Global Change Biology (2001) **7,** 581–589

Effects of elevated atmospheric CO_2 on root decomposition in a scrub oak ecosystem

JOHN J. DILUSTRO,* FRANK P. DAY* and BERT G. DRAKE†
Old Dominion University, Department of Biological Sciences, Norfolk, VA 23529 USA, †Smithsonian Environmental Research Center, Box 28, Edgewater, MD 21037, USA

Abstract

The effects of elevated atmospheric CO_2 on fine root decomposition over a 828-day period were investigated using open top chambers with both ambient and elevated (700 ppm) CO_2 treatments in an oak–palmetto scrub ecosystem at Kennedy Space Center, Florida. Carbon dioxide enrichment of the chambers began 15 May 1996. The experiment included roots grown in ambient and elevated carbon dioxide. Vertical litterbags installed in September 1996 in each elevated and ambient chamber incubated from December 1996 to December 1998 showed no significant treatment effect on fine root or rhizome mass loss. Initial fine root percentage mass loss varied from 10.3% to 13.5% after three months; 55.5% to 38.3% of original mass had been lost after 828 days. A period of nitrogen immobilization occurred in both fine roots and rhizomes in the elevated CO_2 incubation, which is a potential mechanism for nitrogen conservation for this system in an elevated CO_2 world.

Keywords: CO_2, decomposition, litterbags, nitrogen, roots, scrub oak

Received 4 September 2000; revised version received and accepted 23 January 2001

Introduction

The atmospheric concentration of CO_2 is expected to continue to rise and double sometime in the middle to later part of this century (Conway *et al*. 1988). The effects of elevated atmospheric CO_2 on terrestrial ecosystems have major implications for agriculture and human welfare, as well as to the long-term stability of terrestrial and aquatic ecosystems. Because CO_2 is both the major substrate for photosynthesis and a greenhouse gas, global increase has the potential to affect biogeochemical cycling and, thus, global climate change (Schlesinger 1997).

Belowground growth and decay both affect the sequestering of soil carbon. Total soil carbon should increase as a consequence either of increased fine root production or of decreased fine root decomposition. Thus, the ecosystem might gain carbon even if the plant doesn't (Norby 1994). In light of the likelihood of increased root growth under elevated CO_2 (Curtis *et al*. 1994), the extent to which these roots and rhizomes contribute to belowground carbon merits investigation. Root decomposition under elevated CO_2 is influenced by a complex set of factors because any litter quality changes that may be induced are coupled with possible soil environmental changes (e.g. water and nutrients) and soil flora and faunal changes (e.g. microinvertebrates, fungi and bacteria). Temperature, moisture and plant tissue chemistry are considered to have the greatest influence on decomposition rates (Vitousek *et al*. 1994). Nitrogen, phosphorus and carbon content (as cellulose and lignin) all influence root decomposition (Day 1982; Cotrufo *et al*. 1994; Gorissen *et al*. 1995). Microsite environments are also important in regulating decomposition rates (Day 1995).

The extent to which increased CO_2 will result in increased nutrient cycling and carbon accumulation in the soil globally is unknown. However, a shift of allocation seems a likely scenario. As carbon becomes less limiting under increased CO_2 levels, the plant may shift carbon allocation from leaves (carbon catchers) to roots (mineral miners). Increases in photosynthesis, fine roots (which have a higher C:N ratio than foliage), and

Correspondence: Frank P. Day, fax +1/757-683-5283, e-mail fday@odu.edu

© 2001 Blackwell Science Ltd

overall tissue C:N ratio (resulting from elevated CO_2) all point to increased carbon in the terrestrial ecosystem. The resulting lower tissue nitrogen content may decrease decomposition rates. Increased leaf C:N ratios, decreased leaf water and nitrogen content have all been shown in vegetation grown under elevated CO_2 (Pitelka 1994; Coûteaux *et al*. 1999). Although C:N ratio is a crude estimate of litter quality, it contitutes basic information for evaluating how elevated CO_2 and soil N influence litter quality (Pregitzer *et al*. 2000). Cotrufo *et al*. (1994) found that elevated CO_2 resulted in leaf litter with higher lignin concentrations, lower nitrogen, and higher C:N ratios; all of which point to higher carbon storage in soil under higher atmospheric concentrations of CO_2. Murray (1995) suggested that C3 crops were reduced in quality when grown under CO_2-enriched conditions despite the possible increases in C3 crop yield. Also, increased leaf C:N ratios and decreased leaf water and nitrogen contents have all been shown (Pitelka 1994). These changes in tissue quality could slow decomposition rates. This would, in turn, lower available nitrogen, thus eventually lowering primary production. A meta-analysis on the influence of atmospheric CO_2 concentration on quality of plant material and litter decomposition showed a general decrease of carbon mineralization (Coûteaux *et al*. 1999).

Net nitrogen immobilization is the result of the demand for carbon microbial decomposers as the C:N ratio drops. This signals the beginning of lignin decomposition and lowers available nitrogen, thus eventually lowering primary production. However, the view that widespread substrate quality changes will result in a negative feedback on net primary production has recently been questioned (Norby & Cotrufo 1998), because the majority of studies used green plant material. Plant material often demonstrates an effect of elevated CO_2 (e.g. lower tissue nitrogen), but this may not translate to a significant effect after the translocation that precedes natural senescence.

Decomposition is a fundamental process affecting soil carbon accumulation rates. Van Veen *et al*. (1991) hypothesized that owing to naturally high soil CO_2 concentrations, direct effects of elevated CO_2 on soil processes are doubtful. However, this has not been tested extensively. Because substrate quality is a very important factor regulating decomposition, CO_2 enrichment may prove to be indirectly influential. The few root decomposition studies conducted under elevated CO_2 have shown varied results with a trend toward decreased nitrogen concentration in root tissue (Coûteaux *et al*. 1999). Field experimental plots may exhibit changing flora and fauna as a consequence of elevated CO_2 that could affect decomposition. Soil nitrogen transformation under elevated CO_2 is not clearly understood. The fate of any additional carbon is uncertain. One possibility is a stimulation of microbial growth increasing the incorporation of inorganic nitrogen into the litter, resulting in the immobilization of nitrogen. Accumulation of nitrogen in wood is common (Scheu & Schauermann 1994). The final balance of carbon and nitrogen in the soil is uncertain. Zak *et al*. (1993) found that elevated CO_2 increased soil microbial biomass and nitrogen mineralization. Conversely, Diaz *et al*. (1993) suggested the possibility of lower C:N ratio litter, which would, in turn, increase microbial nitrogen demand and immobilize nitrogen. These differing hypotheses of the fate of carbon are not yet resolved. Experiments indicate a great deal of variability, suggesting the possibility that one paradigm will not emerge to predict the fate of carbon in every system.

Decomposition has been studied under CO_2-enriched conditions, but most studies are on aboveground leaf litter. Root decomposition has been largely overlooked, even under ambient CO_2 conditions. A belowground decomposition study using actual root material is necessary because roots are chemically and structurally complex and contain lignins. It is generally acknowledged that larger roots decompose slower than smaller roots. Fine roots are probably the largest input of belowground carbon in the scrub oak system. Rhizomes have a special importance as they function as a woody reservoir for long-term carbon storage and turnover. Gorissen *et al*. (1995) found that grass root decomposition was retarded for grasses grown under elevated CO_2 conditions. Even single studies examining two species have found species differences in response to elevated CO_2 (Ball & Drake 1997).

The objectives of the current study were to quantify root mass loss and nitrogen dynamics of roots grown in elevated and ambient conditions, and incubated in elevated and ambient conditions, using a buried litterbag technique, with analysis spanning 828 days.

Study site

The study site is on Merritt Island, an inland area of the northern part of Kennedy Space Center (KSC), Florida (N28°38′, W80°42′). Merritt Island is a barrier island with topography ranging from sea level to about 3 m. Precipitation averages 131 cm per year with high year-to-year variability (Schmalzer & Hinkle 1987). A dry season occurs from April to May and is optimal for the occurrence of wild fire. A rainy season occurs from May to October; the rest of the year is relatively dry (Mailander 1990). Mean daily temperatures are 22.3 °C for January and 33.3 °C for July; mean daily minimum temperatures are 9.6 °C for January and 21.9 °C for August (Mailander 1990). The main soils are excessively

drained Poala sand (Spodic Quartzpsamment) and moderately well drained Pomello sand (Arenic Haplahumod) (Schmalzer & Hinkle 1987). The soil is acidic and nutrient-poor with a 20-cm organic layer, a mean N content of 0.01% N (Hungate *et al*. 1999), and a spodic horizon (Bh).

At the inception of the study, it had been 10 years since the last burn. The experimental sites comprised mainly *Quercus myrtifolia* Wasd. (76%), *Q. geminata* Small (15%), *Q. chapmanii* Sargent (7%), *Serenoa repens* (Bartram) Small and *Lyonia ferruginea* (Walt.) Nutt. The community is dominated by clonal C3 species that spread through underground horizontal expansion. It is unknown whether the ramets in each chamber are of the same genet. However, studies of oak species with similar life forms show that ramet size is smaller than the area of the chambers (Montalvo *et al*. 1997). The scrub oak system was chosen because it is woody perennial and deciduous, and thus has a nutrient cycle much like the nutrient cycle of forests while still being small enough to study using open top chambers. The belowground biomass of this system is higher than that above ground (Schmalzer & Hinkle 1996).

The scrub community is fire-adapted and maintained with natural fire cycles of 10–15 years (Schmalzer & Hinkle 1987). The area was burned in February 1996 before the chambers were put in place. Schmalzer & Hinkle (1996) suggested that the characteristics of the fire adapted oak-saw palmetto scrub make it especially susceptible to nutrient losses from fire. Their study, however, did not include belowground biomass and nutrient pools. They did suggest the importance of leaching, immobilization and volatilization to nutrient cycling. Fire can lead to nitrogen losses due to volatilization and, consequently, frequent fires can result in nitrogen limitation (Vitousek & Howarth 1991).

Experimental design

Open top chambers were used to maintain enriched CO_2 concentrations (Drake *et al*. 1989). The treatments, initiated on 14 May 1996, were normal ambient CO_2 and normal ambient + 350 ppm CO_2 maintained 24 h a day. Open top chambers are considered best suited for the study of small stature communities such as scrub oak communities (Mooney & Koch 1994). Both ambient and elevated chambers had air circulating through blower systems that ran continuously, with CO_2 blown from the bottom of the cylinder out of the top. The chambers are octagonal with sides 139.9 cm wide, a maximum diameter of 365.6 cm, and a height of 365 cm. The study incorporated 16 chambers – eight CO_2-enriched and eight ambient CO_2 – and eight control plots without chambers (N = 8). Treatments were assigned randomly within triplets with closest initial aboveground biomass values. All resprouting vegetation was clipped to ground level at the onset of the study. Environmental measurements were obtained with a weather station located on site. Temperature and numerous environmental measurements were either continuously recorded or periodically measured in the chambers throughout the experiment.

Methods

Belowground decomposition of fine roots was measured using fine root material grown in CO_2-enriched and ambient CO_2 conditions, harvested in a pilot study in July 1995. The root material was taken from five cores (11.11 cm deep and 31.75 cm diameter) in each of the nine sites (three treatments) of a pilot study, washed to separate sand and organic matter and dried at 70 °C. Roots that were not intact or showing evidence of decay were excluded from the study. The roots had been grown (1992–95) under treatments similar to those in the current study (normal ambient CO_2 and normal ambient + 350 ppm CO_2) (see Day *et al*. 1996). Separately placing roots grown under ambient CO_2 and elevated CO_2 in both ambient CO_2 and elevated CO_2 chambers allowed for separate evaluations of any differences in decomposition resulting from changes in plant tissue vs. any direct effects of elevated CO_2 on the soil environment. The homogenized mixture of roots harvested from these cores was used for a representative assemblage of the root composition of both species and size for the study. Only fine roots less than 5 mm in diameter were included in this experiment. Representing the proportional makeup of root species and size composition is important for accurately simulating community-level decomposition response to elevated CO_2. This is important because root diameter has been related to mass loss (Berg 1984).

The fine root litterbags (n = 200), constructed of 1 mm mesh nylon, were divided into two 10 cm sections, for a total bag length of 20 cm, to incorporate a depth treatment into the study. The litterbags, containing known masses of roots, were inserted into the soil in September 1996 following the methods of Tupacz & Day (1989). A small slit was made in the soil, a bag inserted and the soil closed behind to ensure bag contact with the soil. The fine root experiment was initiated on 5 and 6 September 1996, when 40 bags were inserted into each of the five treatments. Chamberless control plot-grown roots were inserted into chamberless control plots; ambient-grown roots and elevated-grown roots were inserted into ambient and enriched chambers. Large woody rhizomes were also used from the pilot study harvest. Twenty-four 10-cm sections of approximately

2 cm diameter were cut and placed into 24 rhizome litterbags, each sized 10 cm × 4 cm. These bags were inserted horizontally into the soil at a 5-cm depth. This design allowed for a cross of treatments to test for both substrate and chamber effects. Although the roots were alive when collected for this study, it is generally accepted that roots show little or no retranslocation of nutrients when senescing (Nambiar 1987). O'Neill (1994) cautioned that the enhanced nutrient-use efficiency under CO_2 enrichment may increase reallocation and amplify any reduction in litter quality. All material was again dried at 70 °C for 72 h prior to weighing and preparing the bags. Bags were removed randomly from each chamber between December 1996 and December 1998 at 103-, 187-, 296-, 370- and 828-d intervals to establish decomposition rates. Rhizomes were all harvested at 828 days.

A blade was inserted into the soil to cut root ingrowth before removal, and prior to processing, the number of root intersections into the bag was recorded. The litterbags were rinsed of sand with tap water, and root growth into the bag was identified by colour and pliability and carefully removed. The roots were then oven-dried at 70 °C for 72 h and weighed to determine mass loss. Data obtained from the decomposition study are presented as percentage of initial mass remaining. Random pairs of bags were combined from the eight chambers, and samples ($N = 8$) were ground in a Wiley Mill, with subsamples additionally ground in a ball mill to ensure that the small sample used in the chemical analysis was representative and not biased by particle size. Nutrient analysis was performed on material left at the termination of the study to determine rates of carbon and nitrogen loss from the root tissue in addition to mass loss. Roots buried at the different depths were pooled for the nutrient analysis. Total carbon and nitrogen were analysed using a CHN elemental analyser (Carlo Erba 1108, Milan, Italy).

Initial nitrogen and carbon concentrations of fine roots were analysed using one-way ANOVA's; initial nitrogen and carbon concentrations of rhizomes were analysed using *t*-tests (SAS Institute 1990). Fine root differences in percentage of initial mass remaining between CO_2 treatments and depth were tested using a split-plot ANOVA. The data were evaluated using both linear and exponential models to test for the best fit. Relative decomposition rates (k) were then calculated using a fixed intercept negative exponential model (Wieder & Lang 1982) using the formula $X = e^{-kt}$, where X is the proportion of initial mass remaining, k is the decay constant and t is time. The times to reach 1% and 5% were calculated using k-values. The Tukey–Kramer method (Sokal & Rohlf 1981) was used to determine significant differences in decay coefficients (k) for each treatment and depth.

Data from litterbag studies tend to include a higher proportion of larger diameter roots than actually present in the soil (Pregitzer *et al*. 1997), because even the most careful harvesting and bag preparation involves losing a significant portion of the finest roots. Ruark (1993) suggests that the lower estimates of root decomposition using buried bags can result from washing and air-drying root material and less than optimal moisture within the bags. Therefore, turnover rates in this smallest cohort are best measured using minirhizotron observations. For the larger fine roots, litterbags are more appropriate because larger roots are not easily tracked with minirhizotrons. These two methods are complementary in evaluating decay over the broad range of 'fine roots'.

Results

Fine root mass loss did not differ between treatments or depths in this study ($P > 0.1120$) (Fig. 1). There was no significant time–treatment interaction and the time effect was significant ($P > 0.0001$). Decay rates (k) were calculated for each treatment and rates did not differ between treatments or depths (Table 1). Fine root decay rates (k) ranged from 0.17 to 0.22 among treatments. Rhizome mass loss or decay was not affected by either the CO_2 growth or incubation treatments (Table 2). Decomposition coefficients were similar for the rhizomes and ranged from 0.22 to 0.29 (Table 2).

The fine root initial percentage nitrogen ($P > 0.0582$) and percentage carbon ($P > 0.2212$) did not differ significantly (Table 3) between growth treatments. Rhizome initial percentage nitrogen ($P > 0.6839$) and percentage carbon ($P > 0.2256$) also did not differ significantly between growth treatments. Although percentage carbon was similar for both fine roots and rhizomes, the original nitrogen values for the rhizomes were substantially lower (Table 1). Initial fine root nitrogen content ranged from 0.42% to 0.44% and initial rhizome nitrogen content ranged from 0.25% to 0.26%. These fine root values were lower than the 0.77% measured by Schortemeyer *et al.* (2000) on the same site for fresh root material. This lower nitrogen value was likely the result of washing and oven drying the roots used in this study.

The percentage original nitrogen remaining during the decay of fine roots showed increases in percentage nitrogen three months after the beginning of the study (Fig. 2). This nitrogen immobilization was observed in fine roots of all growth and incubation treatments. Although all treatments exhibited some nitrogen immobilization, it was significantly higher in the CO_2 enriched chambers ($P > 0.0001$) (Fig. 2). The highest nitrogen immobilization in fine roots in this study was measured after 12 months and ranged between 130% and 140% original nitrogen. Fine root carbon concentration was

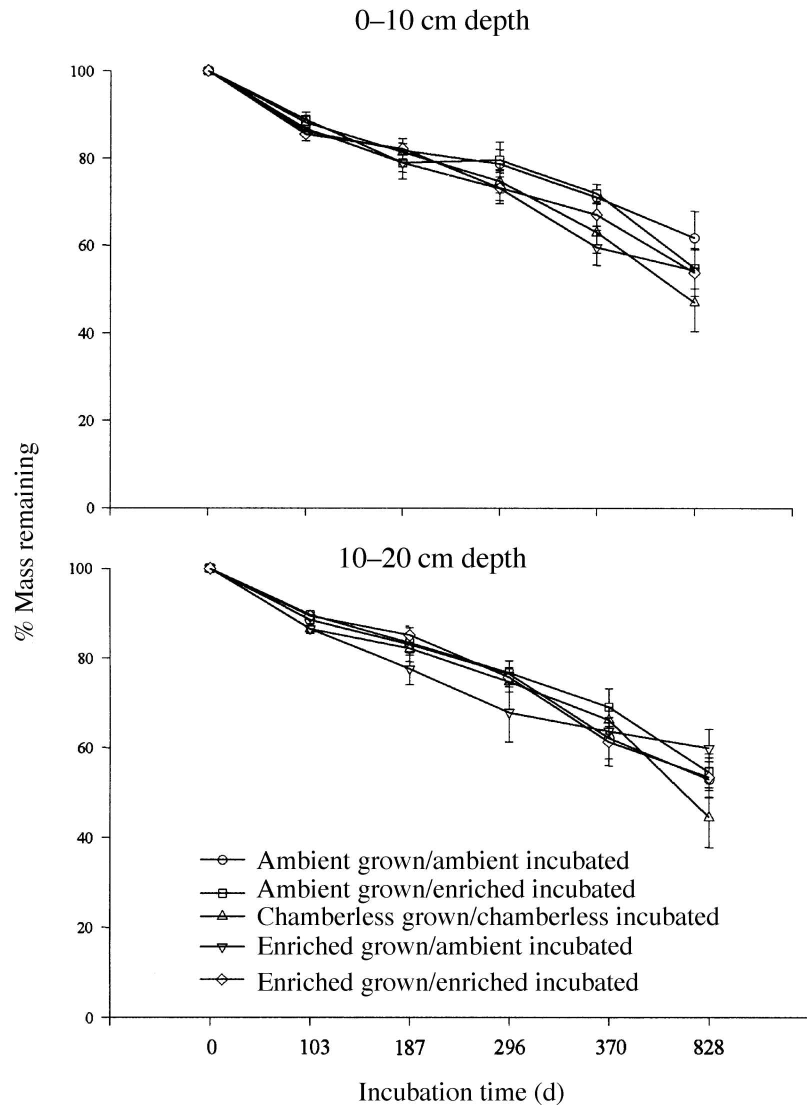

Fig. 1 Percentage mass remaining of fine roots that were harvested from ambient chambers (360 ppm), CO_2-enriched chambers (700 ppm) and chamberless control plots and decomposed in ambient chambers, CO_2 enriched chambers and chamberless control plots.

stable throughout the experiment. Nitrogen immobilization was observed in both roots and rhizomes in this study. Nitrogen immobilization occurred for all rhizome treatments (Table 2). The rhizomes immobilized between 184% and 226% of the original nitrogen, considerably higher than the 102% to 116% immobilized by fine roots after 828 days. The C:N ratio declined over time for both roots and rhizomes as a consequence of the increase in nitrogen coupled with a steady composition of carbon (Fig. 2).

Discussion

Mass loss rates presented herein were lower than those reported for birch and spruce fine roots (40–60% after 155 days) (Cotrufo *et al*. 1994). The present values were closer to those of Lõhmus & Ivask (1995), who observed 22.5% to 43.2% mass loss of Norway spruce fine roots after two years. Both this study and Lõhmus & Ivask (1995) oven-dried the material prior to the experiment, which destroys the decomposer population on the material and may present a time lag for recolonization by decomposers. The lower mass loss rates observed in the present study were likely a consequence of the woody structure, larger roots and oven drying of material. Wood decay occurs over time by leaching, physical weathering, microfaunal and microbial activity. Hungate *et al*. (1999) found reduced rates of gross nitrogen mineralization in soil and lower nitrate recovery from lysimeters in the first 14 months of the current study. Hungate *et al*. (1999) did not detect differences in soil microbial biomass in this study. This was possibly

Table 1 Fine root decay rate constants ($-k\ y^{-1}$), coefficient of determination (r^2), percentage mass remaining after 828 days of decay (%M) and years to reach 99% for depth intervals (n = 48). Individual regressions are significant at P = 0.0001

Litter from	Incubated in	Depth class (cm)	k	SE	r^2	$T_{0.01}$ (y)	Years 99%	Final % M
Ambient	Ambient	0–10	0.17	0.01	0.79	26.43	17.20	61.72
Ambient	Ambient	10–20	0.20	0.01	0.86	22.49	14.63	52.96
Enriched	Ambient	0–10	0.21	0.01	0.85	21.79	14.18	54.27
Enriched	Ambient	10–20	0.20	0.02	0.78	23.16	15.07	59.92
Ambient	Enriched	0–10	0.19	0.01	0.88	24.31	15.82	54.72
Ambient	Enriched	10–20	0.19	0.01	0.88	23.83	15.50	54.58
Enriched	Enriched	0–10	0.20	0.01	0.86	22.76	14.81	53.73
Enriched	Enriched	10–20	0.20	0.01	0.86	22.60	14.71	53.33
Control	Control	0–10	0.22	0.01	0.88	21.08	13.72	46.93
Control	Control	10–20	0.22	0.01	0.90	20.87	13.58	44.45

Table 2 Decay rate constants ($-k\ y^{-1}$), initial nitrogen and carbon content, percentage mass remaining after 828 days of decay and root ingrowth for woody rhizomes in root litter bags. All regressions are significant at P = 0.0001. One SE in parentheses. Different lower case letters indicate significant differences (P = 0.05) between treatments

	Rhizomes from ambient				Rhizomes from enriched	
	Incubated in ambient		Incubated in enriched		Incubated in enriched	
n	8		8		7	
k	0.22	(0.02)	0.22	(0.03)	0.29	(0.02)
Final % remaining	0.51	(0.05)	0.5	(0.06)	0.35	(0.04)
Ingrowth after 828d	17.5 a	(2.2)	20.6 a	(1.5)	28.4 b	(3.7)
T_{01} (y)	21.37		20.8		15.96	
Final % original N	184.11	(15.0)	226.04	(31.7)	225.18	(39.6)
Final % original C	102.14	(1.20)	99.76	(0.68)	100.88	(1.53)
Initial C:N	193	(14.6)	193	(14.6)	191	(1.9)
Final C:N	109	(6.0)	95	(11.4)	96	(10.6)

the result of increased carbon input to the soil by root mass and a decrease in the quality of that carbon (i.e. lignin). Although changes in the quality of the root and rhizome carbon were not detected, the possibility exists for differences in some structural components or in differences in fresh material. Naturally senesced leaf material from the pilot study also did not have significant differences in carbon and nitrogen (Gifford, pers. comm.). Although there were no significant treatment effects, the low decomposition rates do suggest possible soil sequestration of additional carbon resulting from increased production.

The current model for nitrogen dynamics during decay describes an initial phase of leaching followed by a period of accumulation ending with net release (mineralization) (Melillo *et al*. 1989). Nitrogen accumulation can be common during decomposition (net nitrogen immobilization) and can be up to twice the original content (Melillo & Aber 1984). Environmental variability between ambient and elevated chambers drove the increase in nitrogen immobilization observed in the elevated CO_2 chambers. This may have resulted from soil moisture differences (Hungate *et al*. 1997) or from soil fungi differences in the elevated CO_2 chambers. Also, all root litterbags were *in situ* and exposed to growing roots, and possible increased rhizodeposition under elevated CO_2 conditions (Rogers *et al*. 1994) could be instrumental in elevating microsite carbon, thus contributing to enhanced immobilization. Sadowsky & Schortemeyer 1997) suggested the possibility of C:N changes in root exudates similar to the change often observed in root tissue. This could further enhance immobilization. As part of the current study, Schortemeyer *et al*. (2000) found in soil cores taken in early and late July 1998, that on one sampling date the rhizosphere ninhydrin-reactive nitrogen was lower and on the other date the values were not significantly different. This inconsistent finding based on two close

Table 3 Initial root and rhizome nitrogen and carbon concentrations. Mean ± SE (n = 8). The P-value is for one-way ANOVA for fine roots and t-test for rhizomes

Type	Grown in	% N	% C	C:N
Rhizomes	Ambient	0.26 ± 0.0200	48.23 ± 0.08	196 ± 14.60
	Enriched	0.25 ± 0.0002	47.95 ± 0.19	191 ± 1.90
		$P < 0.6839$	$P < 0.2256$	$P < 0.8826$
Fine roots	Control	0.42 ± 0.0040	50.69 ± 0.13	121.02 : 1
	Ambient	0.44 ± 0.0400	50.57 ± 0.11	112.37 : 1
	Enriched	0.42 ± 0.0100	50.26 ± 0.13	121.86 : 1
		$P < 0.2212$	$P < 0.0582$	$P < 0.3297$

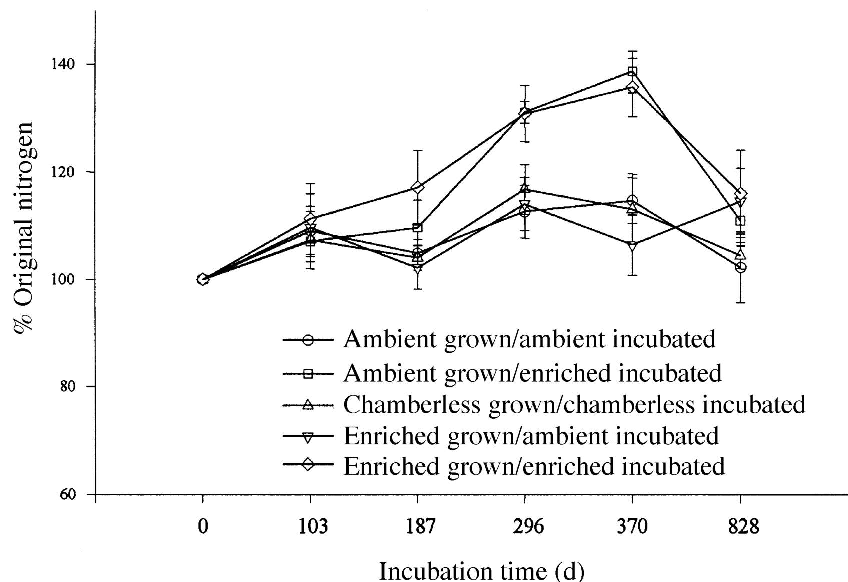

Fig. 2 Percentage original nitrogen content of decomposing roots that were harvested from ambient chambers (360 ppm), CO_2-enriched chambers (700 ppm) and chamberless control plots and decomposed in ambient chambers, CO_2 enriched chambers and chamberless control plots.

sampling dates suggests temporal variability in root exudation and microbial response of this system. Increased rhizodeposition can occur on a root length, a mass or even on a soil volume basis. Even if rhizodeposition on a per-length basis is not affected, it can still result in an increase in total rhizodeposition with increased root biomass (Rogers *et al*. 1994). Seastedt *et al*. (1992) suggested that buried substrates with high C:N ratios do not immobilize substantial amounts of nitrogen in grassland and agroecosystems. Conversely, Ostertag & Hobbie (1999) measured high levels of nitrogen immobilization in tropical forest roots. Immobilization was observed both in roots and in rhizomes in this study, and the initial nitrogen values were slightly lower than the material used in both of their studies (0.49%).

Net nitrogen immobilization was observed across all treatments of both roots and rhizomes because of initially high C:N ratios across all pretreatments. Immobilization may serve as an important mechanism for conserving nitrogen in this system and the enhancement of immobilization under elevated CO_2 conditions may serve to potentially minimize leaching and increase nutrient use efficiency. Vitousek & Matson (1985) showed the minimization of nitrogen leaching by soil microbes following clearcutting. Immobilization exhibited the greatest magnitude in the woody rhizomes. Scheu & Schauermann (1994) also found greater N accumulation in larger roots. Although enhanced immobilization did not persist until the end of the experiment, even short-term immobilization can help conserve nutrients during the critical recovery time after fire.

Plant tissue nitrogen can be controlled by soil nitrogen content (Vitousek *et al*. 1994). The low soil nitrogen values of this system may partially explain the low initial tissue values. Conn & Day (1997) measured grass roots with initial nitrogen concentrations ranging from 59 to 81% nitrogen. Although there was no detectable initial period of leaching, leaching may occur unnoticed if the mineralization occurring is overshadowed by immobilization. Unless it is possible to identify external and internal fractions (e.g. isotopes), the only observation is net immobilization.

Hungate *et al*. (1999) observed no increase in microbial biomass under elevated CO_2, and Langley and Hungate

(pers. comm.) found no difference in mycorrhizal colonization per root in elevated or ambient CO_2. This lack of change in percentage colonization, coupled with increased root length in the elevated chambers, suggests that there is a greater fungal network under elevated CO_2. Greater fungal biomass is a likely contributor to the increased immobilization observed under elevated CO_2 (Fahey 1983). Because mycorrhizae have a ready plant carbon source, they may become more nitrogen limited, resulting in periods of immobilization and mineralization. Enhanced nitrogen immobilization may serve as an important nitrogen conservation mechanism following fire in this system. Increased soil carbon inputs and enhanced immobilization will result in either reduced nitrogen availability or in conservation of nitrogen in this nutrient-limited system. Hungate *et al*. (1999) measured increases in nitrogen fixation under elevated CO_2 in the Florida scrub oak system. However, nitrogen fixation is a rather small nitrogen input to this system and may only have an influence over time. If the immobilized nitrogen balances the increased nitrogen fixation then nitrogen limitation could be avoided and the immobilized nitrogen could potentially be mineralized later for plant use. Thus, although total mass loss was unaffected by rising atmospheric CO_2, immobilization in decaying root litter may be altered. Increased accrual of nitrogen in litter is consistent with the hypothesis that elevated CO_2 will result in increased nitrogen demand by soil microorganisms (Diaz *et al*. 1993; Zak *et al*. 1993). In the long term, nitrogen availability will govern the response of nutrient-limited ecosystems such as the Florida scrub oak to elevated CO_2.

Acknowledgements

This paper is based on a portion of a doctoral dissertation submitted by the first author to Old Dominion University. This work was funded by a subcontract (95–59-MPOOO02) to the Smithsonian Institution's grant from the U.S. Department of Energy (DE-FG-02–95ER61993). We thank Paul Dijkstra and Dave Johnson of the Smithsonian for general assistance and reliable operation of the experiment, and Theresa Dilustro and Michael Farrell for their help at various stages of the study. We especially thank the U.S. National Aeronautical and Space Administration and Dr William Knott, Chief Scientist, Science and Engineering Technology Office, John F. Kennedy Space Center, for providing continual support throughout the project.

References

Ball AS, Drake BG (1997) Short-term decomposition of litter produced by plants grown in ambient and elevated CO_2 concentrations. *Global Change Biology*, **3**, 29–35.

Berg B (1984) Decomposition of root litter and some factors regulating the process: long-term root litter decomposition in a Scots Pine Forest. *Soil Biology Biochemistry*, **16**, 609–617.

Conn CE, Day FP (1997) Root decomposition across a barrier island chronosequence: litter quality and environmental controls. *Plant and Soil*, **195**, 351–364.

Conway TJ, Tans P, Waterman LS (1988) Atmospheric carbon dioxide measurements in the remote global troposphere. 1981–84. *Tellus*, **40B**, 81–115.

Cotrufo MF, Ineson P, Rowland AP (1994) Decomposition of tree leaf litters grown under elevated CO_2: effect of litter quality. *Plant and Soil*, **163**, 121–130.

Coûteaux MM, Kurz K, Bottner P, Raschi A (1999) Influence of increased atmospheric CO_2 concentration on quality of plant material and litter decomposition. *Tree Physiology*, **19**, 301–311.

Curtis PS, Zak DR, Pregitizer KS, Teeri JA (1994) Above- and belowground response of *Populus grandidentata* to elevated atmospheric CO_2 and soil N availability. *Plant and Soil*, **165**, 45–51.

Day FP (1982) Litter decomposition rates in the Great Dismal Swamp. *Ecology*, **63**, 670–678.

Day FP (1995) Environmental influences on belowground decomposition on a coastal barrier island determined by cotton strip assay. *Pedobiologia*, **39**, 289–303.

Day FP, Weber EP, Hinkle CR, Drake BG (1996) Effects of elevated CO_2 on fine root length and distribution in an oak-palmetto ecosystem in central Florida. *Global Change Biology*, **2**, 143–145.

Diaz S, Grime JP, Harris J, McPherson E (1993) Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. *Nature*, **364**, 616–617.

Drake BG, Lendley PW, Arp WJ, Nassiry D, Curtis PS (1989) An open top chamber for field studies of elevated atmospheric CO_2 concentration on salt marsh vegetation. *Functional Ecology*, **3**, 363–371.

Fahey TJ (1983) Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp, *latifolia*) ecosystems, southeastern Wyoming. *Ecological Monographs*, **53**, 51–72.

Gorissen A, Van Ginkel JH, Keurentjes JJB, Van Veen JA (1995) Grass root decomposition is retarded when grass has been grown under elevated CO_2. *Soil Biology Biochemistry*, **27**, 117–120.

Hungate BA, Chapin FS III, Zhong H, Holland EA, Field CB (1997) Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia*, **109**, 149–153.

Hungate BA, Dijkstra P, Johnson DW, Hinkle CR, Drake BG (1999) Elevated CO_2 increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Global Change Biology*, **5**, 781–789.

Lõhmus K, Ivask M (1995) Decomposition and nitrogen dynamics of fine roots of Norway spruce (*Picea abies* (L.) Karst.) at different sites. *Plant and Soil*, **168/169**, 89–94.

Mailander JL (1990) *Climate of the Kennedy Space Center and vicinity*. NASA Technical Memoir 103498. Kennedy Space Center, FL.

Melillo JM, Aber JD (1984) Nutrient immobilization in decaying litter: an example of carbon nutrient interactions. In: *Trends in Ecological Research for the 1980s* (eds Cooley JH, Golley FB), pp. 193–215. Plenum Press, New York.

Melillo JM, Aber JD, Likens AE, Ricca A, Fry B, Nadelhoffer K (1989) Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. *Plant and Soil*, **115**, 189–198.

Montalvo AM, Conard SG, Conkle MT, Hodgskiss PD (1997)

Population structure, genetic diversity, and clone formation in *Quercus Chrysolepis* (Fagaceae). *American Journal of Botany*, **84**, 1553–1564.

Mooney HA, Koch GW (1994) The impact of rising CO_2 concentration on the terrestrial biosphere. *Ambio*, **23**, 74–76.

Murray DR (1995) Plant responses to carbon dioxide. *American Journal of Botany*, **82**, 690–697.

Nambiar EKS (1987) Do nutrients retranslocate from plants? *Canadian Journal of Forest Research*, **17**, 913–918.

Norby RJ (1994) Issues and perspectives for investigation of root responses to elevated atmospheric carbon dioxide. *Plant and Soil*, **165**, 9–20.

Norby RJ, Cotrufo MF (1998) A question of litter quality. *Nature*, **396**, 17–18.

O'Neill EG (1994) Responses of soil biota to elevated atmospheric carbon dioxide. *Plant and Soil*, **165**, 55–65.

Ostertag R, Hobbie SE (1999) Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. *Oecologia*, **121**, 564–573.

Pitelka LF (1994) Ecosystem response to elevated CO_2. *Trends in Ecology and Evolution*, **9**, 204–207.

Pregitzer KS, Kubiske ME, Yu CK, Hendrick RL (1997) Relationships among root branch order, carbon and nitrogen in four temperat species. *Decologia*, **111**, 302–308.

Pregitzer KS, Zak DR, Maziasz J *et al.* (2000) Interactive effects of atmospheric CO_2 and soil-N availability on fine roots of *Populus tremuloides*. *Ecological Applications*, **10**, 18–33.

Rogers HH, Runion GB, Krupa SV (1994) Plant responses to atmospheric CO_2 with emphasis on roots and the rhizosphere. *Environmental Pollution*, **83**, 155–189.

Ruark GA (1993) Modeling soil temperature effects on *in situ* decomposition rates for fine roots of loblolly pine. *Forest Science*, **39**, 118–129.

Sadowsky MJ, Schortemeyer M (1997) Soil microbial responses to increased concentrations of atmospheric CO_2. *Global Change Biology*, **3**, 217–224.

SAS Institute (1990) SAS/STAT User's Guide, v.6, 4th edn, **Vol. 2**. SAS Institute, Cary, NC.

Scheu S, Schauermann J (1994) Decomposition of root and twigs: effects of wood type (beech and ash), diameter, site of exposure and macrofauna exclusion. *Plant and Soil*, **163**, 13–24.

Schlesinger W (1997). *Biogeochemistry: an Analysis of Global Change*, 2nd edn. Academic Press, London.

Schmalzer PA, Hinkle CR (1987) *Effects of fire on composition, biomass and nutrients in oak scrub vegetation on John F Kennedy Space Center, Florida.* NASA Technical Memoir 100305. Kennedy Space Center, FL.

Schmalzer PA, Hinkle CR (1996) Biomass and nutrients in aboveground vegetation and soils of Florida oak-saw palmetto scrub. *Castanea*, **61**, 168–193.

Schortemeyer M, Dijkstra P, Johnson DW, Drake BG (2000) Effects of elevated atmospheric CO_2 concentration on C and N pools and rhizosphere processes in a Florida scrub oak community. *Global Change Biology*, **6**, 383–391.

Seastedt TR, Partin WJ, Ojima DS (1992) Mass loss and nitrogen dynamics of decaying litter in grasslands: The apparent low nitrogen immobilization potential of root detritus. *Canadian Journal of Botany*, **70**, 384–391.

Sokal RR, Rohlf FJ (1981). *Biometry*. Freeman, New York.

Tupacz EG, Day FP (1989) Decomposition of roots in a seasonally flooded swamp ecosystem. *Aquatic Botany*, **37**, 199–214.

Van Veen JA, Lijeroth E, Lekkerkerk LJA, Van De Gerijn SC (1991) Carbon fluxes in plant-soil systems at elevated atmosphere CO_2 levels. *Ecological Applications*, **1**, 175–181.

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*, **13**, 87–115.

Vitousek PM, Matson PA (1985) Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology*, **66**, 1360–1376.

Vitousek PM, Turner DR, Parton WJ, Sanford RL (1994) Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms and models. *Ecology*, **75**, 418–429.

Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, **63**, 1636–1642.

Zak DR, Pregitzer KS, Curtis PS (1993) Elevated atmospheric CO_2 and feedback between carbon and nitrogen cycles. *Plant and Soil*, **151**, 105–117.