

Ozone Effects on Forest Ecosystems under a Changing Global Environment

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Abstract

Tropospheric ozone [O₃] continues to be an important problem for forest ecosystems in many regions of the world. At the same time, atmospheric carbon dioxide [CO₂] is rising at unprecedented rates over the entire globe. Little is known as to how forest ecosystems will respond to [O₃] under elevated [CO₂]. In this paper, I summarize a long-term (7-year) study of the impacts of elevated [CO₂] and [O₃], alone and in combination, on a northern hardwood forest ecosystem consisting of two pioneer species (*Populus tremuloides* Michx. and *Betula papyrifera* Marsh.) and a later successional species (*Acer saccharum* Marsh.) grown under an open-air exposure (FACE) system.

Key words: Aggrading aspen forest, FACE, Interacting pollutants

1. Introduction

Globally, mean [CO₂] and [O₃] have risen 30-36% since pre-industrial times (IPCC, 2001). These increases in [CO₂] are largely due to increased emissions from fossil fuel burning while the increases in [O₃] are primarily related to increasing emissions of oxidized nitrogen (NO_x) and volatile organic emissions from fossil fuel combustion. Nearly 25% of the Earth's forests are currently at risk from [O₃] where peak concentrations exceed 60 nL L⁻¹ (Fowler *et al.* 1999). They predict that half of the Earth's forests will be subjected to peak concentrations exceeding 60 nL L⁻¹ by the year 2100. Little is known about how forest ecosystems will respond to these co-occurring pollutants.

The Aspen FACE experiment was established in northern Wisconsin to examine the long-term effects of these interacting greenhouse gases on the structure and functioning of an aggrading forest ecosystem consisting of trembling aspen, paper birch, and sugar maple and with trees exposed over their entire life history. Here, I present key findings from this long-term project.

2. Materials and Methods

The Aspen FACE project was established in 1997 as the first open-air facility to examine the responses of forest trees to interacting elevated [CO₂] and [O₃] (Dickson *et al.* 2000). This experiment consists of twelve 30-m diameter rings (Fig. 1), assigned to factorial treatments of [CO₂] (ambient and 560 μL L⁻¹) and [O₃] (ambient averaging 39 nL L⁻¹ and approximately 1.5x ambient) during daylight hours throughout the growing season. Treatments are arranged in a randomized complete block design (n=3). In one half of each ring, we planted five trembling aspen genotypes of differing CO₂ and O₃ responsiveness. The other half of each ring is further divided into two quarters; one is planted with aspen

and sugar maple and the other is planted with aspen and paper birch; each FACE ring was planted at 1 m x 1 m spacing.

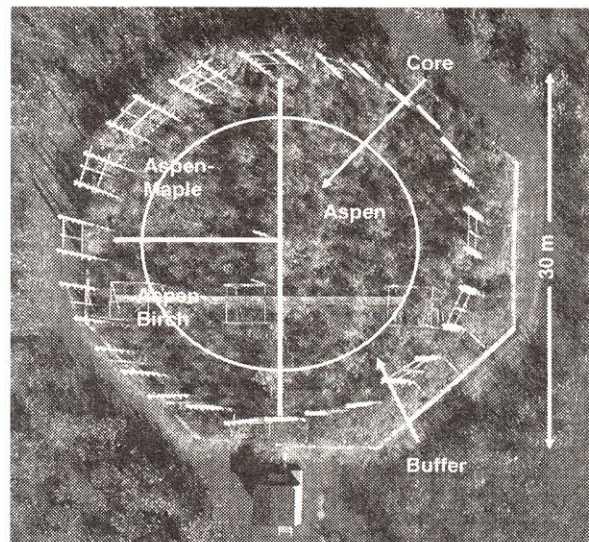


Fig. 1. Each 30-m diameter Aspen FACE ring is divided into three communities. Growth measurements are taken from the trees in the core of each ring.

3. Results and Discussion

We hypothesized that the ecosystem-level responses to elevated [CO₂] and [O₃] would be driven by the responsiveness of the keystone tree species. During establishment phase, the community dynamics of net primary production, community composition, and flows of carbon and nitrogen all are being driven by the responses of the dominant species. While effects of these two greenhouse gases vary by species and by genotype, they have been remarkably consistent across trophic levels through the ecosystem (Table 1).

Table 1. Summary of responses of trembling aspen to elevated [CO₂] (560 μmol mol⁻¹), [O₃] (1.5 x ambient), or [CO₂]+[O₃] compared with control during seven years of treatments at the Aspen FACE project. This table is modified from Karnosky *et al.* 2003.

	CO ₂	O ₃	CO ₂ + O ₃	Source
Foliar Gene Expression and Biochemistry				
Rubisco	↓	↓	↓↓	Wustman <i>et al.</i> (2001), Noormets <i>et al.</i> (2001a)
RbcS ² transcripts	↓	↓	↓↓	Wustman <i>et al.</i> (2001)
PAL transcripts	↓	↑	↓	Wustman <i>et al.</i> (2001)
Ascorbate peroxidase	↓	n.s.	↓	Wustman <i>et al.</i> (2001)
Catalase, Acc oxidase	↓	↑	↓	Wustman <i>et al.</i> (2001), Oksanen <i>et al.</i> (2003)
Glutathione reductase	n.s.	↑	↓	Wustman <i>et al.</i> (2001)
H ₂ O ₂ accumulation	n.s.	↑↑	n.s.	Oksanen <i>et al.</i> (2003)
Phenolic glycosides	n.s.	↓	n.s.	Lindroth <i>et al.</i> (2002), Kopper & Lindroth (2003a, b)
Tannins	n.s.	↓	↑	Lindroth <i>et al.</i> (2002), Kopper & Lindroth (2003a, b)
Foliar nitrogen	↓	↓	n.s.	Lindroth <i>et al.</i> (2001), Kopper & Lindroth (2003a, b), Holton <i>et al.</i> (2003)
C:N ratio of foliage	↑	n.s.	↑↑	Lindroth <i>et al.</i> (2001)
Starch	↓	↓	n.s.	Wustman <i>et al.</i> (2001)
Gas Exchange				
A _{max} , lower canopy	n.s.	↓↓	↑ (young) ↓ (older)	Noormets <i>et al.</i> (2001a), Sharma <i>et al.</i> (2003)
A _{max} , upper canopy	↑↑	↓↓	n.s.	Noormets <i>et al.</i> (2001b)
Stomatal limitation	↓	n.s.	↓	Noormets <i>et al.</i> (2001a)
Stomatal conductance	↓	↓↓	↓	Noormets <i>et al.</i> (2001a), Sharma <i>et al.</i> (2003)
Foliar respiration	n.s.	↑	n.s.	Takeuchi <i>et al.</i> (2001), Noormets, (2001a), Davey <i>et al.</i> (2004)
Soil respiration	↑↑	↓	n.s.	King <i>et al.</i> (2001, 2004a)
Microbial respiration	↑↑	n.s.	n.s.	Phillips <i>et al.</i> (2002)
Stomatal density	n.s.	n.s.	n.s.	Percy <i>et al.</i> (2002), Karnosky <i>et al.</i> (2003)
Chlorophyll content	↓	↓	↓	Wustman <i>et al.</i> (2001)
Chloroplast structure	↑	↓	↓	Oksanen <i>et al.</i> (2001), Wustman <i>et al.</i> (2001)
Peroxisome number	n.s.	↑↑	n.s.	Oksanen <i>et al.</i> (2003)
O ₃ flux	↓	↑↑	↑	Noormets <i>et al.</i> (2001a)
Growth and Productivity				
Leaf thickness	↑	n.s.	n.s.	Oksanen <i>et al.</i> (2001)
Leaf size	↑	↓	↓	Wustman <i>et al.</i> (2001)
Leaf area	↑	↓	n.s.	Noormets <i>et al.</i> (2001b)
LAI	↑	↓	n.s.	Karnosky <i>et al.</i> (2003, 2004)
Height growth	↑	↓	n.s.	Isebrands <i>et al.</i> (2001), Percy <i>et al.</i> (2002), Karnosky <i>et al.</i> (2003, 2004)
Diameter growth	↑	↓	n.s.	Isebrands <i>et al.</i> (2001), Percy <i>et al.</i> (2002), Karnosky <i>et al.</i> (2003, 2004)
Volume growth	↑↑	↓↓	n.s.	Isebrands <i>et al.</i> (2001)
Fine root biomass	↑	↓	n.s.	King <i>et al.</i> (2001) unpublished
Fine root turnover	↑	n.s.	n.s.	King <i>et al.</i> (2001, 2004)
Spring budbreak	n.s.	Delayed	n.s.	Karnosky <i>et al.</i> (2004)
Autumn budset	Delayed	Early	n.s.	Karnosky <i>et al.</i> (2004)
Foliar retention - Autumn	↑↑	↓↓	n.s.	Karnosky <i>et al.</i> (2004)
Fine root biomass	↑	↓	n.s.	King <i>et al.</i> (2001)
Fine root turnover	↑	n.s.	n.s.	King <i>et al.</i> (2001, 2004)
Spring budbreak	n.s.	Delayed	n.s.	Karnosky <i>et al.</i> (2004)
Autumn budset	Delayed	Early	n.s.	Karnosky <i>et al.</i> (2004)
Foliar retention - Autumn	↑↑	↓↓	n.s.	Karnosky <i>et al.</i> (2004)
Wood				
Pith to bark distance	↑	↓	n.s.	Kaakinen <i>et al.</i> (2004)
Vessel lumen diameter	n.s.	↓	n.s.	Kaakinen <i>et al.</i> (2004)
Lignin	n.s.	↑	n.s.	Kaakinen <i>et al.</i> (2004)
Cellulose	n.s.	n.s.	n.s.	Kaakinen <i>et al.</i> (2004)
Hemicellulose	↓	n.s.	↑	Kaakinen <i>et al.</i> (2004)
Leaf Surfaces				
Crystalline wax structure	↓	↓	↓↓	Karnosky <i>et al.</i> (1999, 2002)
Stomatal occlusion	↑	↑	↑↑	Karnosky <i>et al.</i> (1999), Mankovska <i>et al.</i> (2003)
Wax chemical composition	n.s.	Change	n.s.	Karnosky <i>et al.</i> (2002)
Wettability	n.s.	↑↑	↑	Karnosky <i>et al.</i> (2002)
Trophic Interactions				
<i>Melampsora</i> leaf rust	n.s.	↑↑	↑↑	Karnosky <i>et al.</i> (2002), Percy <i>et al.</i> (2002)
Aphids	n.s.	n.s.	n.s.	Percy <i>et al.</i> (2002)
Blotch leaf miner	↓↓	↓↓	↓↓	Kopper & Lindroth (2003a)
Forest tent caterpillar	n.s.	↑	n.s.	Kopper & Lindroth (2003b)
Ecosystem Level				

NPP	↑↑	↓↓	n.s.	King <i>et al.</i> unpublished
Soil carbon formation	↑↑	↓	↓↓	Loya <i>et al.</i> (2003)
Nitrogen mineralization	n.s.	↓↓	n.s.	Holmes <i>et al.</i> (2003), Zak <i>et al.</i> (2003)
Litter decomposition (k-value)	↓	n.s.	↓	Parsons <i>et al.</i> (2004)
Competitive indices	↑	↓	↓↓	McDonald <i>et al.</i> (2002)
Soil invertebrate diversity	↓	↓	n.s.	Loranger <i>et al.</i> (2004)
Microbial enzymes	↑	n.s.	n.s.	Phillips <i>et al.</i> (2002), Larson <i>et al.</i> (2002)
Microbial biomass	↑	n.s.	n.s.	Phillips <i>et al.</i> (2002), Larson <i>et al.</i> (2002)

¹Responses are shown as small but significant increases (↑), large and significant increases (↑↑), small but significant decreases (↓), large and significant decreases (↓↓), nonsignificant effects (n.s.) compared to trees grown in control rings with ambient CO₂ and O₃. 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.

²Abbreviations: RbcS = small subunit of Rubisco; PAL = phenylalanine ammonia-lyase; 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

3.1 Genes to Organelles

Elevated [CO₂] and [O₃] are sensed primarily by leaves and result in dynamic and rapid changes in gene expression and gas exchange. We have documented O₃-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 CO₂, regardless of O₃ exposure, as was PAL, a key enzyme in the shikimic acid pathway. CO₂- and O₃-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 *et al.* 2001) under elevated O₃.

We have been able to visualize and locate O₃-induced H₂O₂ accumulation within leaf mesophyll cells, and relate oxidative stress with structural injuries in aspen and birch. In addition, increased transcript levels for catalase were demonstrated to be related to O₃-induced proliferation of peroxisomes.

CO₂ enrichment appeared to increase scavenging capacity by releasing the resources for peroxisomal antioxidant defense against overproduction of H₂O₂ during oxidative stress (Oksanen *et al.* 2003).

3.2 Leaf Surfaces

The epicuticular waxes are located on the outermost surfaces of plant leaves and are in direct contact with the atmosphere. The role of these waxes in plant defense are well established. Mankovska *et al.* (2003) have documented wax structure changes and increased stomatal occlusion under all treatments but the largest occlusion has occurred repeatedly in the combination treatment. Percy *et al.* (2002) and Karnosky *et al.* (2002) reported significant increases in wax deposits due to enhanced [O₃] as well as changes in wax chemistry.

While stomatal frequency has been shown to be responsive to CO₂ treatment, we have seen no evidence of treatment effects in our experiment on stomatal density (Karnosky *et al.* 2003, Mankovska *et al.* 2003).

3.3 Gas Exchange

Higher [CO₂] enhanced photosynthesis 28-42% in aspen and birch (Karnosky *et al.* 2003) but not in sugar maple (Sharma *et al.* 2003). Contrarily, [O₃] decreased

photosynthesis 29 to 40% in aspen, but had little effect on paper birch or sugar maple (Karnosky *et al.* 2003). Studies of A_{max} of two aspen clones over time suggests that photosynthetic responses over time have remained largely unchanged suggesting photosynthetic acclimation has not occurred either in response to elevated [CO₂] or [O₃].

It has been widely reported in the literature that elevated [CO₂] decreases nighttime foliar respiration. In our cross site comparison using O₂ uptake (rather than CO₂ loss), we found evidence that [CO₂] does not decrease but, in fact, may slightly increase respiration (Davey *et al.* 2004).

3.4 Growth and Productivity

Aboveground growth estimates (diameter, height) and biomass production (sample harvests in 2000 and 2002) both show similar trends in which the dominant plant responses are driving the ecosystem composition and function (Isebrands *et al.* 2001, Percy *et al.* 2002, McDonald *et al.* 2002; Karnosky *et al.* 2003, 2004). Species and genotypes within species (aspen) are highly variable in these responses. The general trends consisted of significantly increased growth and productivity under elevated [CO₂] and significantly decreased responses under elevated [O₃]. Elevated [O₃] generally offset the growth and productivity enhancement by elevated [CO₂]. While long-term growth enhancement has been reported to be unsustainable in some systems, our growth enhancement has continued through the six years of our study, as particularly evidenced by the large stimulation still shown by paper birch. Interestingly, sugar maple has not been enhanced by elevated [CO₂] in our study. Responsiveness of our species to CO₂ are (from most to least enhanced by CO₂): birch>aspen>maple. For O₃, aspen is sensitive to O₃ while birch and maple are more tolerant. In the long term, the interacting treatment has resulted in the strongest growth decrease in sugar maple.

3.5 Pest Interactions

We have found evidence of increased *Melampsora* rust occurrence on aspen under elevated [O₃] (Percy *et al.* 2002, Karnosky *et al.* 2002). We have also documented increased abundance of aphids and a decrease in their natural enemies in aspen under elevated [O₃] (Percy *et al.* 2002). Forest tent caterpillar, a cyclic pest which annually defoliates millions of hectares of aspen and birch forests was found to be

impacted by both elevated [O₃] and [CO₂]. Forest tent caterpillar pupal masses were increased under elevated O₃ (Percy *et al.* 2002, Kopper *et al.* 2003b) and egg mass parasitism was decreased and egg mass foam protection was increased under elevated [CO₂] (Mattson, unpublished).

3.6 Belowground Responses

Whether or not above- and belowground carbon allocation patterns will change under prolonged exposure to elevated [CO₂] and [O₃] remain active research questions. We have detected no changes in allometry in our study (King *et al.* 2004b). While we see stimulation of aboveground growth in both aspen and birch, we see similar enhancement levels in root growth under elevated [CO₂]. Similarly, we see nearly identical shoot and root growth reductions for aspen exposed to elevated [O₃].

Increased carbon inputs to the soil under elevated [CO₂] appear to be largely transient in nature as most new soil carbon inputs are quickly respired (King *et al.* 2004a). Soil carbon formation under elevated [CO₂] is severely restricted by elevated [O₃] (Loya *et al.* 2003).

Soil fauna (Loranger *et al.* 2004) and microorganisms (Phillips *et al.* 2002, Larson *et al.* 2002) are both highly impacted by these two greenhouse gases with soil biodiversity likely to be affected by long-term exposure of forest communities. The changes in soil microorganisms and elevated CO₂ in soils appear to be affecting rates of nitrogen mineralization (Holmes *et al.* 2003, Zak *et al.* 2003).

Conclusions

The Aspen FACE project has demonstrated that [O₃] at moderate levels can dramatically impact the response of forest ecosystems to elevated [CO₂] during the early stand development. It is important to determine if the trends we have shown with the early growth phase for aspen, birch and maple will continue as these stands mature. This study is unique among forest FACE experiments as we have the opportunity to examine responses from establishment through stand maturity.

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