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Overstory community composition and elevated atmospheric CO_2 and O_3 modify understory biomass production and nitrogen acquisition

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Abstract

Elevated atmospheric CO_2 and O_3 have the potential to affect the primary productivity of the forest overstory, but little attention has been given to potential responses of understory vegetation. Our objective was to document the effects of elevated atmospheric CO_2 and O_3 on understory species composition and biomass and to quantify nitrogen (N) acquisition by the understory vegetation. The research took place at the aspen free-air CO_2 and O_3 enrichment (FACE) experiment, which has four treatments (control, elevated CO_2, elevated O_3, and elevated CO_2+O_3) and three tree communities: aspen, aspen/birch, and aspen/maple. In June 2003, each FACE ring was uniformly labeled with 15N applied as NH_4Cl. Understory biomass was harvested in June of 2004 for productivity, N, and 15N measurements, and photosynthetically active radiation (PAR) was measured below the canopy. The understory was divided into five species groups, which dominate in this young aggrading forest: *Taraxacum officinale* (dandelion), *Solidago* sp. (goldenrod), *Trifolium repens* and *T. pretense* (clover), various species from the *Poaceae* family (grass), and composited minor components (CMC). Understory species composition, total and individual species biomass, N content, and 15N recovery showed overstory community effects, but the direct effects of treatments was masked by the high variability of these data. Total understory biomass increased with increasing light, and thus was greatest under the open canopy of the aspen/maple community, as well as the more open canopy of the elevated O_3 treatments. Species were different from one another in terms of 15N recovery, with virtually no 15N recovered in clover and the greatest amount recovered in dandelion. Thus, understory species composition and biomass appear to be driven by the structure of the overstory community, which is determined by the tree species present and their response to the treatments. However, N acquisition by the understory does not appear to be affected by either the overstory community or the treatments at this point.

Introduction

Since the start of the Industrial Revolution, atmospheric CO_2 has increased from 280 to 377 $\mu L\ L^{-1}$ today. Data from free-air carbon dioxide enrichment (FACE) experiments demonstrate that elevated levels of CO_2 led to greater CO_2 assimilation by plants and increased productivity (Ainsworth and Long, 2005; Norby et al., in press; Nowak et al., 2004). However, increased levels of tropospheric O_3 have also accompanied increases in atmospheric CO_2, with the amount

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of increase depending on geographic location (Fishman et al., 2003). Elevated O_3 is harmful to plant tissues, net photosynthesis (Reich and Amundson, 1985), and biomass production (Reich 1987). The interaction between CO_2 and O_3 is not well understood, although evidence suggests that elevated CO_2 will alleviate some of the negative effects of elevated O_3, which include reduced leaf area, leaf and root biomass, net primary productivity, and water-use efficiency (Karnosky et al., 2003).

Elevated CO_2 and O_3 may also alter the cycling of nitrogen (N) within forested ecosystems (McGuire et al., 1995). In order for trees to maintain increased productivity under elevated CO_2, they must increase N use efficiency or N uptake (Pataki et al., 2003). A study of nutrient cycling at the Oak Ridge National Laboratory FACE experiment (Johnson et al., 2004) provided evidence that trees are able to increase their N uptake, likely through greater fine root production, although the source of this additional N is unclear.

Elevated CO_2 research in forests has focused primarily on woody plants (Poorter and Navas, 2003). Existing research on herbaceous species has mostly been in an agricultural setting, and the forest herbaceous understory has been little studied. While understory vegetation does not contribute a significant amount of biomass to forested ecosystems, it is important for biodiversity and wildlife habitat. Meta-analyses of FACE data suggest that herbaceous plants are less responsive than trees to elevated CO_2, (Ainsworth and Long, 2005; Nowak et al., 2004), with fast-growing C3 herbs being more responsive than slow-growing C3 herbs or C4 plants (Poorter and Navas, 2003). Herbaceous plants also experience a greater reduction in leaf nitrogen content compared to woody plants (Nowak et al., 2004).

The direct effects of elevated atmospheric CO_2 and O_3 on understory biomass production and N acquisition, as well as the indirect effects of increased overstory biomass and N demand, are not known. Total understory biomass, individual species biomass, and species composition of the understory vegetation are known to be affected by the amount of light reaching the forest floor, which is driven by overstory species composition, as well as stand and crown structure (Alaback, 1982; Berger and Puettmann, 2000; Hunt et al., 2005; Legare et al., 2002; Peek et al., 2001). Understory species composition and biomass are also affected by leaf litter (Harrington et al., 2003), productivity (Adkison and Gleeson, 2004), soil nutrient concentrations (Hunt et al., 2005), nitrogen deposition rate (Rainey et al., 1999), throughfall precipitation (Anderson et al., 1969), above and below ground competition with overstory vegetation (Harrington et al., 2003; Riegel et al., 1992), disturbance (Moser et al., 1996), and successional dynamics (Gleeson and Tilman, 1990).

The objectives of this research were to study the effects of elevated levels of atmospheric CO_2 and O_3 on understory composition and biomass production and to quantify N acquisition by the understory vegetation using a pulse-chase 15N tracer experiment. We hypothesized that understory species biomass would be lowest in the elevated CO_2 treatment, which is expected to have the lowest light levels, and highest in the elevated O_3 treatment, which is expected to have the highest light levels. We also hypothesized that recovery of the 15N tracer would be lowest in the elevated CO_2 treatments because of greater demand for nitrogen by the overstory trees under elevated CO_2 (Oren et al., 2001).

Methods

Study site

The Aspen FACE site is located at the Harshaw Experimental Farm outside of Rhinelander, Wisconsin, USA. The 32 hectare field contains 12 FACE rings, which are 30 m in diameter. Three rings are exposed to one of four treatments: control, elevated CO_2, elevated O_3, and elevated CO_2+O_3. Elevated levels of CO_2 and O_3 are maintained at approximately 150% of ambient levels using a trace gas monitoring system, high-volume blowers, and vertical vent piping (Dickson et al., 2000; Karnosky et al., 2003). CO_2 levels average 356 and 534 $\mu L\ L^{-1}$ for control and elevated CO_2, respectively. O_3 levels average 36 and 50 nL L^{-1} for control and elevated O_3, respectively. O_3 levels were calculated as 12 h daytime mean O_3 exposure. Detailed hourly O_3 exposure showing maximum daily O_3 concentration can be found in Karnosky et al. (2005). The 12 rings were divided into three blocks, with 1 ring of each treatment composing a block. Each ring was divided into three communities (aspen, aspen/birch, and aspen/maple) by planting half of the ring with five different trembling aspen clones (*Populus tremuloides* Michx.), a quarter with alternating individuals of trembling aspen and paper birch (*Betula papyrifera* Marsh.), and the final quarter with trembling aspen and sugar maple (*Acer saccharum* Marsh.). The seedlings were planted at 1×1-m spacing in June of 1997. The soil was plowed and tilled before planting. Fumigation of the rings began in spring of 1998 (Dickson et al., 2000). The understory vegetation was controlled in 1997, 1998, and 1999 by applying Roundup two times per year using a backpack sprayer. Following the final herbicide application, the understory vegetation was allowed to develop. An ecosystem-scale 15N tracer experiment was conducted in June 2003 in which all FACE rings were uniformly labeled with 15N. The tracer was applied in the form of NH_4Cl at the rate of 0.0153 g 15N m^{-2} using backpack sprayers. Immediately following 15N application, the rings were irrigated with 0.2 cm of water to rinse the 15N solution off the understory plants and into the soil.

The amount of CO_2 and O_3 reaching the forest understory vegetation is not significantly different from that reaching the canopy. Passive samplers installed in an O_3 treatment ring to determine monthly cumulative O_3 show no significant difference between 1 m and canopy samplers (Karnosky, personal communication). Analysis of spatial control of the forest face prototype designed to test the feasibility of using FACE technology to fumigate mature loblolly pine trees found that 3D CO_2 concentrations were acceptably homogenous (Hendrey et al., 1999).

Photosynthetically active radiation

Because the light reaching the understory layer of the forest is directly related to forest overstory biomass production (Chazdon, 1988), we measured the amount of photosynthetically active radiation (PAR) reaching the understory vegetation. A Sunfleck Ceptometer (Decagon Devices, Inc., Pullman WA) was used to measure PAR at four positions in the aspen community and two positions in the aspen/birch and aspen/maple communities on June 23, 2004, at the same time the understory was harvested, and again on July 27, 2004, at the time of approximate peak leaf area for the season. Measurements were taken between 11:00 am and 3:00 pm local time on clear, cloudless days. At each position, the ceptometer was held at arms length, level to the ground and below all tree branches, and turned slowly in a circle. Eight measurements were taken along the circle approximately 45° apart and averaged (Burton et al., 1991). One circle was also established and measured in an open area outside of each ring in the manner described above. Two positions were used in the aspen/birch and aspen/maple communities originally because these areas are half the size of the aspen community. For the July measurement period, four positions were sampled in order to obtain better precision.

Understory harvest

The understory was harvested on June 21–24, 2004, just before the overstory vegetation was sampled for N analysis. The understory was clipped at ground level within four 0.5 m^2 quadrats per community. Quadrat locations were randomly preselected such that, within a community, the quadrats were in the same location in each ring. However, it was necessary to stay away from certain randomly placed equipment and boardwalks throughout the ring. Therefore, the actual quadrat location was the spot nearest to the randomly preselected location that met equipment and boardwalk criteria. Once clipped, the vegetation was sorted into the following fourteen groups: dandelion (*Taraxacum officinale*), goldenrod (*Solidago* sp.), red and white clover (*Trifolium repens* and *T. pretense*), grasses (C3 grasses from the Poaceae family), ferns, tree seedlings, yarrow (*Achillea millefolium*), yellow rocket (*Barbarea vulgaris*), annual fleabane (*Erigeron annuus*), strawberry (*Fragaria* sp.), orange hawkweed (*Hieracium aurantiacum*) and its nearly identical counterpart, prickly lettuce (*Lactuca scariola*), plaintain (*Plantago* sp.), and low hop clover (*Trifolium campestre*). Several additional species were seen in the understory, but could not be identified. These were placed in an ‘other’ category. This category never accounted for more than 7% of the biomass in a quadrat and averaged 0.3%. Two samples of dandelion, goldenrod, clover, and grass were also taken in similar habitats outside of the rings to determine the natural abundance of 15N. These species were chosen because they represented over 90% of the total understory biomass.

Laboratory and statistical analyses

The understory samples were dried in a 65 °C oven for 72 h and weighed to the nearest 0.1 g. The samples were then composited by community into five groups: dandelion, goldenrod, clover, grass, and composited minor components (CMC). All composite samples were ground into a powder using a ball mill. Approximately 3 mg of ground sample were weighed into a tin capsule and analyzed for N concentration and δ15N using a Costech Elemental Combustion System connected to a Thermo Finnigan ConfloIII Interface and Delta^{plus} Continuous Flow-Stable Isotope Mass Spectrometer. International Atomic Energy Agency, United States Geological Survey, and National Institute of Standards and Technology certified isotopic standards were run at the beginning of every analysis. Every ten samples were followed by an internal standard and every 25th sample was an analytical replicate. N concentration and δ15N were used to calculate N content, 15N atom percent excess, and 15N recovery.

Statistical analysis of understory biomass, N concentration, N content, atom percent excess 15N, and 15N recovery was performed in SAS (version 8.2, SAS Institute Inc., Cary, NC) using PROC GLM for a split-plot randomized complete block design as detailed in King et al. (2001). An alpha level of 0.05 was used and significant differences were further analyzed using least squared means. Due to uneven variance in the biomass estimates under elevated CO_2 and O_3, we multiplied the biomass values by 10 and log transformed these data. Statistical results were similar to the original analysis. Therefore, the results presented below are for untransformed data.

Results

Photosynthetically active radiation

The amount of PAR reaching the understory was significantly different among the three communities, with the amount of PAR reaching the understory being 30 and 60% lower in the aspen/birch community than the aspen and aspen/maple communities, respectively ($P < 0.001$). In the aspen and aspen/birch communities, CO_2 significantly decreased PAR (main effect $P = 0.04$) and O_3 significantly increased PAR (main effect $P = 0.02$; Figure 1). There were no significant treatment effects in the aspen/maple community.

Species composition and biomass

The understory was dominated by perennial old-field vegetation. More than 30 herbaceous species, 2 fern species, and 5 tree species were found in the understory layer. Dandelion, goldenrod, clover, and grass dominated, accounting for over 90% of the total biomass.

Dandelion, clover, and grass biomass differed significantly among overstory communities ($P = 0.02$, < 0.0001, and 0.03 respectively; Table 1). We found no CO_2 or O_3 main effects or $CO_2 \times O_3$ interaction effects on individual species biomass and total understory biomass. However, some treatment trends were apparent. Simple linear regression analysis showed that mean understory biomass and mean PAR by treatment for the aspen and aspen/birch communities showed a positive correlation (data not shown, $R^2 = 0.69$, $P = 0.01$). Additionally, clover biomass increased in treatments exposed to O_3 compared to those at ambient or elevated CO_2, with the increase ranging from 80–430% in the aspen community, 180–400% in the aspen/birch community, and 30–100% in the aspen/maple community. In the aspen and aspen/birch communities, total understory biomass was highest in the O_3 treatment, while the $CO_2 + O_3$ treatment showed a marked increase in biomass over the control treatment (data not shown).

Nitrogen acquisition

Natural abundance δ15N values were −1.5‰ for clover, −0.71‰ for dandelion, −0.29‰ for goldenrod, 0.33‰ for grass, and −0.22‰ for CMC. The natural abundance δ15N value of CMC was calculated by taking the average δ15N of dandelion, goldenrod, and grass. N concentration differed by species group with clover having the highest N concentration, but N concentration did

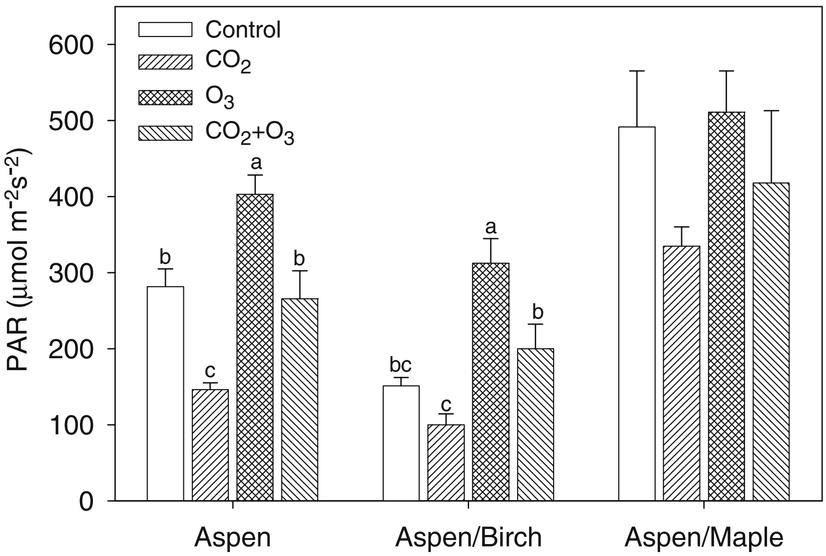

Figure 1. Photosynthetically active radiation under the overstory canopy at the Aspen FACE site on July 27, 2004. Error bars represent one standard error of the mean ($n = 3$). Different letters within a community represent significant differences at an alpha level of 0.05.

not differ among treatments or communities. N content differed in dandelion, clover, and grass between overstory communities (Table 1). 15N recovery varied significantly by species group and within species group by overstory community. Clover recovered 96% less 15N than dandelion in the aspen and aspen/birch communities and 83% less in the aspen/maple community. Clover also recovered over 85% less 15N than goldenrod across all communities (Table 1). No significant treatment differences were found.

Discussion

Species composition and biomass

Understory biomass was on average 3% of total aboveground biomass (aboveground biomass estimates can be found in King et al., in press). Understory biomass appears to be driven by the amount of light reaching the understory vegetation. We had anticipated that the differences in PAR by treatment would have been strong enough to produce significant treatment effects on total and individual species biomass, but this was not the case. Rather, individual species in our study responded to the overstory community, with clover and grass thriving in the aspen/maple community and dandelion thriving in the aspen/birch community. This suggests that clover may out compete dandelion under open canopies or that dandelion is more shade tolerant than clover. There is no indication in our results that the response of the understory to the overstory community is due to differences in N competition among the different overstory communities, as there were no overstory community effects on understory N concentration or atom percent excess 15N.

The individual species responses to light differences among the overstory communities are similar to the nonsignificant species responses to light seen among the treatments. Understory species composition and biomass varied widely between quadrats and FACE rings, resulting in high standard errors in total and individual species biomass. This heterogeneity many have contributed to the lack of treatment response. In the future, a greater sampling intensity may be necessary in order to determine treatment responses.

Besides sampling intensity, several other factors may have contributed to a lack of biomass response to the elevated CO_2 and O_3 treatments. While PAR is significantly different among the

Table 1. Mean biomass, N content, and 15N recovery for understory species groups at the Aspen FACE site

	Biomass ($g\ m^{-2}$)			N Content ($gN\ m^{-2}$)[a]			15N Recovery ($\mu g15N\ m^{-2}$)[b]		
	Aspen	Aspen/Birch	Aspen/Maple	Aspen	Aspen/Birch	Aspen/Maple	Aspen	Aspen/Birch	Aspen/Maple
Clover	15.6 ab (4.0)	9.7 b (4.7)	19.6 a (3.9)	0.44 ab (0.11)	0.29 b (0.13)	0.54 a (0.12)	11.3 (2.3)	13.9 (4.3)	21.1 (6.2)
Dandelion	20.1 b (2.3)	29.5 a (2.6)	12.3 c (1.6)	0.32 b (0.04)	0.53 a (0.06)	0.19 b (0.02)	184.7 b (26.9)	371.4 a (67.4)	127.8 b (17.7)
Goldenrod	15.6 (4.0)	11.1 (3.0)	23.4 (6.4)	0.31 (0.09)	0.24 (0.06)	0.45 (0.1)	92.2 (19.0)	93.6 (28.5)	192 (56.8)
Grass	1.2 b (0.6)	1.4 b (0.6)	4.2 a (1.4)	0.020 b (0.01)	0.026 b (0.01)	0.060 a (0.02)	10.2 b (5.2)	13.0 b (4.6)	33.9 a (9.9)
CMC	4.9 (1.2)	3.1 (0.7)	4.1 (1.4)	0.086 (0.02)	0.066 (0.01)	0.075 (0.03)	47.5 (10.7)	42.9 (8.0)	51.4 (17.0)
Total	57.4 (5.9)	54.8 (8.5)	63.6 (10.1)	1.15 (0.2)	1.11 (0.2)	1.3 (0.2)	328.9 (37.4)	525.8 (74.4)	415.6 (67.3)

Values in parenthesis are one standard error of the mean ($n = 12$). Different letters within a species group represent significant differences at an alpha level of 0.05.
[a]Nitrogen content: biomass multiplied by N concentration.
[b]15N recovery: N content multiplied by atom percent excess 15N.

four treatments, the vast majority of the plants found growing in the understory were shade intolerant species typically found in open fields, not forested understories. Also, the large number of factors that affect understory biomass production makes it difficult to tease apart responses to specific treatments. Differing species responses to environmental and community factors affected the total understory biomass response to the treatments. Clover seemed to flourish with elevated O_3. This could be attributed to several causes, including a direct positive response to O_3, a response to negative growth by other species because of O_3, or a response to greater light availability. Environmental and individual species responses were also considered to be the factors driving understory biomass at the Oak Ridge National Laboratory FACE experiment (Belote et al., 2004).

Additionally, under low light conditions, the relative rate of photosynthesis is expected to increase under elevated CO_2 relative to ambient CO_2 (Long and Drake, 1991). Osborne et al. (1997) documented greater carbon uptake in understory Indiana strawberry when grown under elevated CO_2 (*Duchesnea indica*). Hattenschwiler and Korner (1997) found that when grown under elevated CO_2, shade-intolerant species were able to obtain greater biomass and grow under low light. In our study, the total biomass was higher, although not significantly different, in the $CO_2 + O_3$ treatment compared to the control, despite similar light levels, and biomass was the same in the control and CO_2 treatments, despite significantly lower light levels in the CO_2 treatment, possibly indicating that understory plants were able to obtain more photosynthate for growth under elevated CO_2.

The different responses of the species groups to the treatments and communities are to be expected, as our species groups were different in life form and life history attributes. Together these differences between species and their responses to overstory species composition, light, interspecific competition, CO_2, and O_3 make it difficult to predict community- and ecosystem-level responses to a changing atmosphere. It is, however, apparent that elevated CO_2 and O_3 influence light transmission through the canopy (Figure 1), and this initiates a series of complex interactions in the forest understory.

Nitrogen acquisition

On average, 3% of the 15N tracer was recovered by the understory vegetation, compared to only 8% in the forest overstory. The majority of the tracer was recovered by the leaf litter and soil organic matter (Holmes, unpublished data). These results suggest that new N from the tracer was available for uptake throughout the growing season as leaf litter turned over. The total amount of N acquired by the understory vegetation, as measured by N content and 15N recovery, was not significantly affected by the treatments. Other elevated CO_2 experiments have also found that overstory and understory vegetation are able to obtain approximately equal amounts of N in control and elevated CO_2 treatments (Finzi et al., 2002; Johnson et al., 2004). Our results demonstrate that, at least in the understory, elevated levels of CO_2 and O_3 have not influenced total N acquisition.

N content and 15N recovery of dandelion and grass differed by overstory community. These differences are likely driven by biomass, as there were no community effects on N concentration and 15N atom percent excess. However, due to differences in understory species composition between the three overstory communities, total understory biomass was highest in the aspen/maple community, while total 15N recovery was highest in the aspen/birch community. This is largely due to the fact that dandelion dominated the aspen/birch community, while clover, which recovered very little 15N, along with goldenrod, dominated the aspen/maple community. Clover likely obtained the majority of its N through biological fixation, rather than through uptake of inorganic N, and therefore acquired little of the 15N tracer.

Individual species N content and 15N recovery did not differ significantly by treatment. Other studies addressing the N content of individual species have found a variety of responses to elevated CO_2. A review of FACE data by Nowak et al. (2004) found that all but one herbaceous species studied had reduced leaf N content under elevated CO_2. However, a study of understory vegetation in a sweetgum plantation found four of five understory taxa showed no significant change in C:N ratios when grown at elevated CO_2 (Sanders et al., 2004). Even though N content was unaffected by elevated CO_2 and O_3, species differences in N concentration and changes in species composition with overstory community and treatment could affect N distribution within the understory and perhaps the amount of N remaining in the soil.

In conclusion, overstory community composition, light, and interspecific competition affected species composition and biomass. The effects of the elevated CO_2 and O_3 treatments were manifested indirectly through overstory community response. Further, total N content and total 15N recovery in the understory were unaffected by CO_2 and O_3 or community type. However, N concentration and 15N recovery did differ by understory species groups with clover recovering virtually none of the 15N tracer regardless of treatment. Elevated CO_2 and O_3 appear to have little effect on the understory component of the N cycle in this experiment. Nevertheless, changes in the atmosphere did appear to contribute to alterations in species composition of the understory and responses were specific to groups of herbaceous taxa, demonstrating both direct and indirect responses of the forest understory to changes in the Earth's atmosphere.

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