Scaling ozone responses of forest trees to the ecosystem level in a changing climate

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ABSTRACT

Many uncertainties remain regarding how climate change will alter the structure and function of forest ecosystems. At the Aspen FACE experiment in northern Wisconsin, we are attempting to understand how an aspen/birch/maple forest ecosystem responds to long-term exposure to elevated carbon dioxide (CO2) and ozone (O3), alone and in combination, from establishment onward. We examine how O3 affects the flow of carbon through the ecosystem from the leaf level through to the roots and into the soil microorganisms in present and future atmospheric CO2 conditions. We provide evidence of adverse effects of O3, with or without co-occurring elevated CO2, that cascade through the entire ecosystem impacting complex trophic interactions and food webs on all three species in the study: trembling aspen (Populus tremuloides Michx.), paper birch (Betula papyrifera Marsh), and sugar maple (Acer saccharum Marsh). Interestingly, the negative effect of O3 on the growth of sugar maple did not become evident until 3 years into the study. The negative effect of O3 effect was most noticeable on paper birch trees growing under elevated CO2. Our results demonstrate the importance of long-term studies to detect subtle effects of atmospheric change and of the need for studies of interacting stresses whose responses could not be predicted by studies of single factors. In biologically complex forest ecosystems, effects at one scale can be very different from those at another scale. For scaling purposes, then, linking process with canopy level models is essential if O3 impacts are to be accurately predicted. Finally, we describe how outputs from our long-term multispecies Aspen FACE experiment are being used to develop simple, coupled models to estimate productivity gain/loss from changing O3.

Key-words: Populus tremuloides; carbon accumulation and allocation; carbon dioxide; C and N cycling; climate change; ecosystem scaling; modelling; pest interactions; trembling aspen; tropospheric ozone.

Abbreviations: AAQS, American air quality standards; AOT40, accumulated hourly O3 exposure over 40 ppb; C14, radioactive isotope of carbon; CDIAC, Carbon Dioxide Information Analysis Center; CL, critical level; CWS, Canadian Wide Standard; ECOPHYS, an ecophysiological model to grow individual trees; FACE, Free-Air CO2 Exposure; LAI, leaf area index; N, nitrogen; PAR, photosynthetically active radiation; ppb, parts per billion; ppm, parts per million; SOM, soil organic matter; SUM60, accumulated hourly exposure over 60 ppb.

INTRODUCTION

Tropospheric ozone (O3), a secondary pollutant generated downwind of major metropolitan areas from nitrogen oxides and volatile organic compounds reacting in the presence of sunlight, was first identified as a problem in the 1950s (Dunn 1959) for plant communities downwind of the Los Angeles area. Among the first forest ecosystems found to be impacted by O3 was the pine-fir forest in the San Bernardino Mountains (Miller et al. 1963; Miller & Millec 1971). Subsequently, O3 effects on forest trees also were identified in the Sierra Nevada Mountains of southern California (Miller, McCutcheon & Milligan 1972). About the same time, researchers in the eastern United States identified visible symptoms of O3 damage on sensitive genotypes of eastern white pine (Dochinger et al. 1970; Costonis 1970).

Since these early days, thousands of papers have been published on the effects of tropospheric O3 on the physiology, biochemistry, community structure, and population dynamics of forest trees (see reviews by Chappelka & Samuelson 1998; Skárby et al. 1998; Miller & McBride 1999;
Samuelson & Kelly 2001; Percy, Legge & Krupa 2003a). However, despite numerous studies on individual plants, still very little is known about the impacts of O₃ on forest ecosystem structure and function (Karnosky et al. 2003a; Laurence & Andersen 2003). This is especially true in light of rapid increases in atmospheric carbon dioxide (CO₂) (Keeling et al. 1995). The interaction between increasing CO₂ and O₃ is especially important because of large areas of Earth are impacted by O₃ (Fowler et al. 1999; Fig. 1). Furthermore, it is important to understand how tropospheric O₃ may affect carbon sequestration of forest trees exposed to elevated CO₂ (Beedlow et al. 2004).

The Aspen FACE experiment was established in 1997 in northern Wisconsin to examine the impacts of tropospheric O₃, alone and in combination with elevated atmospheric CO₂, on the structure and function of a northern forest ecosystem dominated by the rapid-growing, pioneer species trembling aspen (Populus tremuloides Michx.) but including also another rapid-growing, pioneer species paper birch (Betula papyrifera Marsh) and the slower-growing, later-successional species sugar maple (Acer saccharum Marsh). Trembling aspen is the most widely distributed tree species in North America. Aspen forest types make up over 8.8 million ha in the USA and 17.8 million ha in Canada. In Wisconsin, alone, where this experiment is located, aspen, birch and maple stands comprise over 50% of the State’s vast forest resource. Aspen and birch comprise some 70% of the pulpwood harvested in the states bordering the Great Lakes (Piva 1996).

The Aspen FACE experiment is unique in that it was established to examine the long-term effects of these two greenhouse gases on development of the ecosystem from seedling establishment onward. The experiment utilizes a state-of-the-art open-air fumigation system (Dickson et al. 2000) that is devoid of artifacts that often occur in chamber systems such as low-winds, higher-than-ambient temperature, altered hydrology, higher humidity, and reduced light levels (Hendrey et al. 1999; McLeod & Long 1999; Karnosky et al. 2001). Furthermore, the plot sizes (30-m-diameter rings) are large enough to examine effects that are difficult to detect in small chambers such as intraspecific and interspecific competition, carbon fluxes to soil and pest epidemiology. Trophic interactions are facilitated by the unencumbered movement of insects into and out of the rings.

In this paper, we present a synthesis of results from the first 7 years of this unique experiment including studies of above-ground physiology and growth, canopy development, stem wood quality, community dynamics, below ground growth, carbon flux and community structure, and pest interactions. Finally, we discuss ways to scale up our experimental data to landscape or regional levels via various modelling strategies and development of appropriate O₃ dose–response functions to project impacts of O₃. These

**Figure 1.** Projected maximum 1 h surface ozone values for July, 2050 from the model output of the STOCHEM model (C.E. Johnson and David Fowler, personal comm.).

could eventually be useful in determining O₃ standards to protect forest vegetation.

THE ASPEN FACE EXPERIMENT

The Aspen FACE experiment consists of a full factorial with 12 30-m-diameter treatment rings with three control rings, three rings with elevated O₃, three rings with elevated CO₂, and three rings with elevated O₃ + elevated CO₂ (Fig. 2); 100 m is the minimum distance between any two FACE rings. The rings were planted in late 1997 and treatments ran from budbreak to the end of each growing season from 1998 to 2004. The eastern one-half of each ring was randomly planted in two-tree plots at 1 m × 1 m spacing with five aspen clones differing in O₃ tolerance (8L, 216 and 271 = relatively tolerant; 42E and 259 = relatively sensitive). The north-western quadrant of each ring was planted at the same spacing with alternating aspen clone 216 and sugar maple seedlings, and the south-western quadrant of each ring was planted as above with aspen clone 216 and paper birch seedlings.

Carbon dioxide and O₃ are delivered via a computer-controlled system modified from Hendrey et al. (1999) during the daylight hours with our target CO₂ being 560 ppm, which is about 200 ppm above the daylight ambient CO₂ concentration. Ozone was applied at a target of 1.5 × ambient and was not delivered during days when the maximum temperatures were projected to be less than 15 °C or when plants were wet from fog, dew, or rain events. Additional details of the experimental design and pollutant generation and monitoring can be found in Karnosky et al. (2003b). Actual treatment summaries for CO₂ and O₃ were published in Karnosky et al. (2003b). Hourly O₃ values for one control and one O₃ ring (Fig. 3) show that our O₃ expo-
Figure 3. Hourly O₃ concentrations from ambient air (black) and one elevated O₃ ring (grey) in the Aspen FACE project during 1998–2003.
sure levels matched our 1.5 × ambient target quite well. In addition, we monitored a number of micrometeorological parameters at our site including wind speed, wind direction, PAR, net radiation, relative humidity, rainfall, air temperature at five heights to 20.0 m and soil temperature at the soil surface and at five depths to 2.0 m and soil moisture. Relevant web sites for the Aspen FACE project include: (1) the general site for the Aspen FACE (http://aspen-face.mtu.edu); (2) the micrometeorology data collected at the Aspen FACE site (http://climate.usfs.msu.edu/FACE/meteorology/); (3) the treatment gas concentrations are shown at the BNL web site (http://www.face.bnl.gov/FACE_Site_Data_Archive/FACETSII.htm) and the CDIAC data depository web site (http://cdiac.ornl.gov/programs/FACE/facts-IIdata/factsIIdata.html).

EXAMINATION OF CARBON FLOWS

In order to prioritize research at the Aspen FACE project, our site’s investigator team spent a considerable amount of time developing a conceptual model of carbon cycling in our ecosystem (Fig. 4). Our research team has focused attention on control points (red triangles) in an attempt to develop a comprehensive understanding of ecosystem carbon flow under elevated CO$_2$ and O$_3$. We hypothesized that ecosystem level responses to these two greenhouse gases would be driven by the responsiveness of the three keystone tree species (Karnosky 2005). In this paper, we will summarize the effects of O$_3$ on carbon uptake, allocation, distribution, and release at background and elevated levels of CO$_2$. Finally, we discuss our progress scaling our results to regional levels and we present our results in terms of O$_3$ metrics as best predictors of O$_3$ effects.

ABOVE-GROUND RESPONSES

Gas exchange

All carbon flows into trees through leaves via the process of photosynthesis. Thus, the impacts of greenhouse gases on leaf morphology, chlorophyll content, Rubisco content, stomatal density, stomatal conductance, leaf area in the canopy, and phenology of leaf display play critical roles in carbon budgets of forest trees. In Fig. 5, it is shown that there is interspecific variability in the effects of elevated O$_3$ and/or CO$_2$ on maximal photosynthesis as the rapid-growing pioneer species, trembling aspen and paper birch, are both quite responsive to these two greenhouse gases but the slower-growing, later-successional species sugar maple.

Figure 4. A conceptual model developed for the Aspen FACE project describing the flow of carbon from photosynthesis through forest ecosystems. The red switches indicate processes that serve as control points where we hypothesize that genotypic and species-specific responses to atmospheric CO$_2$ and O$_3$ will alter the flow of carbon to and through aboveground and below-ground food webs.

Figure 5. 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 (From: Karnosky et al. 2003b).
maple is not very responsive to either gas (Noormets et al. 2001a,b; Karnosky et al. 2003b; Sharma et al. 2003).

The effects of O$_3$ on photosynthesis have generally been negative for aspen at either CO$_2$ concentration (Karnosky et al. 2003b), whereas birch photosynthesis was most affected at the elevated CO$_2$. The depression of photosynthesis under elevated CO$_2$+O$_3$ suggests co-occurring elevation of O$_3$ could decrease the projected stimulation of photosynthesis under future CO$_2$ concentrations (Kull et al. 1996).

Ozone effects on photosynthesis vary by aspen genotype, leaf age (Noormets et al. 2001a,b) and crown position (Sharma et al. 2003). Average maximal photosynthesis was depressed by 29–40%, depending on the aspen clone at ambient CO$_2$ and by 19–31% under elevated CO$_2$, compared with photosynthesis at elevated CO$_2$ alone. Older leaves tended to be more severely affected by O$_3$ at either CO$_2$ concentration (Noormets et al. 2001a,b). The limitations to maximal photosynthesis were primarily driven by altered mesophyll processes, primarily by impacts on Rubisco (Noormets et al. 2001b). In addition, O$_3$ decreased chloroplast size, starch content, and altered foliar ultrastructure (Oksanen, Sober & Karnosky 2001) in aspen but not in birch leaves. More recently, O$_3$-induced decreases in mesophyll cell wall thickness and starch grain size were detected for both aspen and birch trees (Oksanen et al. 2003).

While no effects of elevated CO$_2$ have been found in foliar respiration at our site (Davey et al. 2004), increased levels of foliar respiration have been detected in O$_3$-damaged aspen leaves, particularly later in the growing season (Noormets et al. 2001a,b).

**Growth**

Since we have shown decreased maximal photosynthesis for aspen (see above), it is not surprising that we have documented a relatively consistent and statistically significant, O$_3$-induced 10–15% decrease in both height and diameter growth in aspen from O$_3$ at both ambient and elevated CO$_2$ (Isebrands et al. 2001; Percy et al. 2002; Fig. 6). In contrast, birch has not shown adverse effects of

![Figure 6](image-url)  
**Figure 6.** Height (a) and diameter (b) growth for trembling aspen, paper birch and sugar maple seedlings exposed to elevated CO$_2$ and/or O$_3$ at the Aspen FACE project. Means ± SE.
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O₃ in ambient CO₂. However, consistent and significant 14–18% decreases in growth of birch have been seen for elevated O₃ in the elevated CO₂ environment compared to birch in elevated CO₂ alone.

The most interesting growth response we have found was that of sugar maple in that no significant O₃ effects were detected for the first few years but growth has been significantly decreased since year four. After age 5, O₃ had significantly decreased both height and diameter growth of sugar maple, regardless of the CO₂ treatment. While we have not yet determined the cause for either the stronger O₃ response in birch in the CO₂ + O₃ combination treatment or the significant long-term decrease in sugar maple growth under elevated O₃. These two findings show the importance of long-term studies of interacting stresses in decreasing uncertainties about the impacts of O₃ on forest ecosystems and the need to examine interacting stresses as the responses found were not predicted from the single-factor treatments.

Carbon allocation

Shifts in carbon allocation under elevated O₃ are expected in our experiment because O₃ often decreases carbon allocation to root systems (Andersen 2003). Our previous open-top chamber research with aspen suggested that O₃ may alter C¹⁴ distribution to roots (Coleman et al. 1995) and that O₃ differentially impacts root growth (Karnosky et al. 1996; Coleman et al. 1996). While a trend was seen in decreased soil respiration under elevated O₃ suggesting possible adverse effects on root growth for our site (King et al. 2001), we did not detect any shifts in carbon allocation in sample whole-tree biomass harvests in 2000 (Pregitzer, unpublished) and 2002.

Canopy dynamics and phenology

In addition to photosynthetic rates, leaf area and leaf display duration contribute to carbon gain potential in forest trees. In our study, we have shown that O₃ can have major negative impacts on both LAI (Fig. 7) and leaf display duration. LAI was significantly decreased under elevated O₃ throughout the growing season and this is due to several factors. First, bud break is delayed so that leaf out is later in the spring, as has been previously reported by Oksanen (2003). Second, leaf senescence and leaf abscission are accelerated under elevated O₃, regardless of CO₂ concentration, as can be seen in late-season aerial photos (Fig. 8). Accelerated leaf aging is a well-documented phenomenon with O₃ (Pell et al. 1990; Bielenberg, Lynch & Pell 2002) and we have previously reported on it in aspen (Karnosky et al. 1996). Third, the reduced LAI may have been partially due to decreased tree sizes (Isebrands et al. 2001; Percy et al. 2002), reduced branch and leaf sizes (Oksanen et al. 2001), or changes in crown architecture (Dickson et al. 2001).

Competitive interactions

Competition for light, nutrients, and water in a forest environment can have major impacts on the responses of trees to elevated levels of O₃ and CO₂ (Matyssek & Sandermann 2003). At the Aspen FACE experiment, we are testing both the effects of interspecific as well as intraspecific competition. Clear evidence has been presented from our project that the magnitude of the O₃ effects on growth depended on the particular aspen genotype and its competitive status (McDonald et al. 2002). After 6 years of treatments, we can readily see the effects of CO₂ and O₃.

Plot–level mean of three different methods.

*Figure 7.* Estimated seasonal trends for LAI for aggrading aspen stands in the Aspen FACE experiment in northern Wisconsin during the 2002 growing season based on plot-level means in the aspen one-half of each ring for litterfall, optical (hemispherical fisheye approach), and ceptometer data. Values are means ± SE. (From Giardina et al. unpublished)
on the competitive ability of aspen clones (Fig. 9). Clone 259 is not a good competitor in our experiment as seen by its poor growth in all treatments, but we have evidence that its fitness is particularly decreased under elevated O₃ as evidenced by its decreased survival and inability to produce seed (Karnosky et al. 2003c). Interestingly, clone 8L appears to thrive in elevated O₃ as it is growing at faster rates under high O₃, regardless of CO₂ treatment. We have previously seen enhanced growth in low levels of O₃ (i.e. in 0.5 × ambient versus ‘O₃-free air’ produced by charcoal filtering) (Karnosky et al. 1996) that was attributed to adaptation to elevated background O₃ exposures at the location from which the clone originated. In general, however, the lowest growth rate of aspen is in the elevated O₃ treatment and the CO₂ + O₃ treatment is nearly identical to growth under control conditions (Isebrands et al. 2001; Fig. 9).

**Stem wood properties**

Ozone significantly decreased volume of xylem as shown by decreased distance from the pith to the bark in our juvenile aspen stems but did not affect birch or maple stems (Kaakinen et al. 2004). Gravimetric lignin concentration increased under elevated O₃ in four of five aspen clones and in birch (Kaakinen et al. 2004). This suggests a possible change in carbon allocation leading to enhanced activity of the phenylpropanoid biosynthetic pathway as we previously documented in our Aspen FACE project with increased PAL transcripts under elevated O₃ (Wustman et al. 2001).

Another wood structure change elicited by O₃ was that vessel lumen diameter decreased, which could decrease water transport efficiency in the xylem (Kaakinen et al. 2004). In birch, hemicellulose increased under elevated O₃.
Elevated CO₂ largely offset adverse effects of O₃ on both aspen and birch wood structure and chemistry (Kaakinen et al. 2004).

**Pest interactions**

A large uncertainty for future forests growing under elevated levels of O₃ and CO₂ is how forest pests will be affected (Harrington, Woiwood & Sparks 1999; Chakraborty, Tiedemann & Teng 2000). Our Aspen FACE results suggest that elevated O₃ can impact forest pests in several ways that can result in increased or decreased pest occurrence, depending on the pest. For example, O₃ altered the nutrient and defense compound composition of aspen and birch foliage in our study (Lindroth et al. 2001) and O₃ decreased the tremulacin concentration of aspen by about 20%, adversely affecting aspen blotch minor development (Kopper & Lindroth 2003a). However, the performance (as measured by pupal mass and fecundity) of the forest tent caterpillar, a major pest of aspen-birch forests in the Lake States region, was enhanced under elevated O₃ (Kopper & Lindroth 2003b; Holton, Lindroth & Nordheim 2003). Similarly, aphid populations were significantly higher on aspen trees under elevated O₃ (Percy et al. 2002; Awmack, Harrington & Lindroth 2004; Mondor et al. 2004). Interestingly, the impact of O₃ on aphids appeared to be an indirect one on their natural predators (Percy et al. 2002; Awmack et al. 2004) or due to exaggerated escape behaviour due to increased production of alarm pheromones under elevated O₃ (Mondor et al. 2004).

For diseases, Karnosky et al. (2002) have reported a three- to five-fold increase in aspen leaf rust, caused by *Melampsora medusae*, under elevated O₃ at the Aspen FACE over several growing seasons. This disease was particularly enhanced under O₃ for O₃-sensitive aspen clones. We believe that the mechanisms for this rust infection increase is that the surface of aspen leaves is altered structurally by elevated O₃ (Mankovska, Percy & Karnosky 1998, 2003; Karnosky et al. 1999) and chemically (Percy et al. 2002) making the leaves more wettable (Percy et al. 2003b). These effects do not appear to be alleviated under elevated CO₂ (Mankovska et al. 1998, 2003).

**BELOW-GROUND RESPONSES**

While the role of tropospheric O₃ in altering plant growth and development has been thoroughly studied over the
recent decades, there is still limited understanding regarding the effects of O₃ on tree roots and soil processes (Andersen 2003). From our open-top chamber research with aspen, we knew that carbon allocation and partitioning to roots could be dramatically altered by O₃ (Coleman et al. 1995). This, in turn, could lead to decreased root growth of aspen (Coleman et al. 1996) and altered root/shoot ratios (Karnosky et al. 1996). Thus, we expected going into the Aspen FACE experiment that we would likely be able to detect effects of O₃ on root growth in aspen but did not know if birch or maple would be adversely affected. Furthermore, we were uncertain as to how interacting elevated CO₂ and O₃ would affect root growth and soil processes of any of the three species.

**Root development**

Early in our Aspen FACE experiment, we found that live fine-root biomass (<1.0 mm) averaged over community types was 263 g m⁻², of which 81% was composed of roots <0.5 mm in diameter (King et al. 2001). Elevated O₃ resulted in a decrease in fine root biomass, which was marginally significant after three growing seasons (King et al. 2001). Elevated O₃ has increased fine root turnover (Pregitzer, unpublished), as was previously found from our open-top chamber studies of O₃ effects on aspen fine root dynamics (Coleman et al. 1996). As with our above-ground studies, elevated CO₂ alleviated the negative effects of O₃ on aspen roots. Conversely, elevated O₃ offset increases in soil respiration caused by elevated CO₂ when the two gases were applied in combination (King et al. 2001). Taken together, root studies at Aspen FACE suggest that elevated CO₂ increases the flux of carbon from root systems to the soil, while elevated O₃ alters whole plant source–sink relationships, resulting in more rapid root turnover and a smaller crop of standing fine root biomass (Karnosky & Pregitzer 2005).

**Soil carbon**

Carbon inputs to the Aspen FACE soils were increased under elevated CO₂ as seen by the increase in soil respiration (King et al. 2001, 2004). However, under the combination of elevated CO₂ + O₃, stable soil carbon formation was decreased by 50% compared to that under elevated CO₂ alone (Loya et al. 2003; Fig. 10). This suggests that NPP-induced changes in the atmosphere may have a significant impact on the formation of stable soil carbon. These findings have begun to influence air pollution control strategies in Europe (see Grennfelt 2004).

Decomposition of leaf litter is another important part of carbon input into the forest ecosystem. Elevated CO₂ altered birch litterfall chemistry at Aspen FACE, decreasing nitrogen content, and increasing condensed tannins, regardless of O₃ concentration (Parsons, Lindroth & Bockheim 2004). Nitrogen content in decomposing litter from elevated CO₂ treatments remained consistently lower up to 350 d. Ozone alone did not affect birch leaf litter quality or litter decomposon (Parsons et al. 2004).

**Soil fauna and micro-organisms**

Since O₃ adversely affected aspen growth at Aspen FACE and since O₃ impacts litter quality in aspen (Lindroth et al. 2001), Loranger, Pregitzer & King (2004) hypothesized that O₃ could impact the abundance of soil fauna. They found significant decreases in Acari (−47%) under elevated O₃, but these responses were alleviated by elevated CO₂ (Loranger et al. 2004).

Phillips, Zak & Holmes (2002) presented evidence from Aspen FACE that O₃ may be impacting microbial community composition at Aspen FACE. While microbial respiration was increased under elevated CO₂, this increase was negated by the presence of co-occurring O₃ (Phillips et al. 2002; Fig. 11). Fungal abundance declined under elevated O₃ in both the aspen and aspen-birch communities but not in the aspen-maple community (Phillips et al. 2002).

Holmes et al. (2003) found that soil nitrogen transformations were impacted by O₃ (Fig. 12). Elevated O₃ significantly decreased gross N mineralization and microbial biomass N. Effects were consistent across all three communities (Holmes et al. 2003). The authors suggested that by decreasing plant litter inputs, O₃ appeared to be decreasing microbial biomass and activity.
SCALING ASPEN FACE RESPONSES WITH MODELS

Scaling responses from 30 m plots studied over 7 years at Aspen FACE to the landscape or regional levels over decades or centuries requires making a series of assumptions to bridge these gaps in scale. Through simulation modelling we can extrapolate the consequences of these assumptions over space and time (Laurence & Andersen 2003). Since the direct effects of O₃ and CO₂ occur as physiological effects on photosynthesis in individual leaves (Chappelka & Samuelson 1998), using a leaf-level model is a logical starting point for scaling. The ways that changes in leaf physiology can in turn affect growth of trees and their ability to compete within forest canopies can then be evaluated by using forest community or forest productivity models.

Two alternative models have been used at Aspen FACE to take leaf-level responses and predict their significance for whole-tree health. First, Martin et al. (2001) have developed a process-based model that predicts the relative effects of O₃ on the photosynthetic rate and growth of an O₃-sensitive aspen clone. Modifying the model ECOPHYS, developed by Rausher et al. (1990), Host et al. (1996), and Isebrands et al. 2000, Martin et al. (2001) estimate seasonal growth, biomass accumulation, and leaf drop under various O₃ profiles. Further adaptations enable the simulation of root growth and below-ground water redistribution (The-seira et al. 2003).

A second model is TREGRO (Weinstein, Beloin & Yanai 1991), which simulates carbon, water, and nutrient flows of an individual plant in response to changes in temperature, drought, nutrient deficiency, and exposure to pollutants and CO₂ levels. The TREGRO model evaluates whether a reduction in the rate of photosynthesis in direct proportion to the cumulative O₃ uptake would prevent an individual tree from meeting its carbon demands for growth. TREGRO then calculates how the plant is likely to shift its carbon allocation as a result of the lowered supply of carbon and mobilize stored carbon reserves to continue tissue growth.

Forest community or production models are then used to extrapolate the predictions of these physiological models to tree performance in the presence of competing species. One model that has been used for this purpose is ZELIG (Urban 1990; Urban et al. 1991), a gap-succession of forest growth simulation that predicts whole canopy and landscape processes. The link of TREGRO with ZELIG has been used to evaluate the regional impact of O₃ on several tree species (Laurence et al. 2001; Weinstein et al. 2001a; Weinstein, Gollands & Retzlaff 2001b; Weinstein et al. 2005).

The ZELIG model was applied to extrapolate the results from the Aspen FACE studies to regional forests of Wisconsin over 100 years of simulated stand development. Ozone was predicted to cause P. tremuloides basal area in the approximately 1.4 million hectares of aspen-birch stands throughout Wisconsin to decrease by over 1 million m² cross-sectional area or 12% of the abundance expected in the absence of O₃ (Fig. 13). This level of reduction was expected because of the physiological sensitivity of P. tremuloides to O₃. However, predictions for B. papyrifera demonstrate that scaling is not a simple matter of extrapolating directly from experimental results. Betula papyrifera was predicted to increase in abundance despite the absence of sensitivity to O₃. The scaling methodology clearly must be capable of considering changes in the competitive opportunities among species, since in this case B. papyrifera thrived (11% increase) despite O₃ because P. tremuloides was injured more severely. Betula papyrifera was then able to compete for resources in situations where previously it had not been able.
Elevated levels of CO$_2$ caused 20% growth increases in $B$. papyrifera and 30% increases in $P$. tremuloides (Fig. 13). For $P$. tremuloides, this amounted to an increase of over 1 million m$^2$, similar in size but opposite in direction to the effect of O$_3$. Simultaneous exposure to O$_3$ and CO$_2$ had offsetting effects in $B$. papyrifera and $P$. tremuloides. Unpredictably, the competitive advantages $B$. papyrifera was simulated to have under O$_3$ exposure disappeared when CO$_2$ was also present. In another result from the landscape level that would not have been predictable from the physiological effects, the presence of CO$_2$ exacerbated the negative effect of O$_3$ on Acer saccharum abundance, causing it to decrease by over 30%.

How predictable were these landscape level effects from the individual plot responses? While it is somewhat difficult to compare 5 years of tree plot results to 100 years of landscape predictions, the changes in the landscape abundance of species were generally a reflection of responses that had been noted in average growth in the experimental plots (Table 1). For example, $P$. tremuloides decreased by 14% in the experimental plots but only by 12% in abundance by year 2100 in the simulation. In no case did the competitive dynamics among species on the landscape predicted in the simulation result in the opposite response to that observed in the plots. However, $P$. tremuloides was predicted to have twice the response to CO$_2$ on the landscape as the plots suggested, and $B$. papyrifera had twice the response to O$_3$.

**SCALING FOR RISK ANALYSIS**

North America and Europe have adopted different approaches to ambient O$_3$ standard setting, with the latter opting for an approach to specifically protect vegetation. In North America, ambient air quality standards (AAQS) are used for compliance purposes and are balanced against social, economic and political considerations (see Ashmore 2005). AAQS do not implicitly assume the existence of a concentration threshold for receptor (i.e. tree) response (Percy et al. 2003a), and therefore, target values are often substituted for regulatory purposes. In North America, the
correlation does not necessarily mean causality. The effect of regression models. However, even a statistically significant relationship that has been established has used empirically dominant factor. There are meteorological (e.g., precipitation, soil moisture, solar radiation, temperature, etc.) factors, co-occurring air pollutants, and many other variables that exert large effects on tree growth.

In order to meaningfully assess the risk of increasing O₃ concentrations, it is vital to build a predictive model comprising all important predictors. Krupa et al. (2003) have recently developed a multivariate statistical model including meteorological variables (global radiation, air temperature, relative humidity and wind speed, variables that influence plant O₃ uptake through stomata). With the addition of soil moisture data to the main meteorological variables listed, an approximation of first-order atmospheric O₃ flux can be achieved. After verification of validity and significance of such a model, it is then necessary to factor out the effect of O₃ itself, while controlling all other predictors. This is a complicated procedure requiring integrated experiments such as Aspen FACE, which provide systematic and reliable monitoring of pertinent predictors.

Coincidentally, evidence from our Aspen FACE experiment is pointing to the multitropic nature of forest ecosystem responses to long-term, low-level O₃ exposures. Feedbacks to growth have included a large reduction in both aspen height (~12%) and diameter (~13%) growth at the stand level (Percy et al. 2002). We have now taken the initial steps towards linking a multivariate statistical model (Krupa et al. 2003) with multipoint plant response data. After computing O₃ exposure within each of the three replicate FACE rings using established AAQS, CL, and related descriptors, O₃ dose–response functions relevant to regulatory processes have been calculated.

Initial analysis using The Best Subsets Regression Algorithm (Percy et al. unpublished) suggests the best predictor of aspen growth was the 4th highest daily maximum 8 h O₃ concentration (Table 2) followed by tree age. As a second step in the process, meteorological data (T, RH, PAR, precipitation) are being combined with soil moisture data at the stand level to develop an approximation of first-order atmospheric O₃ flux and aspen stomatal uptake. If such efforts are coupled to multipoint plant response measurements, meaningful cause–effect relationships can be derived regarding the nature of the so-called background

### Table 1. Comparison of responses at the scale of physiology, plot, and predicted landscape

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Acer saccharum</th>
<th>Betula papyrifera</th>
<th>Populus tremuloides</th>
</tr>
</thead>
<tbody>
<tr>
<td>FACE Amax reductions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O₃</td>
<td>0%</td>
<td>0%</td>
<td>-20%</td>
</tr>
<tr>
<td>O₂ + CO₂</td>
<td>0%</td>
<td>64%</td>
<td>27%</td>
</tr>
<tr>
<td>Face plot effects measured</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O₃</td>
<td>-18%</td>
<td>5%</td>
<td>-14%</td>
</tr>
<tr>
<td>CO₂</td>
<td>-15%</td>
<td>26%</td>
<td>15%</td>
</tr>
<tr>
<td>O₃ + CO₂</td>
<td>-25%</td>
<td>3%</td>
<td>-3%</td>
</tr>
<tr>
<td>ZELIG landscape effects predicted in 2100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O₃</td>
<td>-28%</td>
<td>11%</td>
<td>-12%</td>
</tr>
<tr>
<td>CO₂</td>
<td>-23%</td>
<td>18%</td>
<td>31%</td>
</tr>
<tr>
<td>O₃ + CO₂</td>
<td>-35%</td>
<td>4%</td>
<td>-1%</td>
</tr>
</tbody>
</table>

O₃ concentrations and their significance in more remote forested areas (Krupa et al. 2003). The future development of new flux-based critical levels in Europe and biologically based dose–response functions in North America will allow policy makers and regulators for the first time to more accurately predict O₃ risk to the world’s forests in the future.

**SUMMARY AND CONCLUSIONS**

We have examined over 7 years the effects of elevated levels of O₃ at two atmospheric CO₂ levels, current ambient (360 ppm) and 560 ppm (projected for about year 2050), on northern Wisconsin aspen, aspen-birch, and aspen-maple forest communities. In this paper, we elucidate how O₃ affects the flow of C from the leaf and canopy level through tree roots to soil and soil microorganisms, under ambient and elevated CO₂. Our long-term, multidisciplinary research project has consistently shown adverse effects of O₃ on the above-ground growth and physiology of all three species. These impacts on above-ground biochemistry, physiology and morphology with feedbacks to growth and pest occurrence have cascaded through the ecosystem via multiple food webs and trophic levels ultimately affecting ecosystem C cycling. While CO₂ generally moderated the detrimental responses of O₃, there were some noticeable exceptions, including the long-term growth suppression of sugar maple and paper birch, which could not have been predicted by studies of these two important greenhouse gases applied singly or for a short-term.

Our results suggest that fine roots are key mediators of ecosystem response to these greenhouse gases, regardless of forest community type. Secondly, they highlight the importance of bottom-up changes caused by the combined effects of CO₂ and O₃ on food quality and the long-term population dynamics of forest pests. Furthermore, they suggest establishing links between net primary productivity, the biochemical constituents of plant litter, and the metabolic responses of microbial communities which are crucial to a mechanistic understanding of how these greenhouse gases will alter soil C and N cycling, as well as the long-term forest ecosystem productivity.

We are attempting to scale up our results to project O₃ responses of forest regions using various process-based models linked to canopy gap models. In addition, we are using a regression approach to find the best policy-relevant predictors of our observed O₃ effects on growth.

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