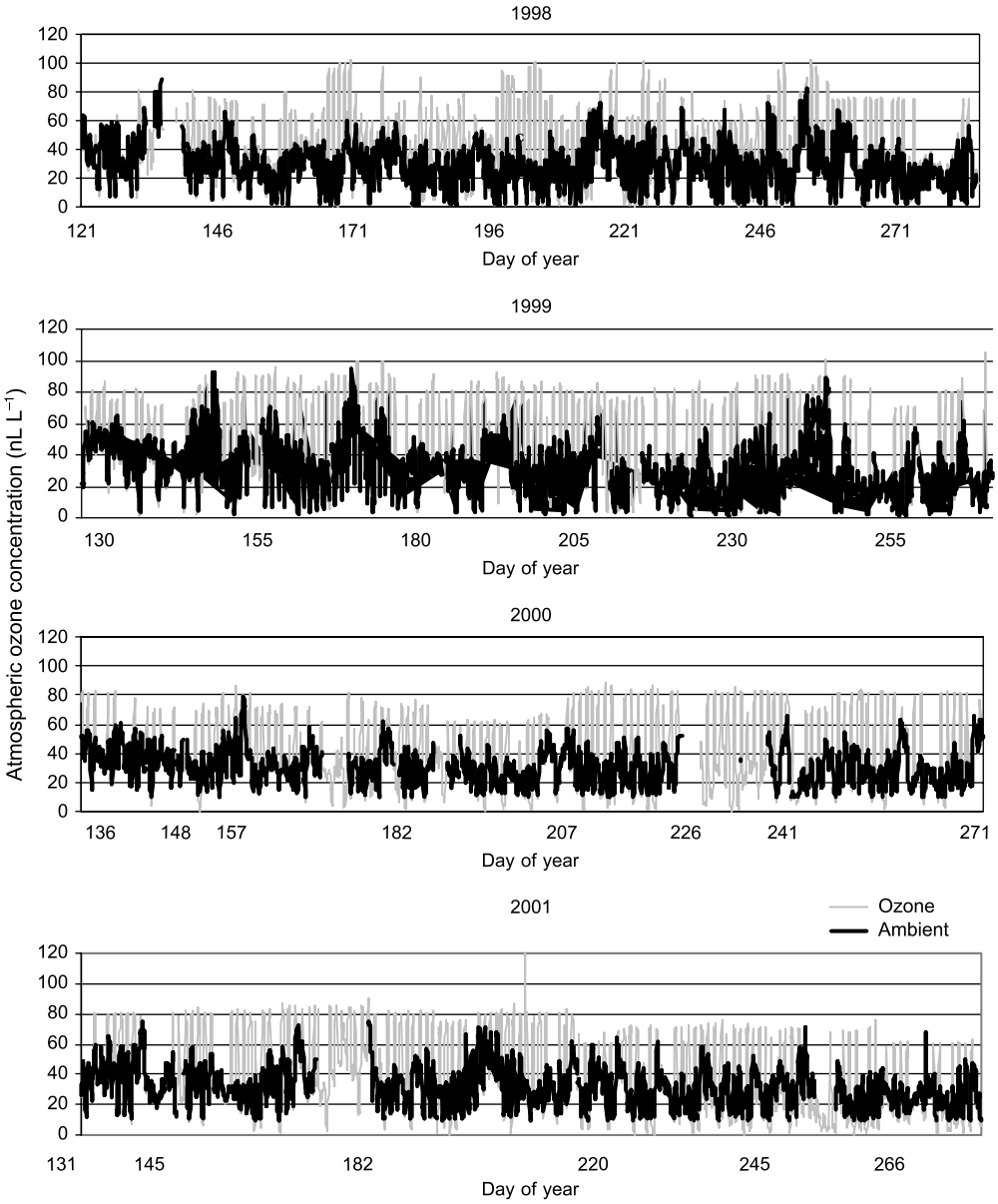

Fig. 3. Hourly O_3 concentrations from ambient air (black) and one elevated O_3 ring (grey) in the Aspen FACE project during 1998–2001.

in the O_3-tolerant genotype, in that A_{max} was 35% greater than that of clone 216 plants in the controls (Noormets *et al*. 2001a). In the O_3-sensitive genotype, however, A_{max} in the $CO_2 + O_3$ treatment was equivalent to that of clone 259 individuals from the controls. These responses occurred across leaves of different developmental stages and throughout the growing season.

Significant effects of elevated CO_2 and O_3 were also found for stomatal conductance (g_s). Generally, the stomata of Maple were much more responsive than those of Aspen and Birch to changing environmental conditions (light, CO_2 and relative humidity) across all treatments. Elevated CO_2 tended to reduce g_s for all three species, as expected (Noormets *et al*. 2001a; A. Sôber & P. Sharma, unpublished results). The largest decreases in g_s for Maple were under the combined $CO_2 + O_3$ treatment (A. Sôber & P. Sharma, unpublished results).

Increased leaf A_{max} of Aspen and Birch under elevated CO_2 was accompanied by significantly greater canopy leaf-area production (Fig. 5), a finding we believe is simply linked to the trees being larger in the elevated CO_2 rings, as we have not found changes in allometry associated with treatments. The O_3-induced decline in A_{max} of Aspen (Fig. 4) was also reflected in the decreased LAI of the Aspen canopies. Interestingly, Paper Birch had no O_3-induced decline in A_{max}, and the Aspen–Birch canopies exhibited no significant decrease in LAI under elevated O_3, reflecting the contribution of Birch to total canopy leaf area. The combination of elevated $CO_2 + O_3$ did not affect canopy LAI of either pure Aspen or Aspen–Birch.

The differences in A_{max} and LAI that we observed indicate that CO_2 and O_3 will alter carbon assimilation into terrestrial ecosystems in a manner consistent

Table 1. Summary of responses of Trembling Aspen to elevated CO_2 (+200 µmol mol^{-1}), O_3 (1·5 × ambient), or $CO_2 + O_3$ compared with control during 3 years of treatments at the Aspen FACE project

	CO_2	O_3	$CO_2 + O_3$	Source
Foliar gene expression and biochemistry				
Rubisco	↓*	↓	↓↓	Wustman *et al*. (2001); Noormets *et al*. (2001a)
RbcS transcripts†	↓	↓	↓↓	Wustman *et al*. (2001)
Chalcone synthase transcripts	n.s.	n.s.	n.s.	Wustman *et al*. (2001)
PAL transcipts	↓	↑	↓	Wustman *et al*. (2001)
SOD	n.s.	n.s.	n.s.	Wustman *et al*. (2001)
ACC oxidase	↓	↑	↓	Wustman *et al*. (2001)
Ascorbate peroxidase	↓	n.s.	↓	Wustman *et al*. (2001)
Catalase	↓	↑	↓	Wustman *et al*. (2001)
Glutathione reductase	↓	↑	↓	Wustman *et al*. (2001)
Phenolic glycosides	↑	↓	n.s.	Lindroth *et al*. (2002); Kopper & Lindroth (2002)
Tannins	n.s.	↑	↑	Lindroth *et al*. (2001); Kopper & Lindroth (2002)
Foliar nitrogen	↓	n.s.	↓	Lindroth *et al*. (2001); Kopper & Lindroth (2002)
C : N ratio of foliage	↑	n.s.	↑↑	Lindroth *et al*. (2001)
Starch	↓	↓	n.s.	Wustman *et al*. (2001)
Gas exchange				
A_{max} lower canopy	n.s.	↓↓	↑(young leaves) ↓(older leaves)	Takeuchi *et al*. (2001); Noormets *et al*. (2001a)
A_{max} whole canopy	↑↑	↓↓	n.s.	Noormets *et al*. (2001b)
Carboxylation efficiency	n.s.	↓	↓↓	Sôber *et al*. (2002)
Stomatal limitation	↓	n.s.	↓	Noormets *et al*. (2001a)
Stomatal conductance	↓	↓↑	↓	ôber *et al*. (2000), Noormets *et al*. (2001a)
Foliar respiration	n.s.	↑	n.s.	Takeuchi *et al*. (2001), Noormets (2001)
Soil respiration	↑↑	↓	n.s.	King *et al*. (2001)
Microbial respiration	↑↑	n.s.	n.s.	Phillips *et al*. (2002)
Stomatal density	n.s.	n.s.	n.s.	Percy *et al*. (2002a)
Chlorophyll content	↓	↓	↓	Wustman *et al*. (2001)
Chloroplast structure	↑	↓	↓	Oksanen *et al*. (2001), Takeuchi *et al*. (2001), Wustman *et al*. (2001)
O_3 flux	↓	↑↑	↑	Noormets *et al*. (2001a)
Growth and productivity				
Leaf thickness	↑	n.s.	n.s.	Oksanen *et al*. (2001)
Leaf size	↑	↓	↓	Wustman *et al*. (2001)
Leaf area	↑	↓	n.s.	Noormets *et al*. (2001b)
LAI	↑	↓	n.s.	Noormets (2001)
Height growth	↑	↓	n.s.	Isebrands *et al*. (2001)
Diameter growth	↑	↓	n.s.	Isebrands *et al*. (2001)
Volume growth	↑	↓	n.s.	Isebrands *et al*. (2001)
Leaf biomass	↑	↓	n.s.	McDonald & Isebrands, unpublished
Stem biomass	↑	↓	↓	McDonald & Isebrands, unpublished
Coarse root biomass	↑	↓	n.s.	King & Pregitzer, unpublished
Fine root biomass	↑	↓	n.s.	King *et al*. (2001)
Fine root turnover	↑	n.s.	n.s.	King *et al*. (2001)
Spring budbreak	n.s.	Delayed	n.s.	Isebrands & Karnosky, unpublished
Autumn budset	Delayed	Early	n.s.	Isebrands & Karnosky, unpublished
Foliar retention (autumn)	↑↑	↓↓	n.s.	Isebrands & Karnosky, unpublished
Wood chemical composition				
Lignin	n.s.	↑	n.s.	Anttonen *et al*. (2001)
Cellulose	n.s.	n.s.	n.s.	Anttonen *et al*. (2001)
Hemicellulose	n.s.	n.s.	n.s.	Anttonen *et al*. (2001)
Extractives	n.s.	n.s.	n.s.	Anttonen *et al*. (2001)
Leaf surfaces				
Crystalline wax structure	↓	↓	↓↓	Karnosky *et al*. (1999); Karnosky *et al*. (2002a)
Stomatal occlusion	↑	↑	↑↑	Karnosky *et al*. (1999)
Wax amount	↑	↑	n.s.	Karnosky *et al*. (2002a); Percy *et al*. (2002a)
Wax chemical composition	n.s.	Change	n.s.	Karnosky *et al*. (2002a)
Wax fatty acid *de novo* synthesis	↑↑	↑↑	↑	Percy *et al*. (2002a)
Wax hydrocarbon biosynthesis	↑↑	↑↑	n.s.	Percy *et al*. (2002a)
Wax carbon-chain length	↑↑	↑	↓	Karnosky *et al*. (2002a)
Wettability	n.s.	↑↑	↑	Karnosky *et al*. (2002a)

Table 1. *Continued*

	CO_2	O_3	$CO_2 + O_3$	Source
Trophic interactions				
Melampsora leaf rust	n.s.	↑↑	↑↑	Karnosky *et al.* (2002a); Percy *et al.* (2002b)
Aspen aphids	n.s.	n.s.	n.s.	Percy *et al.* (2002b)
Birch aphids	n.s.	n.s.	n.s.	Awmack & Lindroth, unpublished
Aspen Blotch Leafminer	↓	↓	↓	Kopper & Lindroth (2002)
Forest Tent Caterpillar	n.s.	↑	n.s.	Kopper (2001), Kopper & Lindroth (2002)
Oberea woodborer	↑	n.s.	↑	Mattson, unpublished
Ecosystem level				
NPP	↑	↓	n.s.	Kruger & McDonald, unpublished
Litter decomposition (*k* value)	↓	n.s.	↓	Parsons *et al.* (2000)
Nutrient mobilization	↑↑	n.s.	↑	King, unpublished
Water-use efficiency	↑	↓	↑	Sober *et al.* (2000)
Soil moisture	↑	↑	↑	King, unpublished
Competitive indices	↑	↓	↓↓	McDonald *et al.* (2000); McDonald *et al.* (2002)
Soil invertebrate diversity	n.s.	↓	↓	Loranger & Pregitzer, unpublished
Microbial enzymes	↑	n.s.	n.s.	Phillips *et al.* (2002); Larson *et al.* (2002)
Microbial biomass	↑	n.s.	n.s.	Phillips *et al.* (2002); Larson *et al.* (2002)

*Responses are shown as small but significant increases (↑), large and significant increases (↑↑), small but significant decreases (↓), large and significant decreases (↓↓), non-significant effects (n.s.) compared to trees grown in control rings with ambient CO_2 and O_3. Foliar analyses and leaf surface properties were largely determined from recently mature leaves of all three species during mid-season. Gas-exchange data were taken from all leaf ages and throughout the growing season.
†RbcS = small subunit of Rubisco; PAL = phenylalanine ammonialyase; SOD = super oxide dismutase; ACC = 1-aminocyclopropane-1-carboxylic acid; C = carbon; N = nitrogen; A_{max} = maximum photosynthesis rate; LAI = leaf area index; NPP = net primary productivity.

with the physiological response of the dominant vegetation. This key observation supports our hypothesis that ecosystem C assimilation, allocation and cycling are strongly influenced by the life-history traits of the dominant plant taxa, coupled with the manner in which plants increase or decrease amounts of C and N allocated to plant growth, storage and defence.

GROWTH AND PRODUCTIVITY

The photosynthetic responses of the species and genotypes in our experiment have influenced growth and litter production above and below ground (Parsons, Bockheim & Lindroth 2000; Isebrands *et al.* 2001; King *et al.* 2001). Enhanced rates of photosynthesis under elevated CO_2 contributed to increased above-ground growth of Aspen and Birch (Fig. 6). In contrast, decreases in photosynthesis by O_3 depressed above-ground growth in Aspen, but not Birch. Interacting CO_2 and O_3 resulted in intermediate responses in Aspen and Birch, such that these treatments did not generally differ significantly from controls. Although Maple photosynthesis exhibited little response to any of the treatments, we did observe an overall negative above-ground growth response to all treatments. Nevertheless, variability in above-ground growth was extremely high in the smaller Maple saplings (CV = 250%), and it is premature to conclude that the overall growth of Maple will decline as CO_2 and O_3 accumulate in the atmosphere.

As with photosynthesis, above-ground growth responses varied widely in magnitude among Aspen genotypes. For example, the response to elevated CO_2 was least in genotype 42E and greatest in genotype 271 (Isebrands *et al.* 2001). Similarly, O_3-sensitive genotype 259 had the greatest reduction in above-ground biomass under elevated O_3, consistent with its reduced A_{max}. In contrast, mean above-ground biomass of genotype 8L was not influenced by elevated O_3 to any extent. Given the photosynthetic and above-ground growth responses of these genotypes, we expect those genotypes that are most responsive to CO_2 and least responsive to O_3 will eventually dominate our aggrading stands. By observing the growth and allometry of individual genotypes over the next several years, our intensive measurements of each plant in the experiment will enable us to document mortality and dominance at the genotype level over time, as well as to study interspecific interactions (McDonald *et al.* 2002).

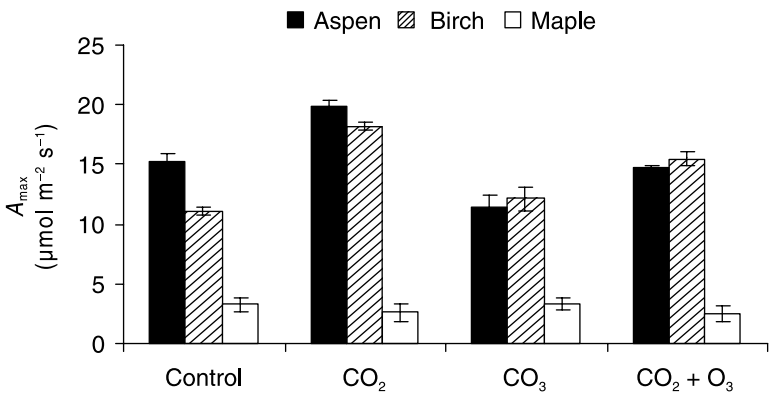

Fig. 4. Light-saturated CO_2 assimilation rates of Aspen, Birch and Maple growing under experimental atmospheric CO_2 and O_3 treatments. Data represent the mean and SE of three trees from each of three replicates for three to five measurement times over the 1999 and 2000 growing seasons.

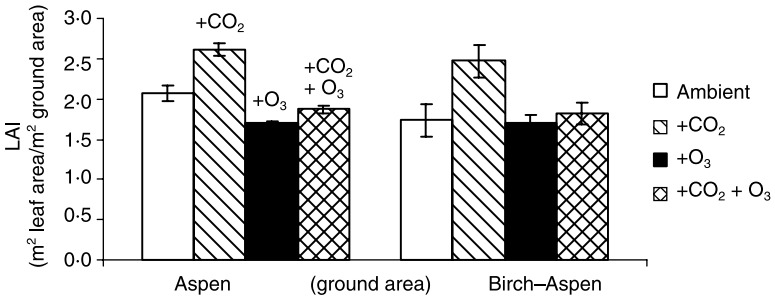

Fig. 5. Estimates of leaf area index (LAI, m^2 leaf area per m^2 ground area) for Aspen and Aspen–Birch stands in mid-season 2000. A destructive subsample harvest in August 2000 was used to calibrate the relationship between total leaf area and stem basal diameter. Significant linear regressions of log–log-transformed leaf area and diameter data were developed ($R^2 = 0{\cdot}80$, $P < 0{\cdot}0001$), with specific intercepts for each species. Whole-stand estimates of LAI were obtained by estimating individual tree leaf area from mid-season basal diameter measurements using the regression equations, summing the total leaf area of all trees in each stand, and dividing by the total ground area in each stand type (means ± 1 SE).

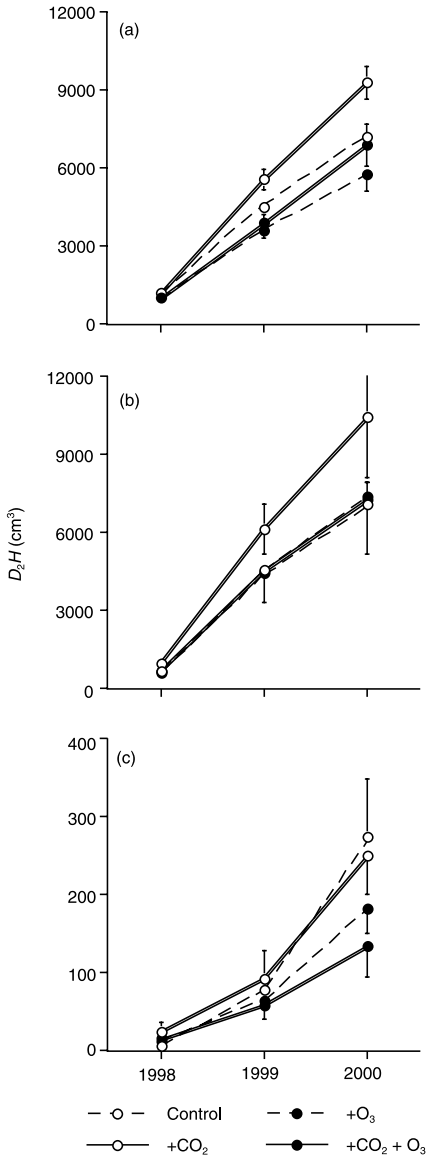

Fig. 6. Volume growth index (diameter^2 × height) of Aspen (a), Birch (b) and Maple (c) grown for 3 years in full factorial combinations of elevated atmospheric CO_2 (solid lines) and elevated O_3 (solid symbols).

WOOD CHEMISTRY

Concentration of total lignin (= gravimetric + acid-soluble lignin) in stem wood of Aspen increased by 2·5% under elevated O_3 as compared to the control, while elevated CO_2 had no effect. This result agrees with a previous study where no changes in lignin concentration caused by elevated CO_2 were found (Hättenschwiler, Schweingruber & Körner 1996). Increases in total lignin concentration under elevated O_3 are interesting, as there was previously no evidence for O_3 effects on wood chemical composition. Increase in lignin may indicate changes in carbon allocation leading to enhanced activity of the phenylpropanoid biosynthetic pathway, which is consistent with the finding that PAL transcripts increased under O_3 exposure (Wustman *et al.* 2001). The concentrations of the other main structural components of cell wall, α-cellulose and hemicellulose, were not affected by any treatment, nor were the minor nonstructural components (acetone-soluble extractives). A CO_2 effect on N dilution was also evident in Aspen branch wood, although there was a significant CO_2–O_3 interaction, with low-CO_2/high-O_3 branches containing 30% more N per unit dry mass (W.J. Mattson & R. Julkunen-Tiitto, unpublished results). In the case of Aspen branch wood, the sum total of phenolics (total per g dry weight) tended to increase under high CO_2, but the differences were not statistically significant. Out of 14 molecular species of phenolics, the concentrations of only four increased significantly, whereas the others did not. Likewise, neither starch nor fibre content of branch wood changed in response to CO_2 and O_3 (W.J. Mattson & R. Julkunen-Tiitto, unpublished results).

Apart from the environmental control, genetic factors also have a strong impact on wood properties (Costa e Silva *et al.* 1998; King *et al.* 1998; Denne, Calahan & Aebischer 1999; Hylen 1999). In Aspen, genotype significantly affected total lignin and acetone-soluble extractives (Anttonen *et al.* 2001). The O_3-sensitive clone 259 had 3% higher total lignin concentration than the O_3-tolerant clone 216. The O_3-sensitive clone 259 also differed from the other clones in having 26% lower concentration of acetone-soluble extractives. Genotype did not have an effect on α-cellulose and hemicellulose. Wood chemical composition and fibre properties may be different in the juvenile phase from that in mature trees (Zobel & van Buijtenen 1989; Hatton & Hunt 1992); further studies are needed as these trees reach maturity to predict the effects of future climate on wood chemical composition.

FOLIAR CHEMISTRY, SURFACE PROPERTIES AND HETEROTROPHIC INTERACTIONS

Our hypothesis is that changes in the quantity and chemistry of plant tissues, elicited by CO_2 and O_3, cascade through terrestrial ecosystems and alter the performance of heterotrophic organisms, and thus

potentially the entire community structure. Elevated CO_2 and O_3 can alter foliar chemistry and surface properties. Foliar N concentrations in Aspen and Birch declined by 16–21% in response to enriched CO_2, but declined only marginally in response to elevated O_3 (Lindroth *et al*. 2001). Decreased N concentrations in foliage under elevated CO_2, as has been commonly reported in CO_2 studies with other tree species (Cotrufo, Ineson & Scott 1998; Norby *et al*. 2000), increased C : N ratios in Aspen and Birch foliage, particularly under the combination of elevated CO_2 and O_3 (Lindroth *et al*. 2001). For example, as N declined in late-season Birch leaves, starch concentrations increased threefold under elevated CO_2 (W.J. Mattson & R. Julkunen-Tiitto, unpublished results). Differences in C : N ratios among the treatments were maintained through leaf senescence and litterfall (Lindroth *et al*. 2001; Parsons, Bockheim & Lindroth 2000). CO_2 enrichment, regardless of whether it was combined with O_3 or not, increased litter C : N by 39% in Aspen, and by 24% in Birch, relative to the controls.

Elevated CO_2 and O_3 altered concentrations of C-based secondary metabolites in Aspen and Birch (Lindroth *et al*. 2001; Lindroth, Wood & Kopper 2002); but the direction and magnitude of response differed among particular metabolites and between Aspen clones. Common secondary compounds, such as tannins and the phenolic glycosides of Aspen, were responsive to these two gases (Kopper & Lindroth 2002; Lindroth, Wood & Kopper 2002). Eight of 11 Birch leaf phenolic compounds increased 15–30% under high CO_2 (W.J. Mattson & R. Julkunen-Tiitto, unpublished). As was the case with C : N ratios, secondary metabolite concentrations were highest in litter originating in the CO_2-enriched rings and lowest in the rings exposed to high O_3 (W.F.J. Parsons, R.L. Lindroth & J.G. Bockheim, unpublished results).

Elevated CO_2 and O_3 also altered rates of leaf epicuticular wax biosynthesis with increases or decreases depending on clone and treatment, modified amounts of carbon allocated to various wax forms, and changed chemical composition, with O_3 increasing the ratio of long-chain alkane compounds (Karnosky *et al*. 1999, 2002a). O_3 modified wax structure from crystalline to amorphous masses (Mankovska *et al*. 1998) in Aspen and Birch. These changes in leaf surface properties may have contributed to the threefold to fivefold increased incidence of the Aspen leaf rust *Melampsora medusa* Thuem. f.sp. *Tremuloidae* in the O_3 and CO_2 + O_3 treatments (Karnosky *et al*. 2002a; Percy *et al*. 2002b) by altering the wettability of the leaf surface and providing a leaf surface more conducive to spore germination.

Elevated CO_2 and O_3 may alter the performance of insects through changes in bottom-up (plant) and top-down (natural enemy) factors. Colonization of Aspen trees by the Aspen Blotch Leafminer (*Phyllonorycter tremuloidiella*) declined under enriched CO_2 and O_3, a response probably caused by changes in epicuticular waxes easing insect attachment and leaf surface penetration (Kopper & Lindroth 2002). Tent Caterpillar (*Malacosoma disstria*) pupal weights improved under elevated O_3, but this was negated under enriched CO_2, responses consistent with changes in concentrations of foliar phenolic glycosides. Such effects were not always consistent, however, across Aspen clones. In contrast to well established findings with potted Aspen trees in greenhouses (Lindroth, Kinney & Platz 1993; Bezemer & Jones 1998), CO_2 fumigation did not increase leaf foliar consumption by insects. On the other hand, first and late-instar Gypsy Moth larvae consistently increased consumption (>15%) of CO_2-fumigated Birch leaves, though growing no better than control larvae (W.J. Mattson & T. Trier, unpublished results). The beetle *Oberea schaumii*, which bores into the stems and young branches of Aspen trees, responded to CO_2 and O_3 by being least abundant on trees under O_3 fumigation, but most abundant on trees under the CO_2 + O_3 fumigation. Its populations were intermediate in abundance under elevated CO_2, but still exceeded the controls. The Bark Scale, *Chionaspis*, and the Fly Gall-maker, *Hexomyza*, were most abundant on trees growing under CO_2 fumigation, showing no other treatment responses (W.J. Mattson, unpublished results).

Elevated CO_2 and O_3 also have the potential to alter insect community composition. Population censuses of aphids and natural enemies on Aspen revealed that while aphid abundance was unaffected by CO_2 or O_3, natural enemy abundance increased at elevated CO_2 and declined at elevated O_3 (Percy *et al*. 2002b). Awmack & Harrington (2000) showed that the damage caused by aphids increased at elevated CO_2 and negated the large growth stimulations otherwise expected of Bean plants (*Vicia faba*) under elevated CO_2. Therefore increases in pest numbers may have a considerable impact on forest health and productivity in the future. The importance of insect pest and disease eruptions in altering carbon fluxes from ecosystems has been highlighted by Kurz & Apps (1999), who detected a decade-long shift from carbon sink to source in the boreal forests of Canada, attributable to an increase in disturbances by pests and fire.

ECOSYSTEM RESPONSES

Most studies dealing with forest trees and elevated CO_2 and O_3 have been conducted in chambers in which it is not possible to address long-term, large-scale, ecosystem-level questions (Heck *et al*. 1998; Hendrey *et al*. 1999; McLeod & Long 1999; Karnosky *et al*. 2001). After 4 years' research at Aspen FACE, we are beginning to see indications that the physiological and genetic responses, which we detected early in this experiment, are cascading through the ecosystem and resulting in significant ecosystem-level responses to elevated CO_2 and O_3. It should be noted that we have found slight differences in soil fertility across our site, but we accommodated these differences in our experimental

design by using a randomized complete block design with the blocking being done by maintaining rings of common fertility within each replicate (Dickson *et al*. 2000). Our soil fertility levels are in the range of natural Aspen forest soil fertility, but sufficient to ensure that our tree growth responses to elevated CO_2 have been unconstrained by nutrient limitations.

LITTER PRODUCTION, CHEMISTRY AND DECOMPOSITION

Several pieces of evidence collectively suggest that greater rates of carbon assimilation and growth under elevated CO_2 directly influence the amount of organic substrate entering the soil for microbial metabolism, and that this response has been dampened by elevated O_3. Elevated atmospheric CO_2 increased leaf litter production by 36% in Aspen, and Birch leaf litter production doubled in the Aspen–Birch community. Elevated O_3 did not substantially alter leaf litter production relative to the control, but elevated O_3 decreased the CO_2-induced production of litter in Aspen and Birch. Similarly, elevated CO_2 significantly increased the mass of dead fine roots by 140% beneath Aspen, and by 340% beneath Aspen–Birch (King *et al*. 2001). Although elevated O_3 did not influence dead fine-root mass (relative to the control), it did nullify the increase in fine-root mass caused by elevated CO_2. We also found that elevated CO_2 increased live fine root biomass by 113% beneath Aspen and by 83% beneath Aspen–Birch; elevated O_3 did not significantly alter live fine root biomass (King *et al*. 2001). We also observed no change in the lignin content of live and dead fine roots (J.S. King, unpublished results), a result supported by greenhouse studies (W.F.J. Parsons, B.J. Kopper & R.L. Lindroth, unpublished results). Taken together, our results suggest that CO_2 substantially increased above-ground and below-ground litter production beneath Aspen and Aspen–Birch, but this response was almost eliminated by elevated O_3.

The 1 year decay rate (k value) of Birch litter was significantly reduced by elevated CO_2 regardless of O_3 (Parsons, Bockheim & Lindroth 2000). Aspen decay showed similar trends, although differences among treatments were not significant. Initial differences in foliar quality among the treatments were sustained throughout Aspen and Birch decomposition, and these distinctive chemical signatures probably contributed to controlling mass loss from the decomposing litter, whether it was returned to its ring of origin or transplanted into another treatment ring. From reciprocal litter transplant experiments we observed slight moderation of litter quality effects: a weak substrate–environment interaction (Parsons, Bockheim & Lindroth 2000).

SOIL AND MICROBIAL RESPIRATION

Elevated CO_2 substantially increased soil respiration rates beneath Aspen (by 30%) and Aspen–Birch (by 60%); however, soil respiration increased much less (10%) beneath Aspen–Maple. Elevated O_3 had a relatively minor influence on mean soil respiration at both atmospheric CO_2 concentrations except for late in each growing season, possibly due to increased fine root senescence caused by O_3. This pattern of soil respiration was reflected in differences in soil pCO_2 among our experimental treatments (King *et al*. 2001), wherein elevated CO_2 increased soil pCO_2 by 27% (averaged over three depths from 15 to 125 cm and two growing seasons), and O_3 had little effect. We believe this result is important because higher soil pCO_2 could lead to more carbonic and organic acids in the soil, leading to more rapid mineral weathering, nutrient leaching, and the export of dissolved inorganic C. Like soil respiration, microbial respiration under elevated CO_2 was significantly increased beneath Aspen (33%) and Aspen–Birch (55%), but the increase beneath Aspen–Maple was small (1%) and not significant (Phillips *et al*. 2002). We also observed that elevated O_3 did not significantly decrease microbial respiration relative to the control, but elevated O_3 did reduce rates of microbial respiration under elevated CO_2 (in the $CO_2 + O_3$ treatment). Greater rates of microbial respiration indicate that increased litter inputs under elevated CO_2 are being metabolized by a soil microbial population that is larger, more active, or both. We observed a nonsignificant increase in soil microbial biomass under elevated CO_2 (28%) across two growing seasons (Larson *et al*. 2002), while microbial biomass in the O_3 and $CO_2 + O_3$ treatments were equivalent to that of the control (data not shown). We have not yet determined if microbial respiration changes are in any way related to changes in the biochemical composition of the plant litter.

MICROBIAL COMMUNITY FUNCTION

We believe that changes in the quantity of organic substrate entering the soil from our experimental treatments have altered the metabolism of soil microbial communities. Again, we do not yet know if litter quality changes are also having an effect. Elevated CO_2 increased the activity of enzymes involved in plant and fungal cell-wall degradation at O_3 concentrations. We detected CO_2-induced increases in cellobiohydrolase, an enzyme catalysing the release of cellobiose during cellulose degradation, and *N*-acetylglucosaminidase, which catalyses the release of *N*-acetylglucosamine during chitin degradation (we did not find significant interactions between CO_2 and species or O_3 treatments; Larson *et al*. 2002). These results suggest that greater inputs of plant and fungal cell-wall substrates (cellulose and chitin) under elevated CO_2 have altered the metabolism of these plant-derived compounds in soil and the transport of C through the soil food web. This response was confirmed by increased recovery of $^{13}CO_2$ that was respired from labelled cellobiose and *N*-acetylglucosamine added to soil in a preliminary soil

incubation experiment (Phillips *et al*. 2002). It is possible that these responses are driven largely by greater inputs of dead fine roots and associated mycorrhizal fungi, and we intend to explore this possibility.

SOIL N CYCLING

Results from a short-term ^{15}N tracer experiment suggest that changes in microbial metabolism among experimental treatments have altered rates and patterns of soil N cycling. We followed the flow of $^{15}NH_4^+$ and $^{15}NO_3^-$ in soil collected from each FACE ring during the 1999 field season. O_3 had no effect on the recovery of ^{15}N in microbial biomass or soil organic matter. In contrast, elevated CO_2 (main effect) significantly increased the amount of $^{15}NO_3^-$ recovered in microbial biomass and soil organic matter. Recovery of $^{15}NH_4^+$ in these pools was greater under elevated CO_2, but this increase was not significant. These results indicate that larger amounts of N are forming soil organic matter under elevated CO_2. Because the C : N ratio of soil organic matter is relatively constant, this finding suggests that greater amounts of C also are forming soil organic matter in our experiment. This indicates that more C may be stored in soil as the atmospheric CO_2 concentration increases, a finding not strongly supported in the Duke FACE study (Schlesinger & Lichter 2001).

WATER BALANCE

There has been much speculation that ecosystem water balances will be altered under elevated CO_2 (Curtis 1996; Curtis & Wang 1998). However, this type of response has been impossible to test in greenhouse chamber or open-top chamber studies. We have found two independent lines of evidence suggesting possible water balance changes attributable to elevated CO_2 and O_3. First, water-use efficiency calculations by Sôber *et al*. (2000) suggest that water-use efficiency was highest for Aspen clones exposed to elevated CO_2 and lowest in those exposed to O_3. Trees exposed to elevated $CO_2 + O_3$ were intermediate between treatments, but still greater than controls in water-use efficiency. Second, during a relatively dry year (1999) but not in relatively wet year (2000), changes in volumetric soil moisture, as determined by time domain reflectometry, were detectable throughout the growing season under elevated CO_2, O_3 and $CO_2 + O_3$ (J.S. King & K.S. Pregitzer, unpublished results).

BIODIVERSITY

While elevated CO_2 (Vasseur & Potvin 1998) and O_3 (Berrang *et al*. 1986; Barbo *et al*. 1998) have been implicated in altering plant communities and biodiversity, few studies have investigated the impacts of the interacting effects of CO_2 and O_3 on community composition. We have evidence that the composition of forest communities may be altered under these two greenhouse gases. First, in a study of competitive interactions between Aspen clones differing in O_3 sensitivity, McDonald *et al*. (2000, 2002) found that elevated CO_2 exacerbated growth reductions as elevated O_3 decreased growth 35% in elevated CO_2 compared with 24% in ambient CO_2. Clone-competitive interactions were significant, suggesting that interacting CO_2 and O_3 could exacerbate clonal competition for fitness, as previously described under elevated O_3 by Karnosky *et al*. 1999, 2002b). We expect these competitive interactions to increase over the next few years as interactions among crowns and among root systems intensify, and as seed production and dispersal occur in the pioneer species.

IMPLICATIONS FOR CARBON SEQUESTRATION AND NET PRIMARY PRODUCTIVITY MODELS

Our results suggest that elevated O_3 at relatively low concentrations can significantly reduce the growth enhancement by elevated CO_2. Our results follow similar trends found for many agricultural crops, other hardwood trees and a few conifers (Fig. 7). Together, these studies on plants of different genetic backgrounds, growth characteristics and life histories suggest that O_3 can seriously alter the capacity of vegetation to grow under elevated CO_2 and to sequester carbon. For example, the projected co-occurrence of elevated O_3 (as predicted by Fowler *et al*. 1999a) over a large portion of the natural range of the circumpolar Leuce (Aspen) section of Poplar (Fig. 8) may mean that worldwide growth stimulations will not be as great as predicted from previous studies of elevated CO_2. It is important to bring an understanding of O_3 as a moderator of CO_2 responses to global models of terrestrial net primary productivity. It is also important to expose forests for their entire rotation or life cycle to understand the practicality of using forests and forest plantations to sequester carbon and to offset anthropogenic CO_2 emissions.

Conclusions and research needs

The suite of responses to elevated CO_2 and/or O_3 at the Aspen FACE project have been remarkably consistent across functional groups, species and genotypes differing in O_3 tolerance, and from molecular to ecosystem levels. However, it must be noted that these responses are being found in a young, aggrading forest. We have not yet detected a diminishing of CO_2 growth enhancement, as has been reported for Loblolly Pine (Oren *et al*. 2001) and Sweetgum (Norby *et al*. 2001b). However, our forest is in a much younger stage of development than these other two sites. Comparisons among FACE sites are difficult because several factors differ, including soils, climate, species and treatments. Several new areas of study at our site – such as the occurrence and abundance of mycorrhizal fungi; the diversity and

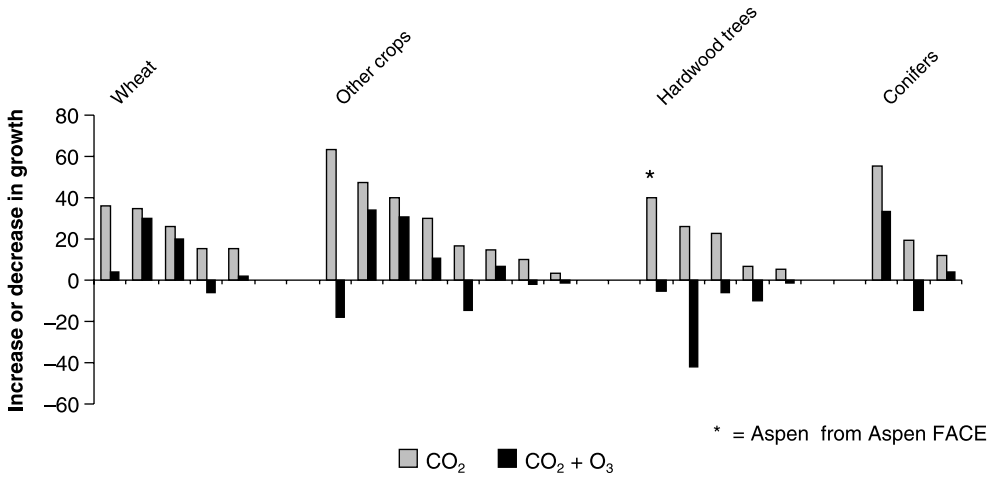

Fig. 7. Relative effects of controlled exposure to elevated CO_2 on normalized plant growth under CO_2 alone (striped bars, 500–713 μmol mol^{-1} CO_2) and elevated CO_2 plus ozone (dotted bars). (Modified and expanded from Barnes & Wellburn 1998.) Data presented for wheat (*Triticum aestivum*) from Barnes, Ollerenshaw & Whitfield (1995); Rudorff *et al*. (1996); McKee, Bullimore & Long (1997); Bender, Herstein & Black (1999); Hudak *et al*. (1999); soybean (*Glycine max*) from Heagle, Miller & Pursley (1998) and Miller, Heagle & Pursley (1998); tomato (*Lycopersicon esculentum*) from Olszyk & Wise (1997) and Hao *et al*. (2000); rice (*Oryza sativa*) from Olszyk & Wise (1997); potato (*Solanum tuberosum*) from Donnelly *et al*. (2001) and Lawson *et al*. (2001); corn (*Zea mays*) from Rudorff *et al*. (1996); hardwood trees including hybrid poplars (*Populus* hybrids) from Dickson *et al*. (1998); Trembling Aspen (*Populus tremuloides*) from Volin & Reich (1996); Volin *et al*. (1998); Isebrands *et al*. (2001); oak (*Quercus petrea*) from Broadmeadow & Jackson (2000); conifers including Ponderosa Pine from David Olszyk (personal communication); Scots Pine (*Pinus sylvestris*) from Broadmeadow & Jackson (2000); Utriainen *et al*. (2000). Each pair of bars represents one species.

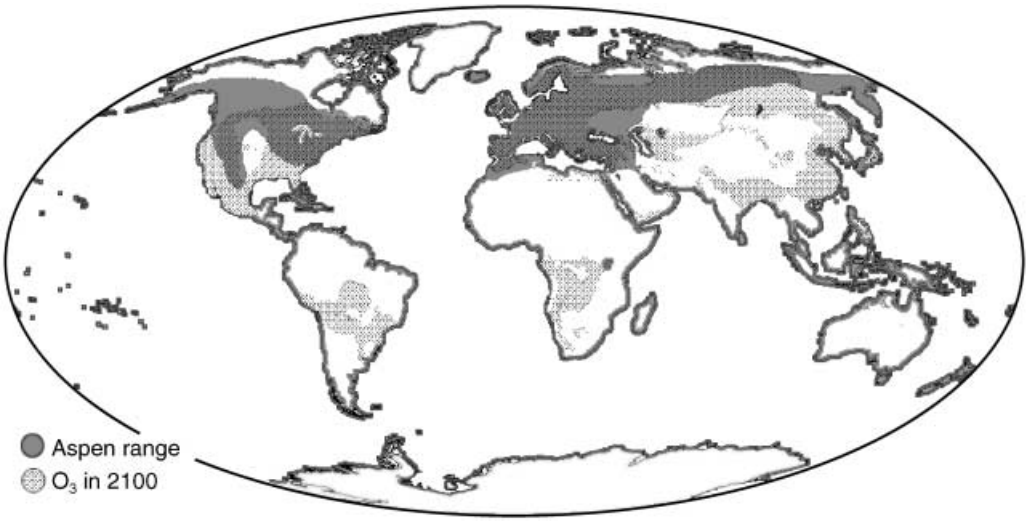

Fig. 8. Worldwide distribution of Aspen and projected areas with elevated O_3 in the year 2100. Ozone map from Fowler *et al*. (1999a).

quantity of understorey vegetation; and canopy-level sap flow – are still premature to discuss at this point, but should be an integral part of our project's future research efforts. Finally, we continue to use our results to parameterize and test various growth models such as ECOPHYS (Martin *et al*. 2001) to broaden the inferences from our results.

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