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Ectomycorrhizal Colonization, Biomass, and Production in a Regenerating Scrub Oak Forest in Response to Elevated CO_2

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Abstract

The effects of CO_2 elevation on the dynamics of fine root (FR) mass and ectomycorrhizal (EM) mass and colonization were studied in situ in a Florida scrub oak system over four years of postfire regeneration. Soil cores were taken at five dates and sorted to assess the standing crop of ectomycorrhizal and fine roots. We used ingrowth bags to estimate the effects of elevated CO_2 on production of EM roots and fine roots. Elevated CO_2 tended to increase EM colonization frequency but did not affect EM mass nor FR mass in soil cores (standing mass). However, elevated CO_2 strongly increased EM mass and FR mass in ingrowth bags (production), but it did not affect the EM colonization frequency therein. An increase in belowground production with unchanged biomass indicates that elevated CO_2 may stimulate root turnover. The CO_2-stimulated increase of belowground production was initially larger than that of aboveground production. The oaks may allocate a larger portion of resources to root/mycorrhizal production in this system in elevated rather than ambient CO_2.

Key words: ectomycorrhizae; fine roots; ingrowth bags; production; turnover; *Quercus*.

Introduction

An important initiative of global change science is to examine how projected atmospheric CO_2 concentrations will affect the global carbon (C) cycle. A great deal of attention has been directed towards soil processes in forests where belowground plant C inputs could mediate critical feedbacks between the biosphere and the atmosphere (Diaz 1996). Globally, the amount of C in soil organic matter is four times that contained in plant biomass (Schlesinger 1984). Changes in the quality of inputs into the soil will influence the C cycle much more strongly than changes in the amount of C in live plants alone (Field 1999). Ectomycorrhizal (EM) associations, which occur in most temperate forests, have been considered in CO_2 studies for their ability to improve plant nutrition but also can directly contribute a large amount of C into soil systems. A change in production of EM root tissue could alter the total quality of belowground plant detritus entering the soil.

Mycorrhizal researchers historically have quantified the frequency and type of colonization to assess the symbiosis. Elevated CO_2 tends to increase EM colonization (Norby and other 1986, 1987; Ineichen and others 1995; Godbold and others 1997; Tingey and others 1997; Runion and others 1997) and can induce subtle and species-dependent shifts on EM types (Godbold and Bernston 1997; Rygiewicz and others 2000). Too few EM fungal taxa have been adequately described to draw specific

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conclusions concerning the effect of changes in mycorrhizal community structure on ecosystem processes (Fitter and others 2000). CO_2-induced stimulation of colonization may indicate enhanced C allocation to mycorrhizal mutualists but, because EM root tips can vary widely in size (Smith and Read 1997), colonization frequency does not necessarily correlate with either EM biomass or C consumption.

Although EM fungi can represent a large C sink in temperate forests (up to 75% of tree photosynthate; Vogt and others 1980; Fogel and Hunt 1983), few ecologists have yet examined how the effects of CO_2 on EM associations could directly feed back to the atmosphere via changes in belowground litter amount and quality. Shifting allocation to EM fungal biomass under elevated CO_2 could represent either a mechanism for net soil C storage or a pathway by which photosynthate is rapidly returned to the atmosphere (Hungate and others 1997), depending on its decomposability. Any increase in belowground production, or alteration in the balance of allocation between fine roots and relatively N- rich, chitinous mycorrhizal roots, could drastically alter the overall chemical quality of organic matter entering the soil C pools (Treseder and Allen 2000).

Recently, the direct effects of arbuscular mycorrhizal fungi and their associated products on C cycling have been addressed in response to global change (Rillig and others 1999). Although the direct contributions of ectomycorrhizae to C cycling (in terms of EM root throughput) can be immense (Vogt and others 1980; Fogel and Hunt 1983), these inputs remain experimentally unexamined in a global change context. Rillig and Allen (1999) recommend utilizing a measure of infection intensity to capture mycorrhizal response to CO_2. Ectomycorrhizae do not form readily measurable structures such as arbuscules and vesicles as do arbuscular mycorrhizae. To supplement colonization and estimate intensity of infection in the present study, portions of roots colonized by EM fungi were separated and weighed. Ectomycorrhizal mass includes both the plant and fungal components that compose the "mycorrhiza." Although this parameter neglects other EM organs that function for reproduction (sporocarps, rhizomorphs) and resource capture (external hyphae), it does represent the total exchange surface between fungus and host and provides an estimate of the amount of C allocated to EM roots. Additionally, ingrowth bags were buried at the beginning of the experiment, harvested at two dates thereafter, and subjected to the same analyses. In this manner, we were able to distinguish new growth from old standing mass of ectomycorrhizae to estimate CO_2 effects on EM production.

Materials and Methods

Site Description

The study site is at the Merritt Island National Wildlife Refuge off the east coast of central Florida (28° 38° N, 80° 4° 2 W). The coastal scruboak system lies on well-drained, infertile, sandy soils (Arenic Haplohumod) with low nutrients and low pH (3.9–4.1). Roots and organic matter are largely confined to the top 30 cm, most of it in the top 15 cm (Schmalzer and Hinkle 1996; Day and others 1996). The site is dominated by three species of scrub oak, *Quercus myrtifolia*, *Q. geminata*, and *Q. chapmanii*, along with saw palmetto, *Serenoa repens*. The natural fire cycle is thought to be approximately 7–10 years (Schmalzer and Hinkle 1996), although it has been subject to human suppression over the last 50 years. A controlled burn was executed in the spring of 1996, after which sixteen 9.4-m^2 open-top chambers were erected over the charred ground. Eight of the chambers contained ambient air (mean $[CO_2]$ = 378 ppm, over the study period) and eight contained ambient air plus supplemental CO_2 (mean $[CO_2]$ = 696 ppm). The oaks reestablished by resprouting from intact root systems and after four years have neared canopy closure with a height of approximately 1.5 m. At the time of the final sampling for this study, aboveground oak biomass was approximately 600 and 350 g m^{-2} (Figure 1) in the elevated and ambient treatments, respectively (for further details of the experimental setup, see Dijkstra and others 2002).

Root and Ectomycorrhizal Mass

At five sampling dates (June and July 1998, September and December 1999, and May 2000) three soil cores (1.9-cm internal diameter × 15-cm depth) were taken haphazardly but no less than 30 cm inside of the chamber wall. The three samples were combined into one plastic bag and stored at 4°C until processing. Samples were put through a 1-mm sieve to remove mineral soil. Palmetto roots and organic matter were manually removed based on easily distinguishable colors and shapes. The remaining sample consisted of more than 90% oak roots and associated ectomycorrhizae by mass. A subsample (more than 50 cm long) of fine (less than 1 mm in diameter) roots was scored for colonized root tips per root length, as determined by a gridline intersect method (adapted from Brundrette 1994).

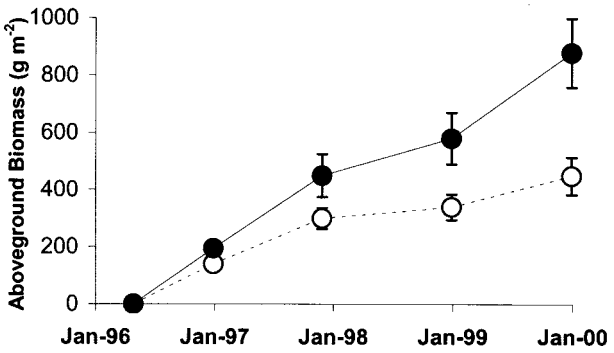

Figure 1. Aboveground oak biomass at the Florida site from the beginning of the experiment through January 2000. Open symbols represent ambient CO_2; solid symbols represent elevated CO_2 treatment. [With permission from Dijkstra and others (2002).]

Morphotypes were tallied on the basis of color, texture, and architecture (Agerer 1987). Because roots were air-dried during the sorting procedure, some root tips had lost integrity. For this reason, if any identifiable portion of mycorrhizal root tip remained, it was recorded as a colonization event. EM roots and clusters were separated from noninfected roots and clusters. Fine roots and EM roots were weighed on a microbalance and analyzed on a Carlo Erba C and N analyzer (Milan, Italy) to adjust mass values for adhering sand. The remainder of the unsorted sample was ground and analyzed for C and N content. The EM and fine roots subsample fractions were multiplied by the whole sample C mass to determine the total amount of fine roots and mycorrhizae in each sample, assuming roots and mycorrhizae contain 43.6% and 48.9% C, respectively, determined from independent measures of samples that were well-rinsed to remove adhering mineral matter. **EM mass** is the weight of plant and fungal portions of ectomycorrhizal roots but excludes the extramatrical hyphal mass or sporocarps. **EM proportion** is EM mass divided by the fine root mass (uncolonized and colonized) for a given sample. **Colonization intensity** is EM mass divided by the number of colonizations in a sample.

Root ingrowth bags were used to estimate EM and fine root production. Mesh bags (1-mm mesh) were filled with C horizon soil (sand with negligible organic matter) to exclude preexisting roots (Vogt and Persson 1991) and buried vertically in the top 15 cm at the beginning of the experiment in May 1996. Any root or root-associated tissue harvested from the ingrowth bags had formed since the bags were buried in May 1996. Sets of bags were collected in December 1998 and May 2000. The contents were sorted as described above.

Because the scruboak vegetation was regenerating, the steady-state assumption to calculate root productivity relative to the standing crop (Tingey and others 2000) was violated. Further more, the bags were allowed to reside in the field for over two years and some root turnover may have occurred. Although absolute productivity estimates measured with ingrowth techniques can have artifacts (Publicover and Vogt 1993), we used the technique to compare differences between treatment groups.

T-tests were used to compare treatment means and to evaluate differences between the parameters that are comparable between the ingrowth and core methods. The effect of CO_2 treatment on ingrowth contents was analyzed using a separate *t*-test. The effects of CO_2 and sampling date on all root/mycorrhizal measures collected from cores were analyzed using a two-way analysis of variance (ANOVA). Repeated measures analyses could not be performed because there were up to two missing cells for some treatment groups. One-way ANOVAs showed no significant effects (all P values greater than 0.1) of individual plots on any measure, suggesting that spatial pseudoreplication through time did not seriously confound statistical analyses. To meet the assumption of equal variances ($P > 0.05$) according to Levene's test, statistical analyses were performed on log transformed parameters; P values therefore refer to the probabilities of differences among log transformed values.

Results and Discussion

Soil Cores

Ectomycorrhizal colonization frequency was higher under elevated CO_2 (less than 0.05) and varied significantly among sampling dates ($P < 0.001$, two-way ANOVA) (Figure 2a). The CO_2 stimulation of colonization averaged 21% over the entire experiment but ranged from 0% to a peak of 77% in September 1999 when overall mean colonization frequencies were at their lowest. The CO_2 stimulation of colonization falls on the low end of estimates from other EM studies which range up to a 220% stimulation in oak roots (O'Neill and others 1987). All previous studies examined were performed on seedlings less than 2.5 years in age (O'Neill and others 1987; Ineichen and others 1995; Godbold and others 1997; Runion and others 1997; Tingey 1997). Of those, the three studies that sampled multiple times revealed decreasing stimulations of colonization with maturation (O'Neill and others 1987; Runion and others 1997; Walker and others 1997), which suggests that CO_2 stimulatory effects

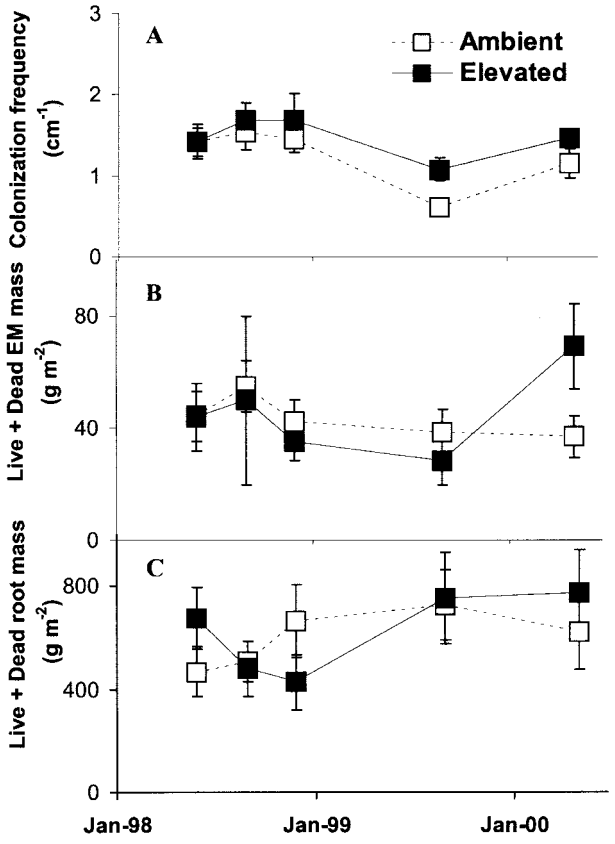

Figure 2. The variation of **A** EM colonization frequency per root length through time, **B** EM mass, and **C** fine root mass. Open symbols represent ambient CO_2; solid symbols represent elevated CO_2.

on EM colonization frequency may not persist on older trees. In general, when absolute colonization frequencies were higher in our study, the CO_2 effect was smaller, indicating that these oaks may approach a dynamic saturation point of mycorrhizal colonization. Tingey and others (2000) found that studies of trees with innately high EM colonization rates tended to find no stimulatory effect of CO_2 on colonization. Our findings demonstrate that elevated CO_2 may accelerate the rate of recolonization after an ebb but does not greatly increase the maximum colonization frequency.

Five distinguishable EM morphotypes were defined, based primarily on color. The most common (from 60% to 90% dominant) was a glossy, black, often large root tip. The presence of grainy, black sclerotia indicated colonization by the fungal genus *Cenococcum*. The dominance of the black morphotype fluctuated throughout the sampling period, generally declining from an initial high of 93% to a low of 68%. At no point was a treatment effect apparent on its relative abundance.

There was no effect of CO_2 or sampling date on standing mass of EM root tips or fine roots at any time (Figure 2b and c). The intensity of infection, which is the EM mass divided by the number of colonization events (Table 1), was higher in the ambient treatment ($P = 0.042$). There was no difference between the two CO_2 treatments in mycorrhizal proportion of total fine root mass (Table 2).

Ingrowth

Elevated CO_2 strongly increased the amount of fine roots ($p = 0.012$) and mycorrhizal tissue ($p = 0.034$) produced in the ingrowth bags (Figure 3). The largest stimulatory CO_2 effect on EM and FR mass occurred in December 1998 (291% and 549%, respectively) and then tapered, but it was still apparent in May 2000 (188% and 185%). The EM proportion of fine roots was much greater in ingrowth bags than in cores ($P < 0.001$, Table 1). Colonization was higher in ingrowth roots than in cores ($p = 0.017$), but no CO_2 treatment effect was apparent in ingrowth colonization (Table 3). The intensity of infection was also much greater in roots from the ingrowth bags than in those from the cores ($P < 0.018$, Table 1). Morphotypic distribution, like that of core samples, was dominated by a black, *Cenococcum*-like EM fungus.

The apparent stimulation of fine root and mycorrhizal root production could reflect the acceleration of stand development (Figure 4) and not direct CO_2 effects on allocation patterns (Staddon 1998). It is notable that belowground production under elevated CO_2 at 2.5 years eclipsed that under ambient at 4 years into the study (Figure 3); aboveground biomass was approximately equivalent, 550 and 500 g m^{-2}, respectively (Figure 1). Belowground production increased proportionately more than aboveground biomass under elevated CO_2 which may indicate that the oaks allocate a greater portion of resources belowground than under ambient CO_2 at this developmental stage. A more rigorous allometric analysis throughout canopy closure is required to decisively separate the effects of elevated CO_2 from those of accelerated ontogeny.

Production and Biomass

The lack of a detectable CO_2 effect on belowground standing root or EM mass is particularly striking considering both the large stimulation of aboveground oak biomass (Dijkstra and others 2002) and the large stimulation of newly grown tissue found in the ingrowth bags. The ingrowth technique may overestimate production because the bags were filled with unexploited, root-free soil.

Table 1. Means of Belowground Parameters from Each Sampling Method and Each CO_2 Treatment Over All Sampling Dates (n = 6–8)

	Core: old + new			Ingrowth: new			
Parameter	Amb (SE)	Elev (SE)	E/A[a]	Amb (SE)	Elev (SE)	E/A[a]	I/C[b]
EM mass (g m^{-2})	42 (4)	41 (7)	0.98	14* (5)	29* (9)	2.07	*
Fine root mass (g m^{-2})	606 (56)	641 (61)	1.06	51* (12)	122* (28)	2.39	*
EM Proportion (% mass)	9.2 (1.5)	8.5 (1.7)	0.92	42.4 (18)	34.0 (7)	0.80	4.32
Intensity (μg col^{-1})	28.6 (4.3)	18.3 (2.4)	0.64	41.6 (10.6)	55.9 (9.4)	1.34	2.08
Colonization (col cm^{-1})	1.23 (0.1)	1.49 (0.1)	1.21	1.78 (0.3)	1.78 (0.2)	1.00	1.31

[a] *E/A = elevated value divided by ambient value.*
[b] *I/C = pooled ingrowth divided by pooled core values.*
**Ingrowth masses represent mass per ingrowth bag and are not comparable to area-based core data (see Methods).*

Table 2. Results of a Two-Way ANOVA of CO_2 Treatment and Sampling Date Effects on Material Harvested from Cores

Response Variable	CO_2	Date	CO_2 × Date
EM mass	0.431	0.772	0.241
Fine root mass	0.910	0.055	0.220
EM proportion	0.378	0.061	0.332
Intensity	0.027	< 0.001	0.115
Colonization	0.024	< 0.001	0.297

However, given the large stimulation present even after 4 years of burial, it is probable that increased production occurred to some extent in the undisturbed soil. Drawing a live/dead distinction in soil core roots was not feasible for this system (Vogt and Persson 1991). Our "fine root mass" fraction included live as well as some dead roots, but not visibly decomposing roots. "Root turnover" in this situation refers to the passage of roots from the live and dead pools to the visibly decomposing pool (Tingey and others 2000). Because there was no treatment effect on standing root mass but an apparent increase in production, either the rate of mortality or the rate of disappearance may have increased under elevated CO_2.

Dilustro and others (2001) reported no change in root, longevity with CO_2 treatment at this site, tracking root cohorts with minirhizotron imaging. In a reciprocal root decomposition experiment, they reported greater microbial N immobilization in elevated CO_2 chambers regardless of whether the roots were taken from elevated or ambient CO_2 (Dilustro and others 2001). Greater flow of C to mycorrhizae, or other decomposing microbes, could enhance decomposition rates of root litter under elevated CO_2. Higher rates of disappearance, along with increased production, could result in no net change in standing root mass.

Accelerated root turnover has been observed elsewhere under elevated CO_2 (Fitter and others 1997; Pregitzer and others 2000; here turnover equals the rates of production and mortality in minirhizotron images). Because our ingrowth data suggest that new roots have higher colonization (Table 1), increased colonization in the standing root crop under elevated CO_2 could indicate that the roots sampled are younger on average (have higher turnover rates) under elevated CO_2. EM fungi selectively colonize the apical region of actively growing roots (Harley and Smith 1983), so higher colonization would be expected in a younger, more active root population.

Recently, we have shown that large, old rhizomes supply a significant portion of the C that supports the oak roots and mycorrhizae, but not aboveground structures (Langley and others 2002). The segregation of above- and belowground C sources may allow increased photosynthetic rates to support an aboveground biomass stimulation (80%, Dijkstra and others 2002) much larger than is found in most studies (38% average stimulation of leaf and stem biomass from 37 studies. (Curtis and Wang 1998). Likewise, this large pool of accessible C stored in rhizomes could, at least transiently, minimize the belowground effects of enhanced photosynthesis under elevated CO_2. The CO_2 stimulation may more strongly affect ingrowth tissues because newly fixed C may be preferentially allocated to building roots in ingrowth bags which may have disturbed connections to rhizomatous reservoirs. Indeed, ingrowth roots did have four times as

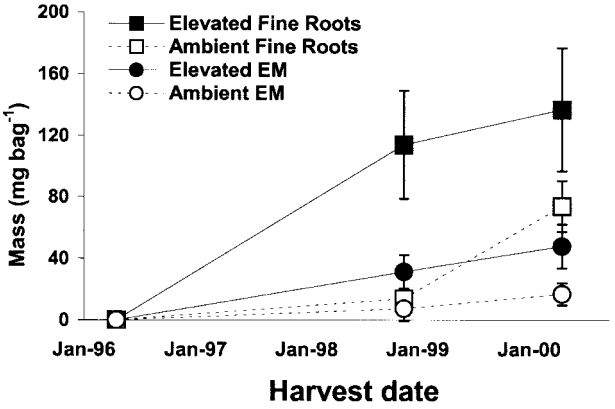

Figure 3. Mass of ingrown ectomycorrhizae (circles) and fine roots (squares) in ambient (open) and elevated (solid) CO_2.

Table 3. Results of Independent *t*-Tests, the Effect of CO_2 on Ingrowth Roots, and the Effect of Method (which Samples Different Ages of Roots) on Comparable Mycorrhizal Indices

Response Variable	CO_2 (ingrowth)	Method (ingrowth vs. core)
EM mass	0.034	NA
Fine root mass	0.012	NA
EM proportion	0.757	<0.001
Intensity	0.167	0.018
Colonization	0.690	0.017

much newly fixed C as roots in cores (Langley and others 2002), indicating a more direct connection to new photosynthate and allowing for a much stronger influence of the CO_2 treatment.

Implications for C Cycling

Retranslocation of nutrients from stems and foliage has been shown to negate CO_2-induced differences in aboveground tissue quality upon senescence therefore resulting in no net change in litter quality (Norby and others 2001). There remains much uncertainty regarding belowground inputs because of technical difficulty in capturing the diverse and enigmatic sources of belowground litter. A shift in allocation between mycorrhizal and nonmycorrhizal fine roots, which differ greatly in chemistry and architecture, could strongly alter belowground litter quality under elevated CO_2. Although growth of roots and mycorrhizae increased with high CO_2, the balance between the two was apparently unaltered. Proportional EM mass and EM colonization were

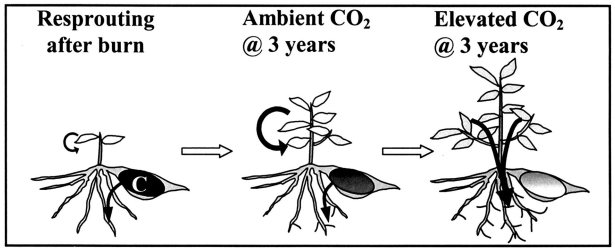

Figure 4. Schematic of oak C allocation scheme after three years under elevated and ambient CO_2. Solid arrows indicate prevailing direction of C flow. Above- and belowground structures use distinct C sources in early stages of development. Fine root production relies heavily on C stored in rhizomes (dark oval), while shoots utilize new photosynthate. Elevated CO_2 may accelerate the progression of oak stand development so that the oaks under elevated CO_2 may deplete C reserves more quickly and utilize new photosynthate. Oaks under ambient CO_2 may follow the same pattern after they reach a similar size.

the same for roots taken from ambient and elevated CO_2 ingrowth bags. Elevated CO_2 may alter only the quantity, not the quality, of root litter inputs in this system. However, the ingrowth data indicate that the balance of above- and belowground litter production may shift with the CO_2 treatment, which could drastically alter the overall intrinsic quality of litter as well as the microenvironmental conditions under which litter decomposes, both of which could impart changes on total C balance (Dukes and Hungate 2002). To draw more refined conclusions about soil/atmosphere feedbacks, we must clarify in a broad range of systems the effects of global change on resource partitioning to each important component of the root/mycorrhizal system (including hyphal litter and root exudates) as well as define the relative decomposability thereof.

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