DE-FG02-95ER62125

IMPACTS OF INTERACTING ELEVATED ATMOSPHERIC CO_2 AND O_3 ON THE STRUCTURE AND FUNCTIONING OF A NORTHERN FOREST ECOSYSTEM: OPERATING AND DECOMMISSIONING THE ASPEN FACE PROJECT

Final Technical Report for the Period September 1, 1995 – March 31, 2014 and highlighting overall findings from the final phase of Aspen FACE, April 1, 2008 – March 31, 2014

submitted June 30, 2014 by

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Executive Summary

Two of the most important and pervasive greenhouse gases driving global change and impacting forests in the U.S. and around the world are atmospheric CO_2 and tropospheric O_3. As the only free air, large-scale manipulative experiment studying the interaction of elevated CO_2 and O_3 on forests, the Aspen FACE experiment was uniquely designed to address the long-term ecosystem level impacts of these two greenhouse gases on aspen-birch-maple forests, which dominate the richly forested Lake States region. The project was established in 1997 to address the overarching scientific question: "What are the effects of elevated [CO_2] and [O_3], alone and in combination, on the structure and functioning of northern hardwood forest ecosystems?"

From 1998 through the middle of the 2009 growing season, we examined the interacting effects of elevated CO_2 and O_3 on ecosystem processes in an aggrading northern forest ecosystem at a free-air carbon dioxide enrichment (FACE) facility near Rhinelander, Wisconsin to compare the responses of early-successional, rapid-growing shade intolerant species (trembling aspen [*Populus tremuloides* Michx.] and paper birch [*Betula papyrifera* Marsh.]) to those of a late successional, slower growing shade tolerant species (sugar maple [*Acer saccharum* Marsh.]). Three replicate FACE rings were established in 1997 for a factorial combination of four treatments (CO_2, O_3, CO_2+O_3 and control) in a randomized block design. Rooted cuttings from five aspen clones previously characterized for O_3 and CO_2 sensitivities were planted 1.0 m apart in one-half of each FACE ring. The other half was divided into equal size plots of aspen/sugar maple and aspen/paper birch, again at 1 m x 1 m spacing. Fumigations with elevated CO_2 (560 ppm during daylight hours) and O_3 (approximately 1.5 x ambient) were conducted during the growing season from 1998 to 2008, and in 2009 through harvest date.

Response variables quantified during the experiment included growth (height, diameter, biomass, leaf area, root production, and fine root mortality), competitive interactions and stand dynamics, physiological processes (photosynthesis, respiration, stomatal conductance, and chlorophyll content), plant nutrient status and uptake (nitrogen), tissue biochemistry (carbohydrates, phenolic glycosides, and antioxidants), litter quality and decomposition rates, hydrology, soil respiration, microbial community composition and respiration, VOC production, treatment-pest interactions, and treatment-phenology interactions. From mid-June to mid-August in 2009, we conducted a detailed harvest of the site. The harvest included detailed sampling of a subset of trees by component (leaves and buds, fine branches, coarse branches and stem, coarse roots, fine roots) and excavation of soil to a depth of 1 m. An excavator and commercial soil sieve were used to recover coarse roots, with additional cores from pit faces used to capture fine root biomass.

Throughout the experiment, aspen and birch photosynthesis increased with elevated CO_2 and tended to decrease with elevated O_3, compared to the control. In contrast to aspen and birch, maple photosynthesis was not enhanced by elevated CO_2. Elevated O_3 did not cause significant reductions in maximum photosynthesis in birch or maple. In addition, photosynthesis in ozone sensitive clones was affected to a much greater degree than that in ozone tolerant aspen clones. Altered photosynthesis had direct effects on net primary productivity (NPP), including production of foliage, which created a positive feedback that led to even greater enhancement of C assimilation under elevated CO_2 for aspen and birch and further reduction of C assimilation under elevated O_3 for aspen.

Treatment effects on photosynthesis contributed to CO_2 stimulation of aboveground and belowground growth that was species and genotype dependent, with birch and aspen being most

responsive and maple being least responsive. The positive effects of elevated CO_2 on net primary productivity NPP were sustained through the end of the experiment, but negative effects of elevated O_3 on NPP had dissipated during the final three years of treatments. The declining response to O_3 over time resulted from the compensatory growth of O_3-tolerant genotypes and species as the growth of O_3-sensitive individuals declined over time. As a result, annual NPP by the end of the project was similar under ambient and elevated O_3. Project results suggest that the changing atmospheric composition could shift the genotypic composition and average pollutant responses of tree populations over moderate timescales. Given the degree to which O_3 has been projected to decrease global NPP, the compensatory growth of O_3 tolerant plants in our experiment, as they replaced senescing O_3 sensitive plants, should be considered in future simulations.

Cumulative NPP over the entire experiment was 39% greater under elevated CO_2 ($P < 0.001$) and 10% lower under elevated O_3 ($P = 0.026$). Enhanced NPP under elevated CO_2 was sustained by greater root exploration of soil for growth-limiting N, as well as more rapid rates of litter decomposition and microbial N release during decay. Overall, our observations indicate that elevated CO_2 has altered SOM cycling at this site to favor C and N accumulation in less stable pools, with more rapid turnover. Results from our long-term measurements at Aspen FACE clearly indicate that plants growing under elevated carbon dioxide, regardless of community type or ozone level, obtained significantly greater amounts of soil N. These results indicate that greater plant growth under elevated carbon dioxide has not led to “progressive N limitation”. In no case did we find significant interactions among plant community, CO_2, or O_3, indicating that NPP in the three plant communities in our experiment responded similarly to both CO_2 and O_3. If similar forests growing throughout northeastern North America respond in the same manner, then enhanced forest NPP under elevated CO_2 may be sustained for a longer duration than previously thought, and the negative effect of elevated O_3 may be diminished by compensatory growth of O_3-tolerant plants as they begin to dominate forest communities.

By the end of the experiment, elevated CO_2 increased ecosystem C content by 11%, whereas elevated O_3 decreased ecosystem C content by 9%. Total ecosystem C content in the interaction treatment (elevated CO_2 and O_3) did not significantly differ from that of the control. Total ecosystem C content responded similarly to the treatments across the three forest communities. The treatment effects on ecosystem C content resulted from differences in tree biomass, particularly woody tissues (branches, stem, and coarse roots), and lower C content in the near-surface mineral soil. For tree C, the negative effect of elevated O_3 was smaller (-15%) than the positive effect of elevated CO_2 (+44%).

During its duration, the Aspen FACE project involved collaboration between scientists from 9 countries, and over the course of the experiment there were over 120 Aspen FACE scientific users. These scientists helped produce 75 publications during the most recent funding period (2008-2014) and 207 peer-reviewed publications (169 in refereed journals) since the beginning of the project. Numerous additional findings beyond those highlighted above or described in this report can be found in the publications listed.

Table of Contents

Final Technical Report Grant No. DE-FG02-95ER62125

Project: Impacts of Interacting Elevated Atmospheric CO_2 and O_3 on the Structure and Functioning of a Northern Forest Ecosystem: Operating and Decommissioning the Aspen FACE Project

The Aspen FACE project occurred due to the vision of efforts of the late Dr. David F. Karnosky and colleagues in the early 1990s. Dr. Karnosky was the Principal Investigator for this project from its initiation until his death in 2008. Without his efforts, Aspen FACE would not have happened, and this report is dedicated in his memory.

Background

Human activities have greatly accelerated rates of global environmental change. Understanding the consequences of these changes for forest ecosystems is a pressing challenge, given the importance of forests in global net primary production (NPP), carbon sequestration, human economies, and as repositories of biodiversity. There is growing recognition that global change and long-range transport of air pollutants have the potential to significantly affect global air quality in the coming decades (Brasseur et al. 2003). Two of the most important and pervasive greenhouse gases driving global change and impacting forests in the U.S. and around the world are [CO_2] and tropospheric O_3 (Felzer et al. 2004, Sitch et al. 2007).

As the only free air, large-scale manipulative experiment studying the interaction of atmospheric [CO_2] and [O_3] on forests, the Aspen FACE experiment was uniquely designed to address the long-term ecosystem level impacts of these two greenhouse gases on aspen-birch-maple forests, which dominate the richly forested Lake States region (USDA 2004, Heath and Smith 2004). The Aspen FACE Project was established in 1997 to address the overarching scientific question:

“What are the effects of elevated [CO_2] and [O_3], alone and in combination, on the structure and functioning of northern hardwood forest ecosystems?”

Data gathered over the decade-long experiment was intended to improve our ability to predict how forest ecosystem productivity, health and composition will respond as the concentrations of both CO_2 and O_3 increase in the future and address the overall hypothesis that: *Genetic differences regulating C assimilation, growth and C allocation are the fundamental controls on changes in ecosystem composition and function as atmospheric CO_2 and O_3 rise*. Under this hypothesis, ecosystem responses to CO_2 and O_3 are mediated through the life history traits of the dominant plants, and responses to CO_2 and O_3 cascade through ecosystems in a predictable manner.

Among the scientific questions the Aspen FACE Experiment was intended to address are:

Where is the missing carbon from global carbon models? Is it being sequestered by forests?
Will more or less CO_2 be sequestered by forest trees as CO_2 levels rise?
Are forests net carbon sources or sinks? Do they change over time?
Is carbon sequestered by trees stored for long time periods in the soil?
Will elevated CO_2 alleviate other stresses (e.g. ozone, drought, low fertility)?
Will our forests become more or less productive over time under elevated CO_2?
How will elevated CO_2 affect insect and disease interactions with trees?

How do CO_2 and the greenhouse gas ozone interact?

This report will focus primarily on results from the last years of treatment and final harvest to answer these questions, but will also describe results from earlier work conducted under this project and others from the entire duration of Aspen FACE, to help explain the changes over time the led to the overall final results of the experiment.

Experimental Design

From 1998 through the middle of the 2009 growing season, we examined the interacting effects of elevated CO_2 and O_3 on ecosystem processes in an aggrading northern forest ecosystem. This study utilized a free-air carbon dioxide enrichment (FACE) facility near Rhinelander, Wisconsin to compare the responses of early-successional, rapid-growing shade intolerant species (trembling aspen [*Populus tremuloides* Michx.] and paper birch [*Betula papyrifera* Marsh.]) to those of a late successional, slower growing shade tolerant species (sugar maple [*Acer saccharum* Marsh.]). Three replicate FACE rings were established in 1997 for a factorial combination of four treatments (CO_2, O_3, CO_2+O_3 and control) in a randomized block design. Rooted cuttings from five aspen clones previously characterized for O_3 and CO_2 sensitivities were planted 1.0 m apart in one-half of each FACE ring (Fig. 1). The other half was divided into equal size plots of aspen/sugar maple and aspen/paper birch, again at 1 m x 1 m spacing, to examine interactions between shade tolerant and intolerant species. The close spacing simulated a naturally regenerating forest. Fumigations with elevated CO_2 (560 ppm during daylight hours) and O_3 (approximately 1.5 x ambient) were conducted over 165, 144, 145, 150, 137, 143, 154, 143, 140, 125 and 140-day growing seasons from 1998 to 2008, respectively, and in 2009 through harvest date.

Measurements made included growth (height, diameter, biomass, leaf area, root production, and fine root mortality), competitive interactions and stand dynamics, physiological processes (photosynthesis, respiration, stomatal conductance, and chlorophyll content), plant nutrient status and uptake (nitrogen), tissue biochemistry (carbohydrates, phenolic glycosides, and antioxidants), litter quality and decomposition rates, hydrology, soil respiration, microbial community composition and respiration, VOC production, treatment-pest interactions, and treatment-phenology interactions. Many of these measurements were not directly supported by this grant, but this grant did provide the infrastructure and site operations that made possible all of the long-term collaborative research at the Aspen FACE facility. Additional details regarding the experimental design, treatments and measurements can be found in Dickson (2000) and the forthcoming Kubiske et al. (2014).

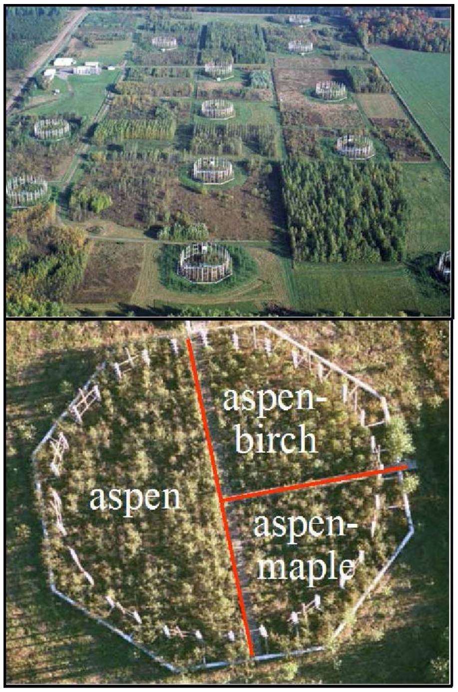

Fig. 1. Aerial views of the FACTS II FACE Experiment. Pictured in panel A is the entire FACE array. Panel B illustrates the division of the FACE rings into sections containing aspen, aspen-birch and aspen-maple.

From mid-June to mid-August in 2009, we conducted a detailed harvest of the site using protocols developed collaboratively between Michigan Tech, the USFS Northern Research Station (Rhinelander), the University of Michigan, and the

University of Nevada, Reno. Portions of the above- and belowground components of the experiment were harvested by block after the entire canopy had developed. Fumigation within a ring was continued to within one week of the harvest. The harvest included detailed sampling of a subset of trees by component (leaves and buds, fine branches, coarse branches and stem, coarse roots, fine roots) and excavation of soil to a depth of 1 m. An excavator and commercial soil sieve were used to recover coarse roots, with additional cores from pit faces used to capture fine root biomass. The destructive harvest produced detailed information on above- and belowground biomass, tree allometry, and soil C and N that far exceeded that which had been obtained by less intensive sampling during the experiment. In addition to the primary measurements and samples for our core scientists, we provided samples and/or data from the final harvest in response to more than 25 requests from researchers with universities and government agencies from five countries.

Findings:

Canopy Gas Exchange

Throughout the experiment, photosynthesis increased with elevated CO_2 and tended to decrease with elevated O_3, compared to the control (Fig. 2, Fig. 3; see Karnosky et al. 2003, Darbah et al. 2010b, McGrath et al. 2010 and earlier reports). Responses were species and genotype specific. In contrast to aspen and birch, maple photosynthesis was not enhanced by elevated CO_2 (Fig. 2). Elevated O_3 did not cause significant reductions in maximum photosynthesis in birch or maple. In addition, photosynthesis in ozone sensitive clones was affected to a much greater degree than that in ozone tolerant clones (Noormets et al. 2001).

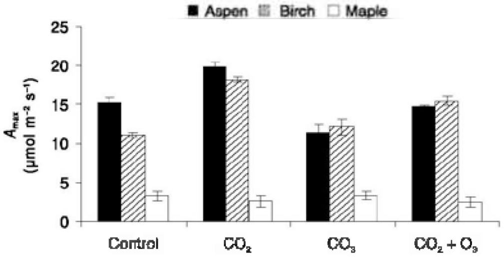

Fig. 2. Light-saturated CO_2 assimilation rates of aspen, birch and maple growing under experimental atmospheric CO_2 and O_3 treatments. Data represent the mean and SE of three trees from each of three replicates for three to five measurement times over the 1999 and 2000 growing seasons. Elevated CO_2 significantly ($P < 0.05$) increased A_{max} in aspen and birch, while elevated O_3 significantly decreased A_{max} in aspen. The figure is from Karnosky et al. 2003 (Fig. 4).

Darbah et al. (2010b) examined two of the aspen clones for evidence of photosynthetic acclimation to the treatments over the first eleven years of exposure and found no evidence indicating changes over time in the positive (CO_2) or negative (O_3) responses to the treatments (Fig. 3). The effects of O_3 and CO_2 on photosynthesis have varied with diurnal and seasonal patterns of environmental stress (drought, high air temperature). The positive impact of CO_2 on net photosynthesis was more pronounced on days with environmental stress but relatively less pronounced during midday depression, while the negative impact of ozone tended to decrease in both cases (Kets et al. 2010).

Altered photosynthesis had direct effects on net primary productivity (see next section), including production of foliage (Fig. 4, Talhelm et al. 2012) which created a positive feedback that led to even greater enhancement of C assimilation under elevated CO_2 for aspen and birch and further reduction of C assimilation under elevated O_3 for aspen (Karnosky 2003).

Elevated CO_2 also conferred increased thermotolerance for both aspen and birch trees while isoprene production in aspen conferred further thermotolerance in aspen (Darbah et al. 2010a). This has potential climatic change implications, as isoprene-emitting trees may have a competitive advantage as temperatures rise.

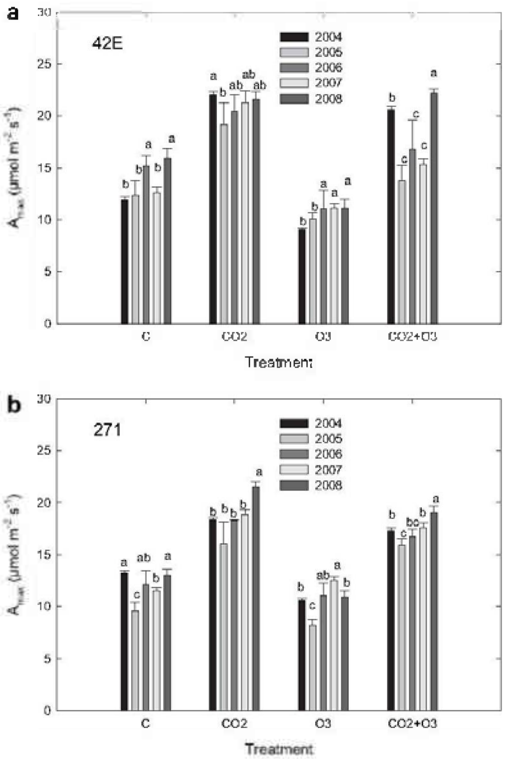

Fig. 3. Average seasonal maximum assimilation rate (Amax) for the growing seasons 2004 through 2008 in aspen clones 42E and 271, showing significant differences among years within each of the four treatments. Measurements were taken from the same trees each year at the Aspen FACE site, Rhinelander, WI, USA. Within a treatment, letters indicate significant differences ($P <$ 0.05) among years. Elevated CO_2 significantly increased Amax in all years. Elevated O_3 significantly reduced Amax in all years except 2007, when O_3 treatment was halted for over a month due to equipment failure. Figure is from Darbah et al. 2010b (Fig. 1).

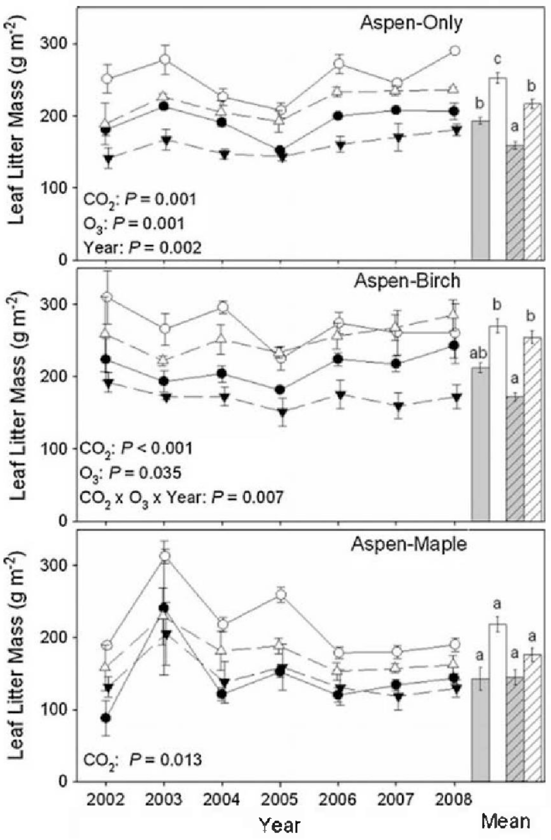

Fig. 4. Annual leaf litter mass (g m^{-2}) in the three community types for the ambient (filled circles, filled bar), +CO_2 (empty circles, empty bar), +O_3 (solid triangles, filled hatched bar), and +CO_2+O_3 (empty triangle, empty hatched bar). Bar graphs are means over the entire collection period. Error bars are ±1 SE. Reported ANOVA P values are from repeated measures analyses within each community. Letters denote significant differences in pair-wise comparisons ($P <$ 0.05) among the treatments within a community. Figure is from Talhelm et al. 2012 (Fig. 1).

Net Primary Productivity

Treatment effects on photosynthesis have contributed to CO_2 stimulation of aboveground and belowground growth that was species and genotype dependent, with birch and aspen being most responsive and maple being least responsive. The positive effects of elevated CO_2 on net primary productivity (NPP) were sustained through the end of the experiment, but negative effects of elevated O_3 on NPP had dissipated during the final three years of treatments (Fig. 5 and Zak et al. 2011).

Relative to NPP under ambient CO_2, NPP was significantly enhanced under elevated CO_2 by 40% in 2006 ($P = 0.009$), 14% in 2007 ($P = 0.013$), and 25% in 2008 ($P = 0.009$), which corresponded to the 10th to 12th years of the experiment. Despite elevated O_3-induced reductions in plant growth that occurred early in the experiment, elevated O_3 had no effect on NPP during the 10th to 12th years of exposure (Fig. 5; $P = 0.128$ to 0.887). In no case did we find significant interactions among plant community, CO_2, or O_3, indicating that NPP in the three plant communities in our experiment responded similarly to both CO_2 and O_3. If similar forests growing throughout northeastern North America respond in the same manner, then enhanced forest NPP under elevated CO_2 may be sustained for a longer duration than previously thought, and the negative effect of elevated O_3 may be diminished by compensatory growth of O_3-tolerant plants as they begin to dominate forest communities.

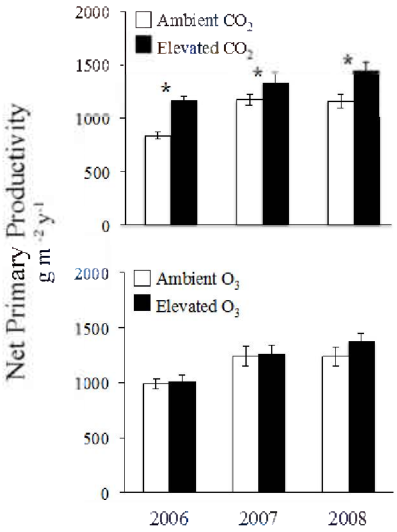

Fig. 5. Net primary productivity (NPP) during the last three years of the Rhinelander FACE experiment. NPP has been sustained under elevated CO_2 and NPP has recovered under elevated O_3 due to compensatory growth of O_3 tolerant genotypes and species.

The treatments are clearly affecting NPP through their effects on photosynthesis and leaf area, and evidence suggests they also may also be affecting NPP by altering growing season phenology. Taylor et al. (2008) reported a significant delay in the decline of autumnal canopy leaf area index in elevated CO_2. Leaf level photosynthetic activity and carbon uptake during the senescence period were enhanced under elevated CO_2. The findings reveal a direct effect of rising atmospheric CO_2, independent of temperature, in delaying autumnal senescence. Riikonen et al. (2008) also observed delayed autumnal senescence under elevated CO_2, as well as accelerated senescence and delayed spring leaf development under elevated O_3, and McGrath et al. (2009) have found that found spring leaf flush is suppressed by elevated O_3 in aspen and stimulated by elevated CO_2. For birch, accelerated senescence under elevated O_3 was associated with decreased expression of photosynthesis- and carbon fixation-related genes, and increased expression of senescence-associated genes (Kontunen-Soppela et al. 2009).

Year-to-year variation in treatment growth responses has occurred at Aspen FACE, and the long-term nature of the project has enabled the research team to explain much of this variation. Kubiske et al. (2006) found the photosynthetically active radiation and temperature during specific times of the year explained 20-63% of the annual variation in growth response to elevated CO_2 and O_3. Cloudy summers and cool autumns were responsible for several years with a decreased CO_2 growth response. Climatic variation has also played a role in predisposing trees to deleterious effects of other stressors. For example, three to five times as many birch in the O_3 treatments succumbed to drought stress in 2005, due to subsequent infestation with bronze birch borer, which does not infect healthy birch trees.

Following the final harvest, estimates of cumulative NPP for the entire experiment were made (Talhelm et al. 2014) in order to understand the magnitude and temporal dynamics of the treatment effects on NPP and to test the hypothesis that the relationship between ecosystem C content and NPP had not been altered by elevated CO_2 and/or O_3. Previous NPP estimates at Aspen FACE included only the first six years (1998-2003; King et al. 2005) or last three years of the experiment (2006-2008; Zak et al. 2011) and had been constructed using different allometric equations and assumptions. Thus, estimating cumulative NPP (1998-2008) was not a simple combination of the earlier analyses. NPP was considered to include fine roots (<2 mm diameter), small roots (1 - 2 mm diameter), coarse roots (>2 mm diameter), stems, branches, leaves, groundcover vegetation, and other plant litter. The NPP estimates were derived from previous publications on the production of leaves, fine roots, and groundcover plants (e.g. Bandeff et al. 2006, Pregitzer et al. 2008, Talhelm et al. 2012) and estimates of tree biomass created from annual stem diameter measurements and allometric equations created from trees harvested in 2000, 2002, and 2009.

Cumulative NPP was 39% greater under elevated CO_2 ($P < 0.001$), 10% lower under elevated O_3 ($P = 0.026$), and varied by more than 27% across communities ($P < 0.001$) (Fig. 6 and Talhelm et al. 2014). Interactions were not significant between treatments ($P = 0.661$) or between the treatments and communities ($P > 0.65$) for cumulative NPP. The O_3 effect on annual NPP gradually disappeared during the final 7 years of the experiment (dashed line in Fig. 6b). Specifically, the O_3 effect on tree productivity (NPP_{tree}) declined from a peak of -95 g m^{-2} in 2002 ($P = 0.002$) to -17 g m^{-2} in 2008 ($P = 0.554$; linear $r^2 = 0.66$, $P = 0.026$). Over a similar period, the absolute effect of elevated CO_2 on NPP_{tree} was fairly consistent, changing from +189 g m^{-2} in 2001 to +200 g m^{-2} in 2008 (linear $r^2 = 0.24$, $P = 0.223$). The declining response to O_3 over time resulted from the compensatory growth of O_3-tolerant genotypes and species as the growth of O_3-sensitive individuals declined over time (see next section), thereby causing annual NPP to attain equivalent levels under ambient and elevated O_3. Given the degree to which O_3 has been projected to decrease global NPP, the compensatory growth of O_3 tolerant plants in our experiment, as they replaced senescing O_3 sensitive plants, should be considered in future simulations. Depending on the generality of this response, this effect could dramatically

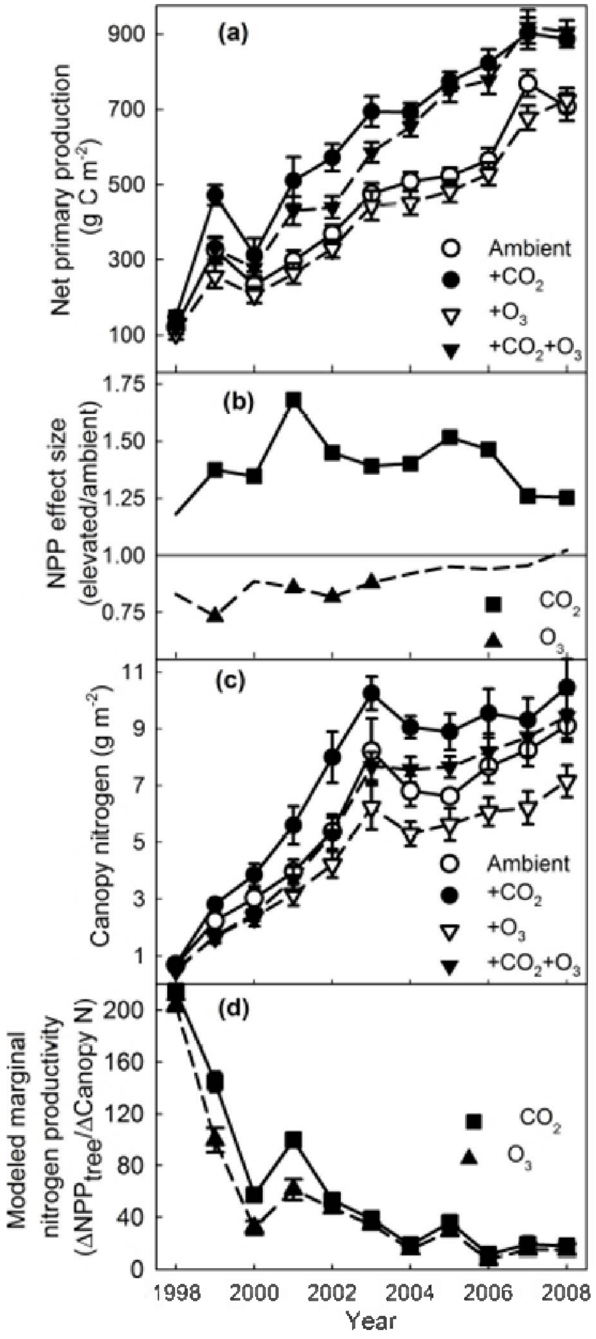

Fig. 6. (a) NPP, (b) NPP effect sizes, (c) canopy N (elevated/ambient, 1 = no effect), and (d) the modeled marginal N productivity ([$NPP_{tree(elevated)}$ - $NPP_{tree(ambient)}$]/ [Canopy $N_{(elevated)}$ – Canopy $N_{(ambient)}$]). In (b), symbols are shown only when NPP effects are significant ($P < 0.05$). Bars are ±1 standard error. Figure is from Talhelm et al. 2014.

diminish the predicted negative effect of elevated O_3 on NPP and C storage on land as well as projected feedbacks to atmospheric CO_2 and climate warming.

Sustaining soil N availability

The inability of maple to respond positively to elevated CO_2 was at least partly due to a superior ability of aspen to acquire N under elevated CO_2 (Zak et al. 2012). Enhanced net primary productivity (NPP) under elevated CO_2 was sustained by greater root exploration of soil for growth-limiting N, as well as more rapid rates of litter decomposition and microbial N release during decay (Zak et al. 2011, 2012). Results from our long-term measurements at Aspen FACE clearly indicate that plants growing under elevated carbon dioxide, regardless of community type or ozone level, obtained significantly greater amounts of ^{15}N tracer as well as soil N. These results indicate that greater plant growth under elevated carbon dioxide has not led to "progressive N limitation".

This is in agreement with accumulating evidence suggesting that elevated CO_2 can supplement the supply of soil N to plants by increasing the production of root exudates, which, in turn, facilitate the decay of soil organic matter and the subsequent release of inorganic N for plant uptake (Zak et al. 1993, Langley et al 2009, Drake et al 2011). This mechanism has sustained enhanced NPP under elevated CO_2 in a loblolly pine (*Pinus taeda*) forest (Drake et al. 2011) as well as a scrub-oak forest (Langley et al. 2009), and several lines of evidence indirectly indicate it may have contributed to the greater plant acquisition of soil N under elevated CO_2 at Aspen FACE. In our experiment, soil organic matter is accumulating at a slower pace under elevated CO_2, despite the fact that both above- and belowground litter production have significantly increased under elevated CO_2 (Talhelm et al. 2009). This observation indicates that the decay of soil organic matter is occurring at a more rapid rate under elevated CO_2, a response that has occurred in parallel with the increased rate of forest floor N cycling. These findings support the idea that greater belowground plant growth under elevated CO_2 has accelerated organic matter decay and increased the supply of N to plants, thereby sustaining the enhancement of NPP under elevated CO_2. This finding differs from those of short-term decomposition studies at Aspen FACE (Liu et al. 2009a,b), highlighting the importance of long-term field measurements for separating true responses from transient effects.

After a decade, NPP remained enhanced under elevated CO_2 and has recovered under elevated O_3 by mechanisms that remain un-calibrated or not considered in coupled climate-biogeochemical models simulating interactions between the global C cycle and climate warming.

Competitive Interactions

The long-term nature of the experiment has enabled assessment of treatment effects on competitive interactions among the tree species and among the aspen clones. Kubiske et al. (2007) utilized trends in species' importance, calculated as an index of volume growth and survival, as indications of shifting community composition. For the pure aspen community, different clones emerged as having the highest change in relative importance values. In the control and elevated CO_2 treatments, clone 42E was rapidly becoming the most successful clone while under elevated O_3, clone 8L emerged as the dominant clone. For the mixed aspen-birch community, importance of aspen and birch changed by -16% and +62%, respectively, in the control, with the presence of elevated O_3 hastening the conversion of stands to paper birch, whereas the presence of elevated CO_2 delayed it. Relative importance of aspen and maple changed by -2% and +3%, respectively, after seven years in the control treatments. Elevated O3 slightly increased the rate of conversion of aspen stands to sugar maple, but maple was placed at a competitive disadvantage to aspen under elevated CO_2. Project results suggest that the changing atmospheric composition could shift the genotypic composition and average pollutant responses of tree populations over moderate timescales (Moran and Kubiske 2013).

Differences among the aspen clones in performance under elevated O_3 are explained in part by reduced early season stomatal conductance and O_3 uptake in clone 8L under elevated O_3, allowing it to avoid damaging exposure (Rouse 2008). Differences in isoprene emissions also may be important, due to the role of isoprene in protection against oxidative stress from O_3 exposure. Working at Aspen FACE, Calfapietra et al. (2008) found isoprene emissions decreased significantly under both elevated CO_2 and elevated O_3 in O_3-sensitive aspen, but only slightly in O_3-tolerant aspen. The ability of O_3-tolerant clones to maintain higher amounts of isoprene emission may be an important factor in strengthening their existing ability to minimize O_3 uptake through lower stomatal conductance. Finally, variation in cellular responses to DNA damage between aspen clones may contribute to O_3 tolerance or sensitivity. Tai et al. (2009) found that exposure to O_3 and CO_2 in combination with O_3 increased DNA damage levels above background. Ozone-tolerant clones 271 and 8L showed the highest levels of DNA damage under elevated O_3 compared with ambient air, but clone 8L also demonstrated the highest level of excision DNA repair.

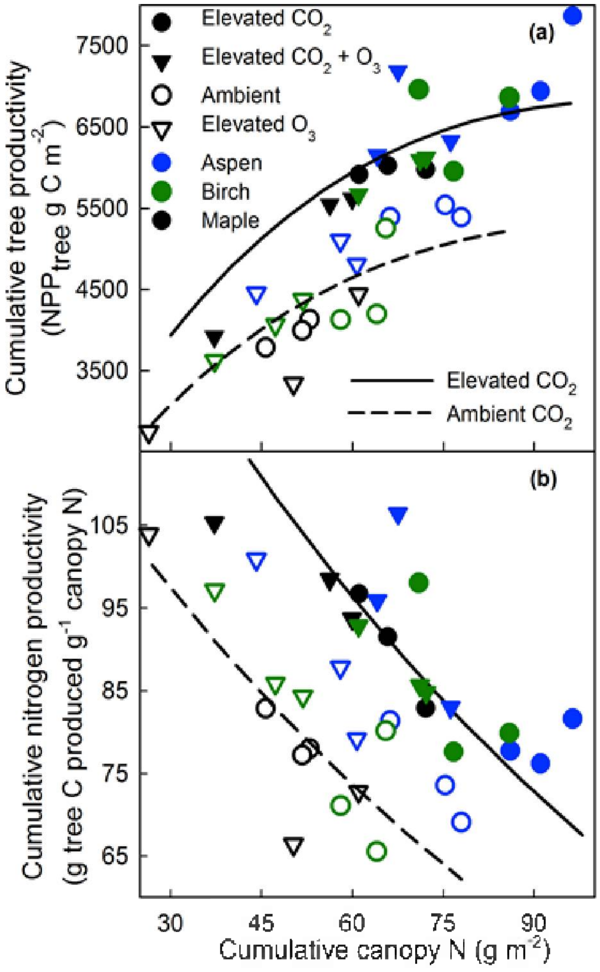

Fig. 7. Cumulative canopy N in relation to (a) cumulative tree productivity and (b) N productivity, with lines displayed representing mixed model estimates of these relationships (community effects not shown for simplicity). Slopes in (b) do not differ, but intercepts differ by community ($P = 0.031$) and between ambient CO_2 and elevated CO_2 ($P < 0.001$). Ozone effects on the slopes and intercepts were not significant ($P > 0.25$). Figure is from Talhelm et al. 2014.

Effects of Canopy Development on NPP

We fit several stand-level models that predict NPP_{tree} based on canopy development metrics (leaf area, canopy N, etc.) and canopy productivity (e.g., produc tivity per leaf area). This allowed us to test the hypotheses that both canopy development and canopy productivity would be stimulated by elevated CO_2 and depressed by elevated O_3 in these young forests (Norby & Zak 2011, Ainsworth et al. 2012). We expected that developmental effects would diminish as all stands reached maximum leaf area index (Körner 2006, Norby & Zak 2011). Through this analysis, we also hoped to gain further insight into the diminishing effect of O_3 on NPP.

We evaluated several canopy attribute stand productivity models using the cumulative NPP data. We tested (1) the N Productivity Model (Ågren 1983), which describes increasing NPP_{tree} with canopy N but a diminishing return as foliar biomass accumulates; (2) the Reich model (Reich 2012), which predicts productivity based upon stand leaf area index (LAI, m^2 m^{-2}), foliar N concentration, and their interaction (LAI × N); and (3) a model developed from remote sensing (Smith et al. 2002) that predicts a base rate of productivity (an intercept) and greater rates of productivity as foliar N concentration increases. We used corrected AIC (AICc) for model selection. In the selected model for NPP_{tree}, stands with more cumulative canopy N (g foliar N m^{-2} of ground area) had greater cumulative NPP_{tree} (Fig. 7a), but N productivity (NPP_{tree} per canopy N) decreased as canopy N accrued (Fig. 7b). Cumulative canopy N, leaf area (m^2 m^{-2}), and canopy leaf mass (g m^{-2}) were correlated with each other (n = 36, $r > 0.80$, $P < 0.001$; not shown). Likewise, annual canopy N (Fig. 6c), leaf area, and canopy leaf mass (Talhelm et al., 2012) responded similarly to the treatments through time. However, canopy N was the best predictor of NPP_{tree}.

Neither CO_2 nor O_3 affected the rate at which N productivity decreased with canopy N accrual (i.e., slopes in Fig. 7b were not different: $P > 0.25$). Cumulative NPP_{tree} was greater under elevated CO_2 because of increases in both canopy N content (+28%, $P < 0.001$) and the maximum rate of N productivity (N $productivity_{max}$, the y-intercept in Fig. 7b; +28%, $P < 0.001$). Communities also differed in both of these traits ($P < 0.035$). In contrast, the negative effect of elevated O_3 on cumulative NPP_{tree} resulted from decreased canopy N (-21%, $P < 0.001$), as there was no meaningful impact on cumulative N $productivity_{max}$ (-2%, $P = 0.659$).

Because NPP_{tree} was a function of canopy N, the disappearance of the O_3 effect on annual NPP (Fig. 6b) despite the consistent negative effect on canopy N (Fig. 6c) might seem to indicate a weakening physiological impact of O_3. For further insight, we fit the NPP_{tree} model to annual data and then applied the annual models for elevated stands to the matching ambient stands (18 pairs at the ring-section level). This allowed us to estimate the marginal increase in NPP_{tree} caused by differences in canopy N between the treatments ($\Delta NPP_{tree}/\Delta N$). This analysis revealed that marginal N productivity decreased by more than a factor of 10 during the experiment (Fig. 2d), meaning that differences in canopy N created by elevated CO_2 or O_3 had gradually smaller impacts on NPP. Notably, the annual O_3 effects on NPP predicted by differences in canopy N closely matched the observed O_3 effects ($r = 0.82$, $P = 0.002$; not shown). Thus, the diminishing impact of O_3 on NPP was due to a declining relative impact of canopy N differences rather than a physiological acclimation to O_3.

Ecosystem C Content

Prior to the experiment, we hypothesized that ecosystem C content would be enhanced by elevated CO_2 and decreased by elevated O_3. We further hypothesized that CO_2 and O_3 would have counteracting effects on ecosystem C content. We observed that the two gases had opposite and nearly equal effects on ecosystem C content (Fig. 8, Talhelm et al. 2014): elevated CO_2 increased ecosystem C content by 11%, whereas elevated O_3 decreased ecosystem C content by 9%. Total ecosystem C content in the interaction treatment (elevated CO_2 and O_3) did not significantly differ from that of the control (Fig. 8). Total ecosystem C content responded similarly to the treatments across the three forest communities (Treatment × Community: $P > 0.25$). There were also no significant interactions between CO_2 and O_3 for any of the largest C pools ($P > 0.1$). The treatment effects on ecosystem C content resulted from differences in tree biomass, particularly woody tissues (branches, stem, and coarse roots), and lower C content in the near-surface mineral soil (Fig. 8). For tree C, the negative effect of elevated O_3 was smaller (-15%) than the positive effect of elevated CO_2 (+44%)

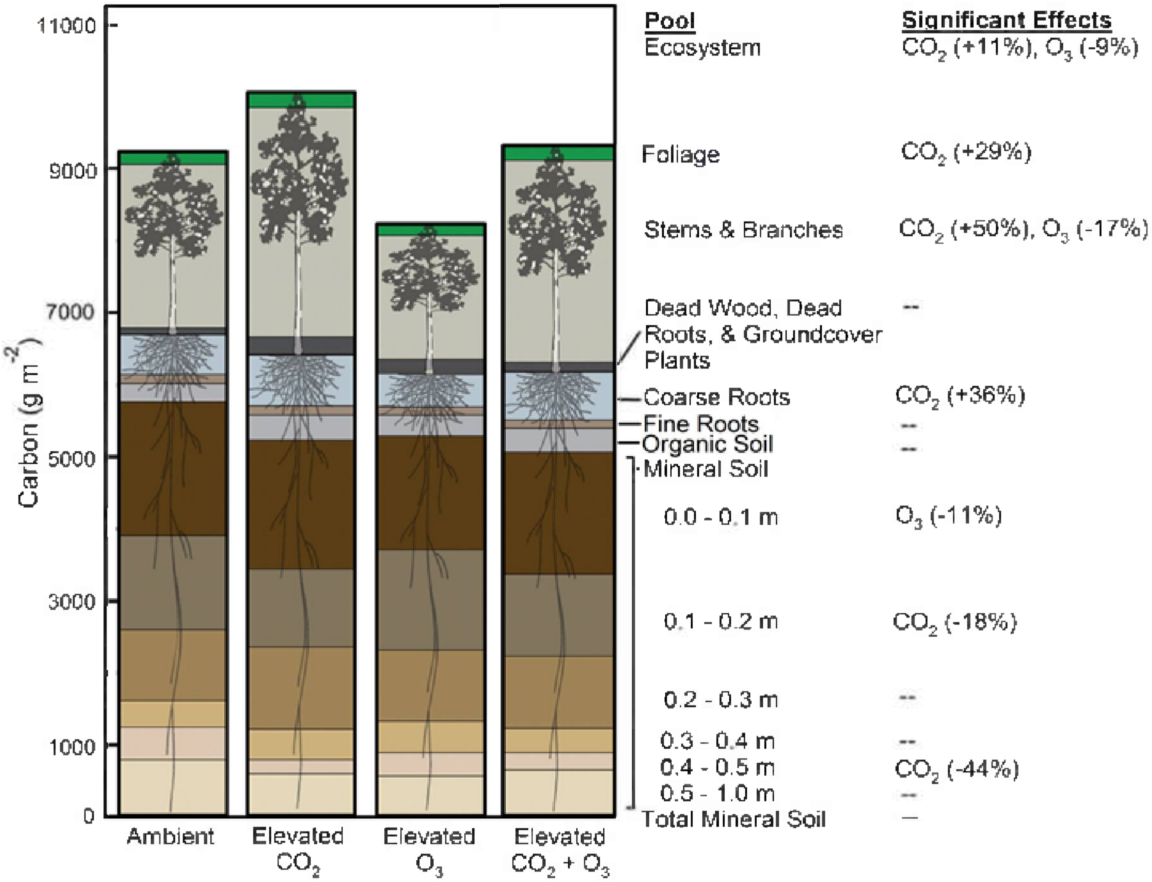

Fig. 8. Ecosystem carbon content at the Aspen FACE experiment. Data are averaged across the three forest community types and include soil to 1 m in depth. The height of each bar segment represents mean size of each pool and the total bar height is represents ecosystem C content for each treatment. Significant ($P \leq 0.05$) effects of the treatment gases and the size of these effects (%) are shown to the right of the figure. Pools without significant treatment effects are denoted with "--". The figure is from Talhelm et al. 2014.

We also assessed tree C at the species level. The two species within the aspen-birch community responded similarly to the treatments and the proportion of tree C represented by aspen within the community was not influenced by CO_2 or O_3 (44 ± 4% aspen; $P > 0.69$). However, there was not a uniform treatment response within the aspen-maple community: elevated CO_2 increased aspen tree C by 76% and decreased maple tree C by 32% (CO_2 × species: $P < 0.001$), while elevated O_3 decreased aspen tree C by 22% and changed maple tree C by <1% (O_3 × species: $P < 0.001$). In interpreting the treatment effects on maple, it should be noted that the faster growing aspen represented 87% (± 2%) of tree C within this community and was taller throughout the experiment than the slower growing maple. In comparison, height differences were not significant between aspen and birch until the final full year of the experiment.

Neither CO_2 nor O_3 affected the total amount of C in the top 1 m of mineral soil. However, each gas significantly decreased mineral soil C content in one of the two depth increments nearest to the surface: soil C within the top 0.1 m of mineral soil was lower under elevated O_3, whereas soil C from 0.1 to 0.2 m in depth was lower under elevated CO_2 (Fig. 8). Soil C was also lower under elevated CO_2 at 0.4 to 0.5 m in depth (Fig. 8), but there were no additional treatment effects on soil C.

After 11 years, there were no significant main effects of CO_2 or O_3 on surface soil (0-20 cm) C content across all three communities, but within the aspen community, elevated CO_2 caused a significant decrease in soil C content (Talhelm et al. 2009). Overall, our observations indicate that elevated CO_2 has altered SOM cycling at this site to favor C and N accumulation in less stable pools, with more rapid turnover (Hofmockel et al. 2011). Elevated O_3 had the opposite effect, significantly reducing cPOM N by 15% and significantly increasing the C:N ratio by 7%. Our results demonstrate that CO_2 can enhance SOM turnover, potentially limiting long-term C sequestration in terrestrial ecosystems; plant community composition is an important determinant of the magnitude of this response. In addition, an initial reduction in the formation of new (fumigation-derived) soil C by O_3 under elevated CO_2 (Loya et al. 2003) proved to be only a temporary effect, mirroring trends in fine root biomass. These results contradict predictions of increased soil C under elevated CO_2 and decreased soil C under elevated O_3 and should be considered in models simulating the effects of Earth's altered atmosphere.

Other Responses

Soil respiration and fine root dynamics

Soil respiration responses paralleled aboveground results in the early years of the project, but not in later years. For example, during the first five years of the experiment, soil respiration increased with elevated CO_2, decreased with elevated O_3 and was fairly similar to the control for elevated CO_2+O_3. In later years, soil respiration was greater in the elevated CO_2 and CO_2 +O_3 treatments for all three plant communities (Pregtizer et al. 2008), but was not affected by elevated O_3 alone. The treatment responses in soil respiration were correlated with fine root biomass, which, for the aspen community was actually stimulated by O_3, and especially CO_2+O_3. After 10+ years of exposure, the CO_2+O_3 treatment induced increases in belowground carbon allocation to fine roots in aspen, suggesting that the positive effects of elevated CO_2 on belowground net primary productivity were not offset by negative effects of O_3.

Aspen fine-root (< 1.0 mm) production rates were not affected by elevated carbon dioxide alone or elevated ozone alone. Fine-root (< 1.0 mm) mortality rates also were not affected by elevated CO_2 alone; however, they were enhanced by elevated ozone in 2003, but not in 2004. Overall, fine-root (< 1.0 mm) production and mortality showed no clear response to treatments, and thus fine-root (< 1.0 mm) survival was fairly consistent across treatments and years. As a result, differences among treatments in annual fine-root production and mortality, expressed on a mass basis, were controlled primarily by treatment differences in standing fine-root biomass. Root production was positively affected by elevated CO_2 alone and elevated O_3 alone and was greatest in the elevated CO_2-O_3 treatment combination, a result that substantially differed from the initial response of fine root biomass to the treatments. Rates of biomass mortality were positively influenced by elevated O_3, but varied from year to year. These results were driven by larger standing fine-root (< 1.0 mm) biomass in the elevated O_3 alone and elevated CO_2-O_3 treatment combination. Seasonal soil respiration in 2005 was correlated to < 2-mm root biomass ($r = 0.87$; $P < 0.001$) and < 1-mm root biomass ($r = 0.72$; $P = 0.008$) for that year. The tendency for the elevated CO_2-O_3 treatment combination to have the greatest values for biomass of fine roots <

1.0 mm in diameter also occurred for seasonal soil C efflux.

Between the 10th and 12th year of the experiment, plants continued to expand their fine root system regardless of treatment, an indication that they had not yet fully exploited soil for growth-limiting resources. For example, averaged across CO_2 and O_3 treatments, fine-root biomass was 155 g/m^2 in 2005 and gradually increased over subsequent years to 168 g/m^2 by 2008. Similarly, fine root production increased from 344 $g\ m^{-2}\ y^{-1}$ in 2006 to 362 $g\ m^{-2}\ y^{-1}$ in 2008; however, increases in fine-root biomass and production from 2005 to 2008 were not statistically significant ($P_{biomass} = 0.108$; $P_{production} = 0.105$). Clearly, at the end our decade long experiment, these developing forests continued to increase the exploration of soil for growth-limiting nutrients.

Treatment-pest interactions

Insect populations have either increased, decreased or shown no response to elevated CO_2, elevated O_3 and elevated CO_2+O_3, depending on insect and/or tree species (Hillstrom and Lindroth 2008). For example, elevated CO_2 reduced abundance of phloem-feeding herbivores and increased abundance of chewing herbivores, although results were not statistically significant. Enriched CO_2 increased numbers of some parasitoids. The effects of O_3 on insect abundance were generally opposite those of CO_2. No significant differences in arthropod family richness were found among treatments.

Changes in foliar tissue quality due to the independent and interactive effects of elevated CO_2 and O_3 have been more pronounced and have the potential to alter the performance outbreak insect herbivore species. Couture et al. (2012) and Couture and Lindroth (2012) examined the effects of aspen and birch phytochemistry changes at Aspen FACE on gypsy moth and forest tent caterpillar performance. Elevated CO_2 nominally affected foliar quality for both tree species. Elevated O_3 negatively affected aspen foliar quality, but only marginally influenced birch foliar quality. Elevated CO_2 slightly improved herbivore performance, while elevated O_3 decreased herbivore performance, and both responses were stronger on aspen than birch. Nitrogen, lignin, and C:N were identified as having strong influences on herbivore performance when larvae were fed aspen, but no significant relationships were observed for insects fed birch. Their results support the notion that herbivore performance can be affected by atmospheric change through altered foliar quality, but how herbivores will respond will depend on interactions among CO_2, O_3, and tree species.

Nabity et al. (2012) examined spatial patterns in chlorophyll fluorescence and the temperature of leaves damaged by leaf-chewing, gall-forming, and leaf-folding insects in aspen trees as well as by leaf-chewing insects in birch trees at Aspen FACE. Both defoliation and gall damage suppressed the operating efficiency of photosystem II in remaining leaf tissue, but the distance that damage propagated into visibly undamaged tissue was marginally attenuated under elevated CO_2. Elevated CO_2 also increased leaf temperatures, which reduced the cooling effect of gall formation and freshly chewed leaf tissue. These results suggest that elevated CO_2 may reduce the effects of herbivory on the primary photochemistry controlling photosynthesis.

Stomatal conductance and ecosystem water use

At the stand level, changes in leaf area have tended to offset the leaf level effects of the treatments on stomatal conductance and thus potential stand water use. Uddling et al. (2010) found stand canopy conductance was significantly increased by elevated CO_2 but not significantly affected by elevated O_3, demonstrating that short-term primary stomatal closure responses to elevated CO_2 and O_3 were completely offset by long-term cumulative effects of these trace gases on tree and stand structure in determining canopy- and leaf-level conductance in pure aspen and mixed aspen-birch forest. In addition, leaves from trees grown in elevated CO_2 and/or O_3 exhibited weaker short-term responses of stomatal conductance to both an increase and a decrease in CO_2 concentration from current ambient level (Onandia et al. 2011). Potential plant water-savings and reduced stomatal air pollution uptake under rising atmospheric CO_2 may not hold for northern forests under concurrently rising tropospheric O3 (Onandia et al. 2011). Thus, model assumptions of large reductions in stomatal conductance under rising atmospheric CO_2 are very uncertain for forests.

Bacterial and fungal responses

Lesaulnier et al. (2008) found that total bacterial and eukaryotic abundance did not change under elevated CO_2, but heterotrophic decomposers and ectomycorrhizal fungi did increase. Andrew and Lilleskov (2009) also found ectomycorrhizal sporocarp biomass was greatest under elevated CO_2, regardless of O_3 concentration, while it was generally lowest under elevated O_3 with ambient CO_2. Mycorrhizal community composition differed significantly among the treatments. These and other changes in soil biota suggest altered interactions between trembling aspen and the microorganisms in the surrounding soil, supporting the theory that greater plant detritus production under elevated CO_2 significantly alters soil microbial community composition.

During 2010 we completed processing and analysis of samples taken to assess fungal community composition and the activities of cellobiohydrolase and N-acetylglucosaminidase (NAG) after ten years of FACE exposure in aspen and aspen-birch forest ecosystems and compared these results to earlier results from the long-term experiment (Edwards and Zak 2011). NAG is an enzyme involved in the depolymerization of chitin, the second most abundant polysaccharide in nature, and an important source of organic N. The forest floor community was dominated by saprotrophic fungi, and differed slightly between plant community types, as did NAG activity. Elevated CO_2 and O_3 had small but significant effects on the distribution of fungal genotypes in this horizon, and elevated CO_2 also lead to an increase in the proportion of *Sistotrema* spp. within the community. Yet, although cellobiohydrolase activity was lower in the forest floor under elevated O_3, it was not affected by elevated CO_2. NAG was also unaffected.

The soil community was dominated by ectomycorrhizal species. Both CO_2 and O_3 had a minor effect on the distribution of genotypes; however, phylogenetic analysis indicated that under elevated O_3, *Cortinarius* and *Inocybe* spp. increased in abundance and *Laccaria* and *Tomentella* spp. declined. Although cellobiohydrolase activity in soil was unaffected by either CO_2 or O_3, NAG was higher (similar to 29%) under CO_2 in aspen-birch, but lower (similar to 18%) under aspen. Time series analysis indicated that CO_2 increased cellulolytic enzyme activity during the first 5 years of the experiment, but that the magnitude of this effect diminished over time. Unlike cellobiohydrolase, NAG activity tended to increase over time. Moreover, NAG activity was strongly stimulated by elevated CO_2, and was slightly lower under elevated O_3, early in the Rhinelander FACE experiment. By year 10 however, NAG response to elevated CO_2 differed between plant communities, being higher in aspen-birch and lower in aspen. Elevated O_3 appears to have variable stimulatory and repressive effects depending on the soil horizon and time point examined.

In our decade-long experiment, stratification of the fungal community between forest floor and soil horizons and differing plant communities had a greater influence on fungal community composition and function than did elevated CO_2 and O_3. Nevertheless, our results demonstrate that plant exposure to elevated concentrations of CO_2 or O_3 can lead to small, but persistent changes in fungal community function, and that these may be related to concomitant changes in fungal community composition. Moreover our results further suggest that O_3 and CO_2 may affect different parts of the fungal community, and that their functional effect may decline or even change entirely over time.

Reproductive fitness

Treatment effects on whole-tree carbon balance also are affecting reproductive fitness in birch (Darbah et al. 2008). Elevated CO_2 has increased both the number of birch trees that flower and the quantity of flowers (260% increase in male flower production), increased seed weight, germination rate, and seedling vigor. In contrasts, elevated O_3 also increased flowering but decreased seed weight and germination rate. In the combination treatment (elevated $CO_2 + O_3$) seed weight was decreased (20% reduction), while germination rate was unaffected. These findings suggest that elevated CO_2 may have a largely positive impact on forest tree reproduction and regeneration while elevated O_3 will likely have a negative impact, at least for some species.

Wood decomposition processes

Although data suggest leaf and root litter decomposition have been affected by the treatments, we found little evidence for altered decomposition of wood grown under or placed in elevated CO_2 and/or elevated O_3 (Ebanyenle 2012). Tree species (aspen vs. birch) and aspen genotype had a much greater impact on the wood-decaying fungal community and initial wood decomposition rate than did growth or decomposition of wood in elevated CO_2 and / or O_3. Thus any changes in ecosystem wood decomposition under future atmospheres would occur via shifts in species and / or genotype composition and under future higher levels of CO_2 and O_3. In terms of wood quality, the effects of the treatments were minor (Ebanyenle 2012). Elevated CO_2 did not have significant effects on wood anatomical properties in trembling aspen, paper birch or sugar maple, except for marginally increasing ($P < 0.1$) the number of vessels per square millimeter. Elevated O_3 marginally or significantly altered vessel lumen diameter, cell wall area and vessel lumen area proportions depending on species and radial position. In line with the modifications in the anatomical properties, elevated CO_2 and O_3, alone, significantly modified wood density but effects were species and / or genotype specific. The effects of elevated CO_2 and O_3, alone, on wood anatomical properties and density were ameliorated when in combination. Based on these results, future higher levels of CO_2 and O_3 may have minor effects on wood quality of northern hardwoods, but for utilization purposes these would not be considered significant.

Brief History of Aspen FACE Funding, Publications and Operation

Initial funding for the experiment came from the NSF/DOE/NASA/USDA Joint Program on Terrestrial Ecology and Global Change (1995-2001) and the NSF Academic Research Infrastructure Program (1996), with additional funding and in-kind support from the National Council for Air and Stream Improvement, Brookhaven National Laboratory, Michigan Technological University, The US Forest Service Northern Global Change Program, and the US Forest Service North Central Experiment Station. Subsequent to 2001, the experiment was principally funded by the US DOE Program for Ecosystem Research, the US Forest Service, Michigan Tech University and Natural Resources Canada, Canadian Forest Service. In addition, the USFS installed, maintained, and archived the extensive micrometeorological monitoring done at the Aspen FACE Project.

The project involved collaboration between scientists from 9 countries, and over the course of the experiment there were over 120 Aspen FACE scientific users. Key investigators from this group are listed in Table 1, but there are many additional scientists and students who participated in the research at the site. These scientists helped produce 75 publications during the most recent funding period (2008-2014) and 207 peer-reviewed publications (169 in refereed journals) since the beginning of the project. In addition to the publications listed in this report, there were numerous other published abstracts from scientific meetings and theses and dissertations from students work on the project.

The Aspen FACE infrastructure was constructed in 1996 and 1997. The development of the Aspen FACE site is detailed in Dickson et al. (2000) and the forthcoming Kubiske et al. (2014). In summary, a team of investigators had been conducting open-top chamber research with aspen and these two greenhouse gases independently in three different locations (Alberta, Michigan [Karnosky, Percy, Isebrands]; Pellston, Michigan [Pregitzer, Zak, Kubiske], and Madison, Wisconsin [Lindroth]. These investigators collaborated with George Hendrey and his Brookhaven National Lab (BNL) team to conceive and engineer the Aspen FACE project with the emphasis being to examine the impacts of these interacting greenhouse gases on the structure and functioning of northern forest ecosystems over their entire life history (Karnosky et al. 2003a).

The experiment consists of twelve 30-m diameter rings, assigned to factorial treatments of [CO_2] (ambient and 560 ppm) and [O_3] (ambient and approximately 1.5 x ambient). Treatments are arranged in a randomized complete block design (n = 3). In one half of each ring, we planted five trembling aspen (*Populus tremuloides*) genotypes of differing CO_2 and O_3 responsiveness. The other half of each ring was further divided into two quarters: one planted with aspen and maple (Acer saccharum) and the other planted with aspen and paper birch (*Betula papyrifera*). Each ring was planted in July 1997 at 1 m x 1 m spacing. Gases were tested in 1997 and full treatments have been run during daylight hours from aspen budbreak to aspen leaf drop from 1998 through mid-2009, except during periods of leaf wetness, when O_3 damage would have been excessive. For CO_2 generation and monitoring, the BNL system in use at the Duke FACE site (Hendrey et al. 1999) was modified. To accommodate fumigation with O_3, the gas delivery was modified to allow for a larger volume of gas to be emitted from the vertical vent pipes so that O_3 could be diluted to nontoxic concentrations. Extensions of the vertical vent pipes were made in 2000, 2002 and 2006. A system of east-west oriented elevated walkways across the aspen and aspen-birch quadrant were established in 2002 to accommodate canopy access. A man-lift was added in 2002 to adjust the slot openings in the vertical vent pipes. The ground and elevated walkways and man-lift were all supported by the USFS Capital Projects Program.

In 2007, a 2700 square foot laboratory building (dedicated in 2009 as the David F. Karnosky Laboratory) was constructed with $450,000 from the USFS Capital Improvement Project Program), along with a new well and septic system, was constructed at the Aspen FACE site to accommodate Aspen FACE users.

Biomass harvests consisting of one aspen tree per clone per ring for each of the 5 clones for the aspen ring-half, one aspen and one birch from the aspen-birch community, and one aspen and one maple from the aspen-maple community were made with trees just outside the scientific core area to examine effects of these greenhouse gases on NPP and to see if allometry of the trees was being changed by either CO_2 or O_3. These harvests were done in 2000, 2002, and 2007. A final detailed harvest and excavation of soil to 1 m depth was conducted during the growing season of 2009, with all remaining trees removed during the winter of 2009/2010.

Wood from the trees from rings with elevated CO_2 is depleted in ^{13}C, allowing it to be used in tracer studies. As a result, wood from Aspen FACE is currently being used in two long-term decomposition studies, examining the environmental and biotic factors that control the movement of wood-derived C into soil carbon pools, and the stability of these C pools.

Table 1. Aspen FACE Investigators

NAME	FIELD	AREAS OF STUDY
C. Awmack (UK)	Ecological Entomologist	Insect biodiversity and community ecology
C. Blackwood (UMich)	Soil Microbiologist	Soil microorganism communities
A. Burton (MTU)*	Forest Ecologist	Carbon and nutrient cycling, physiological ecology of global change, belowground processes
C. Calfapietra (IBAF-CNR/Italy)	Physiologist	VOC emissions
B. Callan (CFS)	Pathologist	Foliar diseases, diagnostics
A. Chappelka (AuburnU)	Physiologist	Understory vegetation quality
R. Cox (CFS)	Ecologist	Passive O_3 sampling
D. Ellsworth (UMich)	Ecophysiologist	Stomatal conductance, stomatal density
A. Friend (USFS)	Ecophysiologist	Nitrogen budgets
C. Giardina (USFS)	Ecophysiologist	Canopy dynamics
E. Gustafson (USFS)	Modeller	Scaling responses
W. Heilman (USFS)	Micrometeorologist	Characterization of micro climate inside and outside of FACE rings
G. Hendrey (QC-CUNY)	Ecologist	Engineering CO2 and O3 delivery systems
D. Herms (OSU)	Entomologist	Bronze birch borer occurance
B. Holmes (UMich)	Microbial	C and N cycling
J. Hom (USFS)	Ecologist	Ecosystem N dynamics, whole-canopy gas exchange
A. Hopkin (CFS)	Pathologist	Foliar pathogen occurrence and affects
G. Host (NRRI-UMinn-D)	Modeler/Ecologist	Growth process modeling - single tree to patch scale. Co-developer of ECOPHYS model. FACTS II Web Site Moderator
J. Jastrow (ANL)	Mycorrhizal specialist	C storage
E. Jepsen (WDNR)	Ecologist	O_3 monitoring and O_3 bioindication

S. Kaakinen (UHelsinki/Finland)	Wood Anatomist	Wood quality and chemistry
J. Kangasjarvi (UHelsinki/Finland)	Physiologist	Birch gene expression
D. Karnosky (MTU) deceased	Geneticist	Steering Committee. Project Director. Genetic interactions, gene expression, project operations.
J. King (NCSU)	Ecophysiologist	Soil respiration and soil carbon dynamics
E. Kruger (UWisc)	Physiologist	Ecosystem C flux, respiration
M. Kubiske (USFS)	Ecophysiologist	Responses of photosynthesis and plant water relations, science coordination
O. Kull (UTartu/Estonia) deceased	Ecologist	Gas exchange/Ozone uptake
K. Lewin (BNL)	Research Engineer FACE Specialist	Facility development and maintenance, equipment-manufacturer liaison
T. Lewis (EPA)	Physiologist	Humming bird behavior
E. Lilleskov (USFS)	Mycorrhizal specialist	Mycorrhizae
R. Lindroth (UWisc)	Entomologist Chemical Ecologist	Plant chemistry, insect herbivory, litter decomposition
S. Long (UIllinois)	Physiologist	Modelling and scaling
J. MacDonald (CFS)	Physiologist	Crown architecture
B. Mankovska (Slovakian Acad. of Science)	Electron Microscopist	Impacts of gases on leaf surfaces
F. Martin (INRA/France)	Physiologist	Gene expression
W. Mattson (USFS) retired	Entomologist	Shoot boring insects, root feeders
E. McDonald (USFS) retired	Ecophysiologist	Canopy dynamics, competitive interactions
M. Miller (ANL)	Mycorrhizal Specialist	Carbon storage dynamics
E. Mondor (Georgia Southern Univ))	Forest Entomologist	Insect behavior
R. Muntifering (AuburnU)	Physiologist	Understory vegetation quality
J. Nagy (BNL)	Physicist	Facility development, software development, exposure controlling systems, technical consultant

N. Nelson (USFS) retired	Tree Physiologist	Steering Commitee. Gas Exchange Dynamics
A. Noormets (NCSU)	Ecophysiologist	Gas exchange dynamics, carbon gain
E. Oksanen (UEF/Finland)	Ecophysiologist	Biochemistry and gene expression for assimilation, rubisco, chlorophyll
K. Percy (Air Quality Effects Consulting, Ltd./Alberta, Canada)	Ecophysiologist	Steering Committee. Leaf surface structure, chemistry, and function; O3 distribution via passive samplers; O3 metrics
G. Podila (UAla-H) deceased	Molecular Biologist	Oversee biochemical and molecular studies of antioxidant gene expression
K. Pregitzer (Univ Idaho)*	Forest Ecologist	Steering Committee. Coordinate studies of roots and C and N cycling
D.Riemenschneider (USFS) retired	Quantitative Geneticist	Experimental analyses and interpretation
J. Riikonen (UKuopio/Finland)	Physiologist	Birch gas exchange
A. Rogers (BNL)*	Ecophysiologist	Steeing Committee. Gas exchange dynamics
P. Saranpaa (Finnish Forest Research Institute)	Physiologist	Wood quality and structure
T. Sharkey (UWisc)	Plant Physiologist	Volitile Organic Compounds (VOC) produced by Aspen
E. Singsaas (UWisc-SP)	Physiologist	Gas exchange
A. Sober (Estonia)	Physiologist	Gas exchange, O_3 uptake
H. Tai (CFS)	Molecular Biologist	DNA dynamics
G. Taylor (USouthhampton/England)	Physiologist	Gene expression
R. Thakur (MTU)	Biotechnologist	Gene expression
T. Trier (GVSU)	Entomologist	Insect interaction
C.J. Tsai (UGeorgia)	Molecular Biologist	Genomics of CO2 and O3 responses in Aspen
J. Uddling (UGothenburg/Sweden)	Physiologist	Canopy-level transpiration
E. Vapaavuori (Finland Forest Institute)	Physiologist	Wood quality and chemistry
D. Weinstein (Boyce Thompson Institute)	Modeler	Scaling up AspenFACE results to the regional level

R. Wise (UWisc-O)	Physiologist	Leaf temperature dynamics
D. Zak (UMich)	Microbial Ecologist	Study mechanisms of C and N cycling; soil microorganisms

* denotes steering committee members

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