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Long-Term Leaf Production Response to Elevated Atmospheric Carbon Dioxide and Tropospheric Ozone

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Abstract

Elevated concentrations of atmospheric CO_2 and tropospheric O_3 will profoundly influence future forest productivity, but our understanding of these influences over the long-term is poor. Leaves are key indicators of productivity and we measured the mass, area, and nitrogen concentration of leaves collected in litter traps from 2002 to 2008 in three young northern temperate forest communities exposed to elevated CO_2 and/or elevated O_3 since 1998. On average, the overall effect of elevated CO_2 ($+CO_2$ and $+CO_2+O_3$ versus ambient and $+O_3$) was to increase leaf mass by 36% whereas the overall effect of elevated O_3 was to decrease leaf mass by 13%, with similar effects on stand leaf area. However, there were important $CO_2 \times O_3 \times$ year interactions wherein some treatment effects on leaf mass changed dramatically relative to ambient from 2002 to 2008. For example, stimulation by the $+CO_2$ treatment decreased (from +52 to +25%), whereas the deleterious effects of the $+O_3$ treatment increased (from −5 to −18%). In comparison, leaf mass in the $+CO_2+O_3$ treatment was similar to ambient throughout the study. Forest composition influenced these responses: effects of the $+O_3$ treatment on community-level leaf mass ranged from +2 to −19%. These findings are evidence that community composition, stand development processes, CO_2, and O_3 strongly interact. Changes in leaf nitrogen concentration were inconsistent, but leaf nitrogen mass (g m^{-2}) was increased by elevated CO_2 (+30%) and reduced by elevated O_3 (−16%), consistent with observations that nitrogen cycling is accelerated by elevated CO_2 but retarded by elevated O_3.

Key words: carbon dioxide; leaf area; long-term; nitrogen cycling; northern temperate forests; ozone; stand age; species dominance.

Introduction

Industrialization has significantly increased the concentrations of atmospheric carbon dioxide (CO_2) and tropospheric ozone (O_3), with greater increases predicted over the next century (Dentener and others 2006; IPCC 2007). Both changes have strong ecological impacts: CO_2 typically stimulates plant productivity (Ainsworth and Long 2005), whereas O_3 is phyto-toxic to a range of plant

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species (Chappelka and Samuelson 1998; Wittig and others 2009). However, despite the large role forest ecosystems play in the global carbon (C) cycle, there is still considerable uncertainly in how changes in atmospheric composition will affect the magnitude and even the direction of forest C storage (Nabuurs and others 2007). This uncertainty hinders efforts to model regional- to global-scale impacts and develop confidence in forest-based C mitigation programs (Nabuurs and others 2007), but relatively few experiments have examined the long-term response of forest ecosystems to elevated CO_2 and/or O_3.

Several of the experiments which have examined the long-term forest response to elevated CO_2 have used the free-air CO_2 enrichment (FACE) technology that minimizes changes to other environmental factors, while allowing for in situ exposure of large trees to increased concentrations of trace gases (Hendrey and others 1999). Results from these forest FACE experiments have emphasized the importance of leaf properties, including physiology, chemistry, and mass, in determining the response of forests to elevated CO_2 (McCarthy and others 2006; Finzi and others 2007). These leaf properties are directly affected by elevated CO_2, but are also affected by factors such as nitrogen (N) availability (McCarthy and others 2006) and species identity (Cotrufo and others 2005), which express important interactions with elevated CO_2. Although at least some of these factors are important determinants of the forest response to elevated O_3 (Chappelka and Samuelson 1998), the number of experiments that have exposed forest systems to both elevated O_3 and elevated CO_2 is too few to draw similar conclusions (Wittig and others 2009).

Although there is considerable evidence demonstrating that CO_2 and O_3 influence the physiology, productivity, and composition of forests, it is less clear how these influences change as stands develop (Körner 2006). Resource (light, water, N) availability typically decreases as stands develop (Ryan and others 1997), and although this shift has the potential to substantially change how forests respond to CO_2 and O_3, the interaction between stand development and these trace gases has not often been examined. For example, although some research indicates that forests can sustain increased productivity under elevated CO_2 by enhancing N uptake (Finzi and others 2007), few studies have followed forests through important stand development phases (for example, establishment, canopy closure, age-related declines in stand productivity) to examine whether the early stimulation of plant productivity by elevated CO_2 persists as stands mature after reaching maximum productivity (Körner 2006).

To date, the Rhinelander FACE experiment is the only long-term forest experiment examining both the independent and interactive effects of CO_2 and O_3 and the only forest FACE experiment designed to examine how competitive interactions among species and genotypes will modify ecosystem responses to these trace gases. In addition, the development of these stands from densely planted seedlings over the 11-year duration of the experiment provides the opportunity for unique insights into how the response of forests to CO_2 and O_3 changes during stand development.

Previous studies at Rhinelander FACE have shown that leaf litter mass and leaf litter N mass increased under elevated CO_2 and decreased under elevated O_3 (Liu and others 2007), whereas green leaf N concentrations were unaffected by the treatments (Zak and others 2007). However, these and other previous studies have been limited to short-term observations or to a subset of the species and communities included in the experiment. These are critical limitations given that leaf litter production is a strong predictor of ecosystem productivity (King and others 2005; Litton and others 2007) and a sensitive assay of ecosystem response to changes in atmospheric chemistry (Liu and others 2007). Therefore, the goal of this study was to use the annual leaf litterfall data from Rhinelander FACE to assess the response of both individual species (aspen, maple, and birch) and communities (aspen-only, aspen–maple, aspen–birch) to elevated O_3 and/or CO_2 and to identify how the relative influences of O_3 and CO_2 on leaf litter production changed as these stands aged over the 7-year period between 2002 and 2008, after which, the experiment was harvested. To do this, we focused on five variables: leaf litter mass (L_{mass}, g m^{-2}), leaf litter area (L_{area}, m^2 m^{-2}), leaf litter N concentration (N_{conc}, mg g^{-1}), leaf litter N mass (N_{mass}, g N m^{-2}), and species canopy dominance (as measured by proportion of aspen L_{mass} in mixed communities, %). Inter-annual variability in plant production at Rhinelander FACE has previously been described (Kubiske and others 2006), so here we specifically conducted our statistical analyses to test for trends through time.

We had several hypotheses in regards to the response of leaf litter properties to the fumigation treatments. First, we expected that because canopy development was thought to be nearly or fully complete in two of the three communities in 2003 (Norby and others 2005), L_{mass} and L_{area} would maintain their responses to the fumigation

treatments over the 7-year sampling period: a positive factorial elevated CO_2 response (+45% in 2003 L_{mass}), a negative factorial elevated O_3 response (−23%), and no significant interaction between CO_2 and O_3 (King and others 2005). However, we did expect that the response to CO_2 and O_3 would vary by species and communities because previous results had observed these effects for productivity (King and others 2005) and stem growth (Kubiske and others 2007). For instance, in results through 2003 for wood production, the reduction caused by the $+O_3$ treatment relative to ambient varied from −8.9% (aspen–maple community) to −27% (aspen-only community; King and others 2005). Lastly, we predicted that there would be no significant effect of the fumigation treatments on N_{conc}, but that N_{mass} would respond proportionately with L_{mass}.

Materials and Methods

The FACE experiment in Rhinelander, Wisconsin, USA (45°40.5′N, 89°37.5′W, 490 m.a.s.l.) consisted of twelve 30-m diameter rings, arranged in three randomized complete blocks (Dickson and others 2000). Treatments included factorial CO_2 and O_3 fumigations, with both ambient and elevated levels of each trace gas randomly assigned within each block. Fumigation began in 1998 and occurred during the daylight hours of the growing season (bud burst to leaf off). Average annual concentrations during fumigation are approximately 40–55 nl L^{-1} for elevated O_3 (elevated average: 45 nl l^{-1}, ambient average: 36 nl l^{-1}) and 515–540 µl l^{-1} for elevated CO_2 (elevated average: 531 µl l^{-1}, ambient average: 374 µl l^{-1}). Soils at the site are Alfic Haplorthods (Pandus series) with a sandy loam Ap horizon overlaying a sandy clay loam Bt horizon. More detailed descriptions of the experimental design, fumigation technique, and fumigation performance can be found in Dickson and others (2000). Annual data on length of the fumigation season, average CO_2 and O_3 concentrations, and meteorological variables are provided in Appendix Tables 1 and 2 (Supplementary material).

Small trees (<25 cm tall) initiated from potted stock were planted in the rings during July 1997. Half of each ring was planted at 1 m × 1 m intervals with five different aspen (*Populus tremuloides* Michx.) genotypes representing a range of responsiveness to elevated O_3 or elevated CO_2 (Dickson and others 2000). The remaining two quarters of each FACE ring were mixed communities planted with either paper birch (*Betula papyrifera* Marsh.) or sugar maple (*Acer saccharum* Marsh.) at equal densities with a single aspen genotype at 1 m × 1 m spacing.

In 2002 and 2003, four litter traps (0.15 m^2) were used to collect leaf litter from the aspen–maple and aspen–birch communities in each ring, with eight litter traps in the aspen-only community of each ring (Liu and others 2007). Starting in 2004, the number of traps in the aspen-only community was increased to twelve and the number of traps in the aspen–birch community was increased to six. Leaf litter was collected bi-weekly during the period of active leaf senescence (late August through early November), and approximately monthly during the rest of the growing season. After collection, the leaf litter samples were sorted by species. A subsample (10–15 leaves) from the litter collected in each community in each ring during September and October was analyzed for leaf area using the LI-3100 Leaf Area Meter (Li-Cor Biosciences, Lincoln, NE, USA). Both the overall sample and the subsample were then oven dried to a constant mass and weighed. Specific leaf area (SLA, cm^2 g^{-1}) of the litter was determined for the subsample (data not shown) and then applied to the overall sample to determine L_{area}. Collections outside of September and October not sub-sampled for leaf area analysis (~15% of overall biomass) were assigned SLA values from the nearest sub-sampling date. Leaf area measurements were not made in the aspen–maple community during 2003 and 2004. Because SLA varied dramatically among communities (by ~20%) and changed consistently through time ($P < 0.01$) in the other two communities, we felt our best option to supply these missing data was to substitute the average aspen–maple community SLA values in 2002 and 2005 for the 2003/2004 values. Annual L_{mass} and L_{area} (m^2 m^{-2}) were the sums of L_{mass} and L_{area} collected over the entire growing season.

The samples collected from throughout the growing season were ground and used to create a biomass-weighted composite annual sample for N analysis using a Costech (Valencia, CA) Elemental Combustion System 4010. Annual leaf N_{mass} (g N m^{-2}) was calculated by multiplying annual L_{mass} (g m^{-2}) by the N_{conc} (mg g^{-1}) of the annual sample. All of the measurements were completed at the species-level within each community. Except in the case of N_{conc}, community-level data in the aspen–birch and aspen–maple communities were simply the sum of the results for the individual species within that community. Community N_{conc} for the aspen–birch and aspen–maple communities was calculated by dividing the combined N_{mass} of the

two species within each community by the combined L_{mass} of those two species. For the aspen–birch and aspen–maple communities, we calculated the canopy dominance of aspen in terms of its proportion of the total community L_{mass}.

Statistical Analysis

The statistical model was a randomized complete block with a split-plot design; the analyses were conducted using the SAS statistical package (Version 9.1.3, SAS Institute, Cary, NC). These tests used type III sums of squares within a repeated measures analysis of variance (Proc Mixed) and post-hoc least squared means adjusted for multiple comparisons. Block was considered a random effect (Parsons and others 2008; Riikonen and others 2008). Because we were more interested in trends through time rather than annual variability, we used year as a continuous rather than categorical variable. With year as a continuous variable, significant year effects reflect changes through time (trends) and significant treatment × year interactions are evidence to reject hypotheses that the rate of change (slope of the trend) was similar among treatments (Littell and others 1996). Starting with the highest-level interaction terms, non-significant ($P \geq 0.1$) interactions between year and fumigation treatments or community were iteratively removed from the model until the only factors that remained were main effects (CO_2, O_3, community, year, and interactions between the first three of these) and significant interactions with year (Littell and others 1996). When year or an interaction with year was significant we used the solution option within SAS, which provides estimates of the rate of change through time and uses a t-test to determine whether these rates are significantly different from zero. When significant treatment × year interactions occurred, we also examined changes in the relative size of the treatment effects (for example, [+CO_2/ambient − 1] × 100) through time using linear regression (Proc Reg; after Norby and Iversen 2006). We should point out that when using this regression analysis for significant CO_2 × O_3 × year interactions, each of the four fumigation treatments are considered as separate treatments rather than factorial treatments. We conducted the overall analyses using community-level data, but we also conducted separate tests for each community individually and explore these results when there were significant community effects in the overall results. Furthermore, data were analyzed for each community component (species) individually to provide mechanistic detail (community and species results provided in Appendix). Data for the proportional dominance (in terms of percent of community L_{mass}) of aspen in the mixed-species communities were arcsine transformed to meet the assumption of normality. We used an alpha equal to 0.05 to determine statistical significance, but we report results where $0.05 \leq P < 0.10$ because nearly significant differences in a study with necessarily low replication may have biological significance (for example, Johnson and others 2004; Norby and Iversen 2006). Data reported throughout are means ± standard error.

Results

Experiment-Wide

As main effects, elevated CO_2 significantly increased both leaf mass (L_{mass}, Figure 1) and leaf area (L_{area}, Appendix Figure 1 in Supplementary material), whereas elevated O_3 significantly decreased L_{mass} and L_{area} (Figure 1; Appendix Figure 1 and Table 1 in Supplementary material). There was no significant CO_2 effect on leaf litter N concentration (N_{conc}), but there was a modest O_3 effect (Figure 2; Table 1). However, the effects of CO_2 and O_3 on leaf litter N mass (N_{mass}, Figure 3) were similar to those for L_{mass} (Table 1). Of the measured properties, only L_{area} exhibited a consistent overall change during the study period ($+0.12 \pm 0.03$ m^2 m^{-2} y^{-1}, $P < 0.001$, Appendix Figure 1 in Supplementary material).

In addition to the overall effects of CO_2 and O_3 on L_{mass}, L_{area}, and N_{mass}, each of these properties had significant CO_2 × O_3 × year, community × year, and CO_2 × O_3 × community interactions (Table 1). The significant interactions with year denote differences in trends through time. For L_{mass}, L_{area}, and N_{mass}, the difference between trees in the +CO_2 treatment and those in both the ambient and +CO_2+O_3 treatments (+CO_2/ambient and +CO_2+O_3/+CO_2) diminished through time ($r^2 \geq 0.578$, $P \leq 0.048$, Table 2 for L_{mass}; effect size data not shown for L_{area} and N_{mass}). In contrast, the difference between trees in the +O_3 treatment and those in both the ambient and +CO_2+O_3 treatments increased through time ($r^2 \geq 0.481$, $P \leq 0.084$), except for +O_3/ambient for N_{mass} ($r^2 = 0.425$, $P = 0.113$). However, the main effects of CO_2 and O_3 did not change significantly through time ($P > 0.2$, Table 2). The CO_2 × O_3 × community and community × year interactions for L_{mass}, L_{area}, and N_{mass} are explored below in the sub-sections for each community. There was a modest CO_2 × community × year interaction for N_{conc}

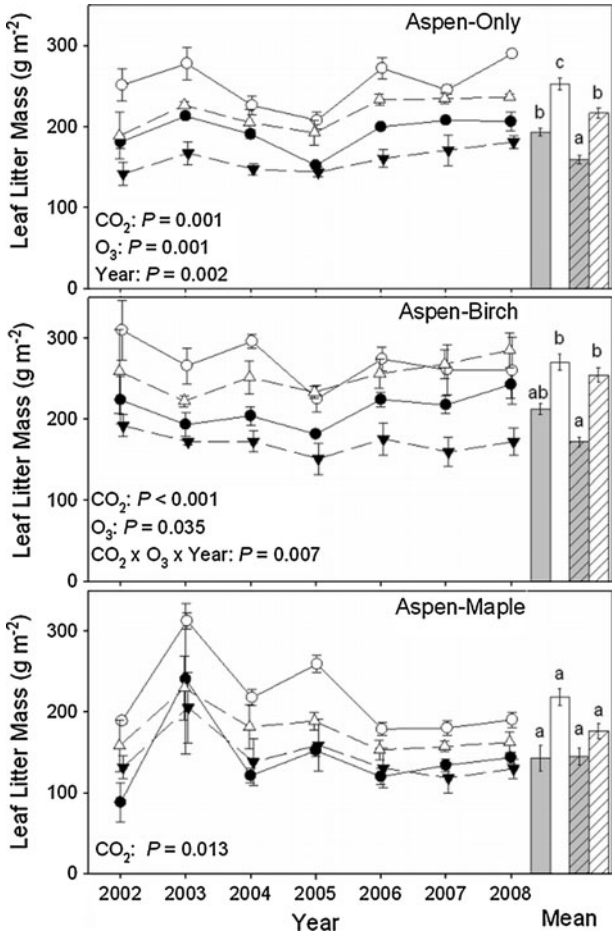

Figure 1. Annual L_{mass} (g m^{-2}) in the three community types for the ambient (*filled circles, filled bar*), $+CO_2$ (*empty circles, empty bar*), $+O_3$ (*solid triangles, filled hatched bar*), and $+CO_2+O_3$ (*empty triangle, empty hatched bar*). *Bar graphs* are means over the entire collection period. *Error bars* are ±1 SE. Reported ANOVA *P* values are from repeated measures analyses within each community. Overall statistical results are found in Table 1; full statistical results for each community are in Appendix Table 3 (Supplementary material). *Letters* denote significant differences in pair-wise comparisons ($P < 0.05$) among the treatments within a community.

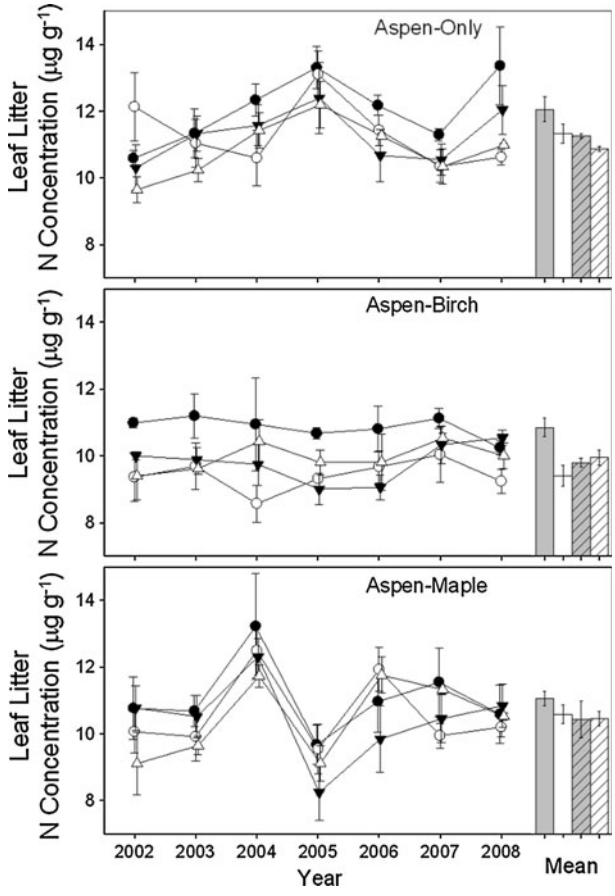

Figure 2. Annual leaf N_{conc} (mg g^{-1}) in the three community types for each fumigation treatment. *Symbols* and *bars* as in Figure 1. Treatment differences within each community were not significant ($P > 0.05$). Overall statistical results are found in Table 1; full statistical results for each community are in Appendix Table 3 (Supplementary material).

that resulted from non-significant CO_2 effects that increased with time in the aspen-only community but decreased with time in the other two communities (Table 1; Figure 2).

Aspen was a much higher proportion of total community L_{mass} in the aspen–maple community than in the aspen–birch community (84.0 ± 1.4% vs. 39.6 ± 1.6%, Figure 4). Trends in the aspen proportion through time varied by community (Table 1), increasing in the aspen–birch community and decreasing in the aspen–maple community (1.3 ± 0.7% y^{-1}, $P = 0.061$ vs. −2.1 ± 0.7% y^{-1}, $P = 0.003$, Appendix Table 3 in Supplementary material). Overall, elevated CO_2 increased the proportion of aspen in the mixed-species communities from 57.4 ± 2.6% to 66.2 ± 3.0% ($P = 0.062$, Figure 4). However, pair-wise differences were only significant when comparing the $+CO_2$ treatment with the ambient treatment in the aspen–maple community ($P = 0.033$, $CO_2 \times O_3 \times$ community: $P = 0.001$).

Aspen-Only Community

In the aspen-only community, there were gradual increases through time in L_{mass}, L_{area}, and N_{mass} (Figure 1; Appendix Table 3 and Figure 1 in Supplementary material). There was no significant increase through time in N_{mass} in the $+CO_2$ treatment ($P = 0.846$; $CO_2 \times O_3 \times$ year: $P = 0.081$), but the relative effects of the treatments on N_{mass} did not change consistently through time ($P > 0.13$).

Table 1. Experiment-Wide ANOVA *P* Values

Source	L_{mass} (g m^{-2})	L_{area} (m^2 m^{-2})	N_{conc} (mg g^{-1})	N_{mass} (g N m^{-2})	Aspen dominance (% of L_{mass})
CO_2	<**0.001** (+36%)	**0.001** (+31%)	0.143 (−4%)	**0.003** (+30%)	0.062 (+15%)
O_3	**0.018** (−13%)	**0.004** (−18%)	0.064 (−4%)	**0.012** (−16%)	0.375 (−6%)
$CO_2 \times O_3$	0.154	0.179	0.925	0.238	0.845
Community (comm.)	**0.001**	**0.046**	**0.002**	0.106	<**0.001**
$CO_2 \times$ comm.	0.313	**0.025**	0.264	0.967	<**0.001**
$O_3 \times$ comm.	0.433	0.127	0.613	0.104	0.424
$CO_2 \times O_3 \times$ comm.	**0.011**	**0.005**	0.186	**0.001**	<**0.001**
Year	0.691	<**0.001**	0.166	0.670	0.420
$CO_2 \times$ year	0.599	0.969	0.739	0.643	–
$O_3 \times$ year	0.444	0.650	0.204	0.255	–
$CO_2 \times O_3 \times$ year	**0.028**	**0.017**	0.103	**0.005**	–
Comm. × year	**0.001**	**0.012**	0.803	**0.002**	**0.001**
$CO_2 \times$ comm. × year	–	–	0.075	–	–
$O_3 \times$ comm. × year	–	–	–	–	–
$CO_2 \times O_3 \times$ comm. × year	–	–	–	–	–

L_{mass}, leaf litter mass; L_{area}, leaf litter area; N_{conc}, leaf nitrogen concentration; N_{mass}, leaf N mass. Results from repeated measures analyses. Fumigation main effect sizes in parentheses. Effects with $P < 0.05$ are in bold. Non-significant interactions ($P \geq 0.1$) between year and species or CO_2/O_3 removed from the analysis (see ''Materials and methods'' section) denoted with ''–''.

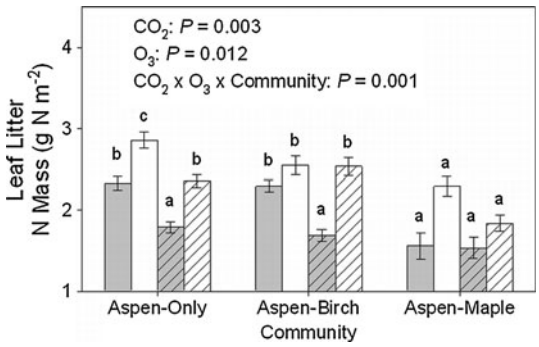

Figure 3. Mean annual leaf N_{mass} (g m^{-2}) for each treatment in the three forest communities averaged across all years. *Bars* as in Figure 1. Overall statistical results are from repeated measures ANOVA. *Letters* denote significant differences in pair-wise comparisons ($P < 0.05$) among the treatments within a community. Overall statistical results are found in Table 1; full statistical results for each community are in Appendix Table 3 (Supplementary material).

Elevated CO_2 increased L_{mass}, L_{area}, and N_{mass} ($P \leq 0.001$), whereas elevated O_3 caused these properties to decrease ($P \leq 0.001$). For N_{conc}, the relative effects of the treatments changed through time ($CO_2 \times O_3 \times$ year: $P = 0.051$; Figure 2). Here, the effect of the $+CO_2$ treatment relative to ambient changed from +15% in 2002 to −20% in 2008, whereas the effect of the $+O_3$ treatment relative to ambient changed from −3 to −10% ($r^2 \geq 0.577$, $P \leq 0.048$ for both).

Aspen–Birch Community

For the aspen–birch community, only L_{area} showed a consistent overall increase with time (Appendix Table 3 and Figure 1 in Supplementary material). L_{mass}, L_{area}, and N_{mass} were all increased by elevated CO_2 and decreased by elevated O_3 ($P \leq 0.018$ and $P \leq 0.038$; Figures 1, 3; Appendix Figure 1 in Supplementary material), but there were $CO_2 \times O_3 \times$ year interactions for each trait ($P \leq 0.061$). Trees in the $+CO_2$ treatment initially had greater L_{mass}, L_{area}, and N_{mass} than trees in both the ambient and $+CO_2+O_3$ treatments, but these differences gradually declined ($r^2 \geq 0.599$, $P \leq 0.041$). Conversely, trees in the $+O_3$ treatment initially had somewhat lower L_{mass} and N_{mass} than trees in the ambient and $+CO_2+O_3$ treatments and these differences gradually increased ($r^2 \geq 0.485$, $P \leq 0.082$).

For both birch and aspen, L_{mass}, L_{area}, and N_{mass} were higher under elevated CO_2 and lower under elevated O_3. However, only the CO_2 effect on L_{area} in birch (+37%, $P = 0.064$) and the CO_2 effect on L_{mass} in aspen approached significance (+47%, $P = 0.090$). Aspen had significant increases through time in L_{mass}, L_{area}, and N_{mass} (Figure 4; Appendix Table 3 in Supplementary material), whereas changes in birch L_{mass}, L_{area}, and N_{mass} through time varied by treatment ($CO_2 \times O_3 \times$ year: $P \leq 0.02$, Appendix Table 3 in Supplementary material). Over time, birch L_{mass} and N_{mass} decreased in the $+CO_2$ treatment and birch L_{mass} decreased in the $+O_3$ treatment ($P \leq 0.051$,

Table 2. Change in Treatment Effects on Overall Leaf Mass Through Time

Contrast	2002 Effect	2008 Effect	Annual change	r^2	*P*
$+CO_2$/Ambient	+52.4 ± 9.5%**	+24.9 ± 1.7%**	−4.0 ± 1.3%	0.654	**0.028**
$+O_3$/Ambient	−5.5 ± 4.0%	−18.5 ± 3.6%*	−1.8 ± 0.8%	0.481	0.084
$+CO_2+O_3$/Ambient	+23.0 ± 11.6%	+15.4 ± 9.9%	−0.1 ± 1.5%	0.001	0.956
$+CO_2+O_3/+CO_2$	−19.3 ± 4.1%*	−7.6 ± 9.0%	2.5 ± 0.7%	0.834	**0.004**
$+CO_2+O_3/+O_3$	+30.2 ± 10.3%*	+41.6 ± 5.9%**	2.8 ± 0.5%	0.649	**0.029**
CO_2 Main Effect	+41.6 ± 15.2%**	+32.4 ± 8.3%**	−0.9 ± 0.9%	0.149	0.392
O_3 Main Effect	−13.8 ± 7.7%	−12.5 ± 5.1%**	0.7 ± 0.5%	0.268	0.234

*Main CO_2 and O_3 effects defined from factorial treatments, for example ($+CO_2$ and $+CO_2+O_3$)/(Ambient and $+O_3$). Effects (mean ± SE) with $P < 0.05$ are in bold. Significant pair-wise comparisons noted by ** for $P < 0.05$ and * for $P < 0.10$. r^2 and P values derived from linear regressions of annual effect size data pooled across communities.*

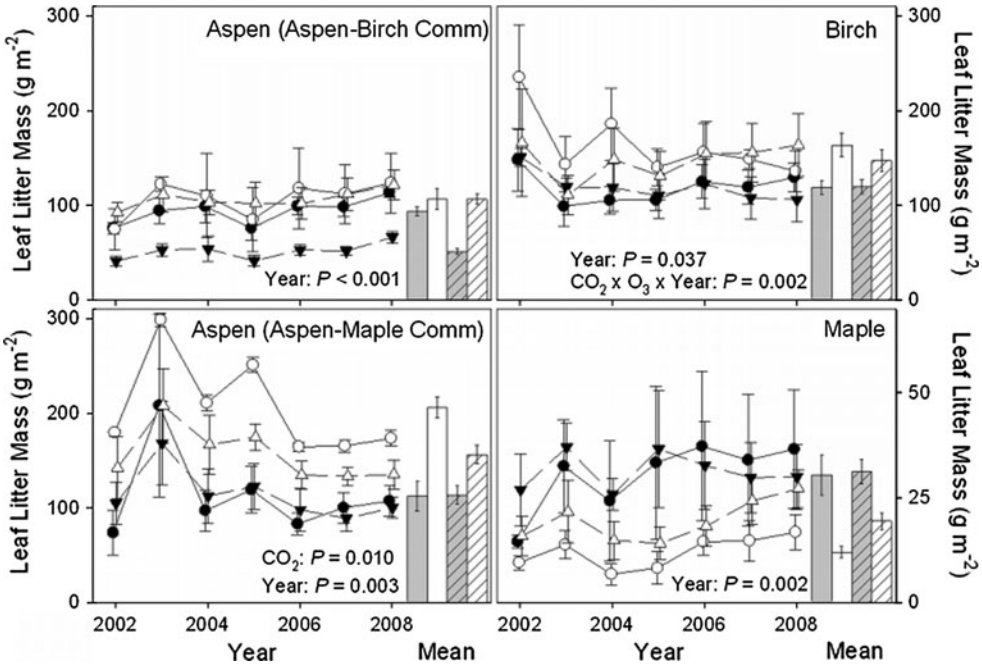

Figure 4. Annual leaf mass (g m^{-2}) of the individual components (species) in the mixed-species communities (aspen–birch and aspen–maple) for each fumigation treatment. *Bars* as in Figure 1. All results where $P \leq 0.05$ in the repeated measures ANOVA conducted for each species are reported. Note the difference in scale for maple. Full statistical results for each community component are in Appendix Table 3 (Supplementary material).

Figure 4). Birch L_{mass} and N_{mass} increased with time in the $+CO_2+O_3$ treatment ($P \leq 0.097$). The L_{mass}, L_{area}, and N_{mass} of birch were larger for trees in the $+CO_2$ treatment than in trees growing in the ambient and $+CO_2+O_3$ treatments, but these differences declined with time ($r^2 \geq 0.472$, $P \leq 0.088$). The same three properties declined with time for trees in the $+O_3$ treatment relative to trees in both the ambient and $+CO_2+O_3$ treatments ($r^2 \geq 0.645$, $P \leq 0.030$, except $+O_3$/ambient for N_{mass} where $r^2 = 0.290$, $P = 0.212$).

At the community level, N_{conc} was 1.4 mg g^{-1} lower for leaves in the $+CO_2$ treatment than for leaves in the ambient treatment ($P = 0.074$, $CO_2 \times O_3$: $P = 0.052$, Figure 2). In aspen, leaves in the ambient treatment had 1.9 mg g^{-1} more N than leaves in the $+CO_2$ ($P = 0.025$) and $+CO_2+O_3$ ($P = 0.027$) treatments and 1.4 mg g^{-1} more N than leaves in the $+O_3$ treatment ($P = 0.086$, $CO_2 \times O_3$: $P = 0.074$). There were no significant effects on N_{conc} in birch ($P > 0.15$).

Within the aspen–birch community, there was a $CO_2 \times O_3 \times$ year interaction for the proportional contribution of aspen to community L_{mass} ($P = 0.013$, Figure 4). Here, early increases in the proportional contribution of aspen in the $+CO_2$ and $+O_3$ treatments relative to both the ambient and $+CO_2+O_3$ treatments declined over time ($r^2 \geq 0.544$, $P \leq 0.04$).

Aspen–Maple Community

For the aspen–maple community, there were no significant trends with time overall or interactions between year and the fumigation treatments for L_{mass}, L_{area}, and N_{mass} ($P \geq 0.249$, Appendix Table 3 in Supplementary material). Community L_{mass}, L_{area}, and N_{mass} were significantly increased by elevated CO_2 ($P \leq 0.047$) and decreased by

elevated O_3, but only the difference in L_{area} approached significance for O_3 ($P = 0.097$; Figures 1, 3; Appendix Figure 1 in Supplementary material).

At the species level, there were significant decreases over time in aspen L_{mass} and N_{mass} (Appendix Table 3 in Supplementary material). Maple L_{mass} and L_{area} significantly increased over time, whereas maple N_{conc} decreased over time (Appendix Table 3 in Supplementary material).

The effects of CO_2 and of O_3 were unique in maple: elevated CO_2 decreased L_{area} (−46%, $P = 0.066$) and N_{mass} (−47%, $P = 0.079$), whereas elevated O_3 slightly (but not significantly) increased L_{mass}, L_{area}, and N_{mass} (+15%, Figure 4). For aspen, L_{mass}, L_{area}, and N_{mass} were increased by elevated CO_2 (all $P \leq 0.012$) and decreased under elevated O_3, but the O_3 effects were not significant ($P \geq 0.102$). There were $CO_2 \times O_3 \times$ year interactions for maple L_{mass} ($P = 0.069$, Figure 4) and N_{mass} ($P = 0.068$). These interactions stem from a steady change from a positive effect of the $+O_3$ treatment relative to the ambient treatment in L_{mass} and N_{mass} to a negative effect ($r^2 \geq 0.491$, $P \leq 0.079$) and a decreasing difference between trees in the $+O_3$ treatment and trees in the $+CO_2+O_3$ treatment for L_{mass} ($r^2 = 0.459$, $P = 0.094$) and N_{mass} ($r^2 = 0.666$, $P = 0.025$).

The only significant treatment effect on N_{conc} was a 0.9 mg g^{-1} decrease in aspen caused by elevated CO_2 ($P = 0.012$).

Discussion

Changes in CO_2 and O_3 Effects Through Time

Over the 7 years of this study (years five through eleven of the experiment), there were clear changes in the effects of the individual fumigation treatments (Table 2). Most dramatically, the average stimulation of L_{mass} by the elevated CO_2 treatment ($+CO_2$) compared to current ambient conditions ($+CO_2$/ambient) dropped by more than half (Figure 1; Table 2). This transient response to $+CO_2$ has been observed in several experiments (Norby and others 1999; Körner 2006). It appears that the initial stimulation of growth by elevated CO_2 allows forests to more quickly reach the point in stand development where environmental factors (light, water, nutrients, and so on) limit canopy production, but eventually, trees growing under ambient conditions reach a similar set of limitations to growth (Körner 2006). For example, in coppiced *Populus* forests (Gielen and others 2003), a stimulatory effect of elevated CO_2 on leaf area was observed only until canopy closure, after which responses declined markedly. A similar pattern appears in our study, where the declining $+CO_2$ effect was most apparent in the aspen–birch community. In 2002, trees in the $+CO_2$ treatment for this community had a L_{area} of 4.1 ± 0.2 m^2 m^{-2}, whereas trees in the ambient treatment had a L_{area} of 2.9 ± 0.2 m^2 m^{-2}. By 2008, trees in both treatments had similar L_{area} values (4.3 ± 0.5 for $+CO_2$, 4.1 ± 0.2 for ambient; Appendix Figure 1 in Supplementary material). This response is less apparent in the aspen-only and aspen–maple communities, but the aspen-only community continued to add both L_{area} and L_{mass} throughout this study and in the aspen–maple community, L_{area} and L_{mass} were considerably lower than in the aspen–birch community and displayed high inter-annual variability (Figure 1). Our overall results are evidence that, relative to ambient conditions, the $+CO_2$ stimulation of leaf production has declined. Although this decline in the $+CO_2$ stimulation has also been observed in annual measures of stem growth (1997–2004; Kubiske and others 2006), some continued stimulation of net primary productivity by the $+CO_2$ treatment relative to ambient is likely because of increases in leaf longevity and leaf-level photosynthesis in the $+CO_2$ treatment (Riikonen and others 2008).

Although the declining CO_2 stimulation of leaf production observed here is supported by theory (Körner 2006) and observations from similar experiments (for example, Gielen and others 2003), less is known about the long-term response of forests to elevated O_3. In earlier work (1997–2004) at Rhinelander FACE, Kubiske and others (2006) found that the negative effect of the $+O_3$ treatment on the relative rate of tree growth was dissipating. However, we observed an increasingly negative effect of the $+O_3$ treatment relative to the ambient treatment on L_{mass} in the aspen–birch community and to a lesser extent in the overall experiment (Figure 1; Table 2). In terms of its consequences for net primary production, the increasingly negative effect of the $+O_3$ treatment on L_{mass} is magnified by the reductions in leaf-level C uptake caused by the lower rates of leaf-level photosynthesis and shorter leaf longevity also observed at Rhinelander FACE (Riikonen and others 2008). Increasing O_3 effects on plant growth have also been found in several other experiments and are likely related to these changes in leaf C uptake (Oksanen 2003; Ottosson and others 2003; Volk and others 2006). In these cases, current year O_3 effects may be compounded due to reduction in the pool of plant resources available to initiate shoot growth due to O_3 effects that accumulated in

the previous growing season (for example, C reserves, bud size; Oksanen and Saleem 1999; Oksanen 2003). At Rhinelander FACE in 2005, Riikonen and others (2008) found that the size of aspen buds and the starch content of birch buds were lower in the $+O_3$ treatment. However, this mechanism does not seem to be affecting leaf mass in the aspen-only and aspen–maple communities, where there is no evidence that trees in the $+O_3$ treatment added or lost leaf mass at a different rate than those in the ambient treatment (as evident from the lack of significant $O_3 \times$ year or $CO_2 \times O_3 \times$ year effects). In fact, the $+O_3$ treatment has had little effect relative to ambient on the L_{mass} of either species in the aspen–maple community (Figure 4). Although maple (*Acer saccharum*) is relatively insensitive to elevated O_3 (Noble and others 1992; Rebbeck and Loats 1997), we are not able to explain why there has been no reduction in aspen leaf mass in this community. For the aspen-only community, Kubiske and others (2007) found using measurements of tree survival and stem volume during the first 8 years of the experiment that the $+O_3$ treatment had diminished the relative importance of O_3-sensitive clones and increased the importance of O_3-tolerant clones.

There were also transient effects when L_{mass} in the $+CO_2$ and $+O_3$ treatments were compared to L_{mass} in the interaction ($+CO_2+O_3$) treatment: the O_3 effect gradually decreased under elevated CO_2 ($+CO_2+O_3/+CO_2$) and the CO_2 effect under elevated O_3 gradually increased ($+CO_2+O_3/+O_3$, Table 2). There are few other multi-year experiments that have exposed trees to $+CO_2+O_3$, but a chamber experiment exposing *Liriodendron tulipifera* (L.) seedlings to 5 years of $+O_3$ and $+CO_2+O_3$ also found increasingly greater plant growth over time under $+CO_2+O_3$ compared to $+O_3$ (Rebbeck and Scherzer 2002). In our experiment, community L_{mass} and L_{area} in the $+CO_2+O_3$ treatment were similar (often slightly greater) to community L_{mass} and L_{area} in the ambient treatment (Figures 1, 4; Appendix Figure 1 in Supplementary material). This is unsurprising because CO_2 and O_3 often have counteracting effects on plant growth (Mulchi and others 1992; Volin and others 1998; Gaucher and others 2003). It is clear from the Rhinelander FACE experiment that this counter-action can be long-lasting.

Effects of CO_2 and O_3 on Species Dominance

Kubiske and others (2007) analyzed tree growth at Rhinelander FACE from 1997 to 2004 and found that elevated CO_2 and elevated O_3 had each shifted the relative dominance of species or genotypes within the three forest community types. Such shifts are important because changes in species abundance can have large effects on community-level properties such as litter chemistry or productivity (Bradley and Pregitzer 2007). Both in our study and in the analysis of tree growth (Kubiske and others 2007), the greatest effect of elevated CO_2 was an increase in the relative dominance of aspen in the aspen–maple community. In general, species with greater relative growth rates are more sensitive to elevated CO_2 and show stronger responses (Poorter and Navas 2003). Our results are consistent with this finding because of the three species included in the experiment, aspen and birch exhibit high relative growth rates, whereas maple is slower growing (Kubiske and others 2007).

Earlier in the development of the forests at Rhinelander FACE (through 2004), it was noted that the $+CO_2$ treatment affected birch more favorably than aspen in both growth and mortality (Kubiske and others 2007). Birch also appeared competitively favored by $+O_3$ in this earlier analysis (Kubiske and others 2007). However, these effects disappeared during the 2002–2008 leaf collections. Here, the proportional contribution of aspen to community L_{mass} increased in all treatments (Figure 4), but the declines in birch L_{mass} in the $+CO_2$ and $+O_3$ treatments meant that increases in the contribution of aspen were stronger in these treatments. Although the contrasting trends between the earlier analysis and this study possibly reflect differences in the way dominance was measured (L_{mass} versus stem volume), it is more likely that the current trends reflect changes over time in how competition between these species is altered by CO_2 and O_3.

Canopy Nitrogen Cycling

As predicted, there was not a significant overall CO_2 effect on N_{conc}. However, there was a modest overall O_3 effect and elevated CO_2 did significantly reduce N_{conc} for aspen in the mixed-species communities. These results are not surprising given similarly mixed findings in previous N_{conc} measurements at Rhinelander FACE for CO_2 and O_3 effects in green foliage (Kopper and others 2001; Takeuchi and others 2001; Zak and others 2007) and leaf litter (Liu and others 2007, Parsons and others 2008). More consistent at Rhinelander FACE is the finding that N_{mass} has been increased by elevated CO_2 and decreased by elevated O_3 (this study, Liu and others 2007; Zak and others 2007).

A similar increase in N_{mass} under elevated CO_2 was observed at Duke Forest FACE (Finzi and others 2001; Drake and others 2011). In contrast, in other forest FACE experiments, N_{mass} has decreased (Cotrufo and others 2005) or there has been no evidence of change in N_{mass} or the pool of green leaf N (Körner and others 2005; Norby and Iversen 2006).

A stimulation of N uptake by elevated CO_2 at Rhinelander FACE has also been observed for roots, stems, and branches (Zak and others 2007). This increase in N uptake rather than an increase in N-use efficiency appears to be supporting higher productivity under elevated CO_2 at Rhinelander FACE (Finzi and others 2007). In addition to the increases in N uptake, the increase in N mineralization (Holmes and others 2006), the greater activity of cellulose-degrading extracellular enzymes (Larson and others 2002), and the lack of soil C accumulation (Talhelm and others 2009) are strong evidence that the additional leaf litter (Figure 1), root litter (Pregitzer and others 2008), and total belowground carbon flux (Giardina and others 2005) under elevated CO_2 is quickly processed by the microbial community. Thus, rather than creating the negative feedbacks on plant N supply that would be consistent with an ecosystem experiencing progressive N limitation (Luo and others 2004), the rate of N cycling has increased under elevated CO_2 (Zak and others 2007). In comparison, elevated O_3 has had effects that suggest a slowed N cycle: decreased L_{mass} (Figure 1) with no corresponding reduction in soil C (Talhelm and others 2009), lower plant N uptake (Zak and others 2007), and reduced N mineralization (Holmes and others 2006).

Summary and Implications

This study was unique in that we were able to examine how leaf production and litter nitrogen in developing northern temperate forest communities of varying composition responded to relatively long-term fumigation (11 years) with elevated atmospheric CO_2 and/or tropospheric O_3. This allowed us insight into how these important gases, which will become more abundant in the atmosphere over the next century, interacted with each other and with ecological factors such as species identity, stand development, and nitrogen availability. Although we observed consistent main effects of CO_2 (positive) and O_3 (negative) on community L_{mass}, L_{area}, and N_{mass}, there were significant $CO_2 \times O_3 \times$ year and $CO_2 \times O_3 \times$ community interactions (Table 1), wherein the differences between individual fumigation treatments changed through time (Table 2) and varied by community (Figure 1). For instance, we observed a declining stimulation of leaf production by elevated CO_2 under ambient O_3, but an increasing stimulation leaf production by elevated CO_2 under elevated O_3 (Table 2). There is little evidence these changes resulted from reduced N availability (Figure 2). As has been observed elsewhere (Gielen and others 2003), it instead appears that the $+CO_2$ treatment affected leaf production largely by advancing the rate of stand development rather than by increasing the long-term community capacity to produce leaves. When comparing trees in the $+O_3$ treatment to those growing under ambient conditions, we found evidence supporting the idea that the negative effects of this gas on leaf production can be cumulative, compounding leaf-level effects to reduce plant C uptake. Perhaps most importantly, when trees were exposed to the treatment most likely to represent the future composition of the atmosphere ($+CO_2+O_3$), community L_{mass}, L_{area}, and N_{mass} were not significantly different than under ambient conditions (Figures 1, 2, 4; Appendix Figure 1 in Supplementary material). However, although these results could be construed to imply that future forests will be functionally similar to current forests, there is considerable evidence that communities exposed to $+CO_2+O_3$ and ambient conditions differ strongly in important functional attributes such as community composition (Kubiske and others 2007) and belowground C cycling (Pregitzer and others 2008; Talhelm and others 2009). Predictions regarding the future function of northern temperate forests are further complicated by the fact that species and communities showed a range of responses to the treatment gases (for example, Figures 3, 4).

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