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Atmospheric CO_2, soil nitrogen and turnover of fine roots

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SUMMARY

In most natural ecosystems a significant portion of carbon fixed through photosynthesis is allocated to the production and maintenance of fine roots, the ephemeral portion of the root system that absorbs growth-limiting moisture and nutrients. In turn, senescence of fine roots can be the greatest source of C input to forest soils. Consequently, important questions in ecology entail the extent to which increasing atmospheric CO_2 may alter the allocation of carbon to, and demography of, fine roots. Using microvideo and image analysis technology, we demonstrate that elevated atmospheric CO_2 increases the rates of both fine root production and mortality. Rates of root mortality also increased substantially as soil nitrogen availability increased, regardless of CO_2 concentration. Nitrogen greatly influenced the proportional allocation of carbon to leaves vs. fine roots. The amount of available nitrogen in the soil appears to be the most important factor regulating fine root demography in *Populus* trees.

Key words: Atmospheric CO_2, nitrogen, roots, turnover, carbon allocation, global warming.

INTRODUCTION

A fundamental understanding of the cycling of C and N in the soil has historically been limited by our inability to quantify fine root demography (Kurz & Kimmins, 1987; Hendrick & Pregitzer, 1992). Ecosystem C and N cycles are intimately linked because leaf N is directly related to photosynthesis (Field & Mooney, 1986; Evans, 1989), and the shedding of plant parts (especially leaves and fine roots) provides the fuel for heterotrophic cycling of C and N in the soil (Zak *et al.*, 1993). Many reports document that photosynthesis and carbon allocation to plant roots increase as atmospheric CO_2 rises (Del Castillo *et al.*, 1989; Norby *et al.*, 1992; Rogers, Runion & Krupa, 1994). It has also been suggested that increased input of C and higher C/N ratios of plant litter will eventually result in microbial immobilization of nutrients, mineral deficiencies, and a dampening of the growth response plants typically exhibit when grown in a CO_2-enriched atmosphere (Schimel, 1990). Root turnover may also be important in the formation of soil organic matter. Changes in carbon flux from fine roots could influence ecosystem carbon storage beyond what is sequestered in biomass in response to elevated atmospheric CO_2.

Reliable estimates and C and N flux from the root system to the soil await a more fundamental understanding of how rates of root production and mortality vary according to changes in environmental parameters such as atmospheric CO_2 and soil nitrogen availability. Limited data from temperate forests suggest that average fine root life expectancy is less than a year (Hendrick & Pregitzer, 1992), and root mortality appears to be sensitive to both soil temperature (Hendrick & Pregitzer, 1993*a*) and N availability (Pregitzer, Hendrick & Fogel, 1993). Until now, there have been no experiments documenting the effect of rising atmospheric CO_2 on fine root demography. The objective of this research was to determine the extent to which increasing atmospheric CO_2 may alter the allocation of carbon to, and demography of, *Populus* fine roots. Because soil N availability plays such an important role in plant carbon allocation, we grew *Populus* trees at two levels

of N availability and at ambient and twice-ambient atmospheric CO_2 in a factorial experiment in the field.

MATERIALS AND METHODS

Populus trees were grown at the University of Michigan Biological Station near Pellston, Michigan (45° 34′ N, 84° 40′ W) in 20 open-bottom root boxes fitted with clear plastic tubes (minirhizotrons) (Zak *et al.*, 1993). Tubes were inserted at an angle of 28·3° and extended from the soil surface to 1·3 m below-ground (vertical depth). Five cuttings of a single genotype (*Populus* × *euramericana* cv. Eugenei) were planted in each root box on 21 May 1992. Cuttings were obtained from stock propagated at Michigan State University and were graded for uniformity in diameter and condition. Mean dry weight (+SD) of cuttings was $5{\cdot}2 \pm 0{\cdot}4$ g.

Two contrasting soil fertility treatments were established by filling the boxes with either 100% locally excavated Kalkaska series topsoil (Typic Haplorthod, high N treatment) or a homogenized mixture of 20% topsoil, 80% native Rubicon sand (Entic Haplorthod, low N treatment). Potential net N mineralization in the two treatments was calculated from the production of ammonium-N and nitrate-N over a 9-wk aerobic laboratory incubation at 25 °C. Net N mineralization was significantly higher ($P < 0{\cdot}001$) in the high-N treatment (348 μg N g^{-1} d^{-1}) than in the low-N treatment (45 μg N g^{-1} d^{-1}). These rates of N mineralization are typical of the range that occurs in Upper Great Lakes, USA, forest ecosystems (Zak & Pregitzer, 1990).

Total soil N was also determined at the beginning of the experiment. Mean soil N was 15·0 and 15·2 g kg^{-1} in the two high-fertility treatments (ambient and elevated CO_2, respectively) and 4·6 and 4·5 g kg^{-1} in the two low-fertility treatments. CO_2 had no effect on total soil N, but the fertility treatments differed greatly ($P < 0{\cdot}001$). Both soil fertility treatments were high in extractable inorganic phosphorus. Extractable PO_4^{-3}, assayed using an acid extraction procedure, was 110 mg kg^{-1} in the low-fertility treatment and 64 mg kg^{-1} in the high-fertility treatment.

Plants were kept well watered throughout the experiment. Three litres of water were added to each box every third day, except during periods of rainfall. To assess the possibility of confounding effects due to water stress, pre-day and midday xylem water potentials were measured on 27 August and 3 September using a Scholander pressure bomb. On these dates trees had received no water for three days (the longest possible interval) and the weather had been warm and sunny. There were no significant differences in water potential at either time among any of the treatments.

Open-top chambers (Curtis & Teeri, 1992) were used to manipulate atmospheric CO_2 around trees growing in the root boxes. Carbon dioxide treatments were crossed with fertility treatments in a factorial randomized block design with two CO_2 levels (ambient and elevated), two fertility levels (high and low N), and five replicate blocks. Carbon dioxide partial pressure inside elevated CO_2 chambers was increased by dispensing 100% CO_2 into an input blower; concentrations were controlled with manual flowmeters. The atmosphere inside the chambers was continuously monitored by an infrared gas analyzer that logged data to a personal computer. Mean seasonal daytime CO_2 partial pressures were $69{\cdot}3 (\pm 4{\cdot}5)$ Pa inside elevated chambers and $34{\cdot}5 (\pm 1{\cdot}5)$ Pa inside ambient chambers. Temperatures inside and outside chambers were monitored every 15 min using shaded thermocouples connected to an LI 1000 datalogger (LICOR Inc., Lincoln, NB). Daytime temperatures averaged 2·7 °C higher inside chambers than outside across the entire season, but there were no significant temperature differences among CO_2 or fertility treatments.

Aboveground growth was monitored throughout the growing season by serial censuses. Non-destructive estimates of leaf area were determined from measurements of leaf length (l) and width (w) and a predetermined regression equation: area = $-0{\cdot}377 + 0{\cdot}578$ (lw), $r^2 = 0{\cdot}99$. Statistical analysis of growth curves consisted of repeated measures analysis of variance, which analyzed coefficients for the mean, linear and quadratic variables of orthogonal polynomials for unequally spaced sample dates (Robson, 1959; Meredith & Stehman, 1991).

Fine root production and mortality were measured by inserting a microvideo camera system into the minirhizotrons and recording sequential images of the soil and fine roots in the numbered frames of both minirhizotrons. The two minirhizotrons buried in the rooting zone of each box were etched with a transect of 130 numbered, 1·17 cm^2 frames (see Hendrick & Pregitzer, 1992). Video images of roots within frames were digitized, categorized according to condition (e.g. new, live, dead), and compiled by length using a computer program we developed (Hendrick & Pregitzer, 1992; Pregitzer, Hendrick & Fogel, 1993). Wang *et al.* (1995) studied several different species and found that visual estimates of live vs. dead roots made with a camera and minirhizotrons like ours have a mean accuracy of 85% when compared to proportions of live vs. dead roots determined by staining roots with 2,3,5-triphenyltetrazolium (TTC). Visual determinations of physiological status (live vs. dead) may be further improved if individual roots are observed over time (Wang *et al.*, 1995), a procedure we routinely follow (Hendrick & Pregitzer, 1992, 1993*a*).

Root lengths were summed for both mini-

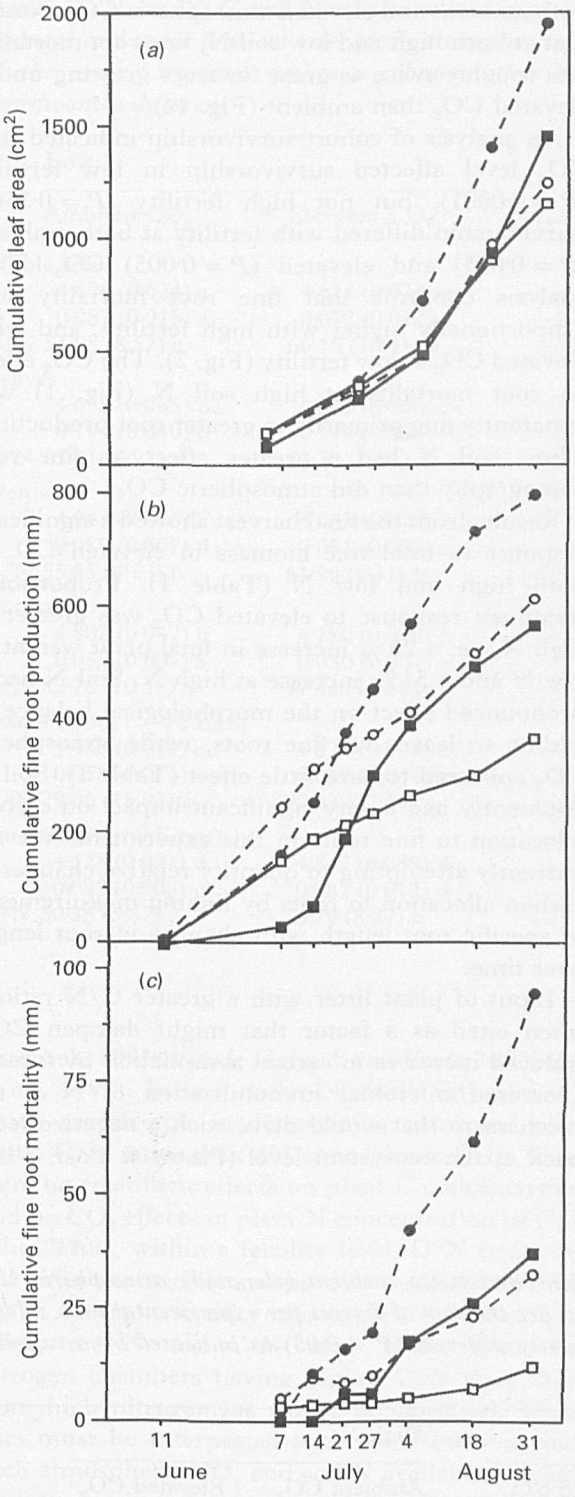

Figure 1. Cumulative leaf area, cumulative fine root production (length of roots < 0·5 mm diam.) and cumulative fine root mortality of *Populus* trees grown in ambient (squares) and twice ambient (circles) atmospheric CO_2 at low (open symbols) and high (closed symbols) soil N.

rhizotrons in a box and consisted of equal numbers of frames sampled, by block. Cumulative production included new and live roots at time t plus root mortality since time t-1. Statistical analyses of root production and mortality curves were similar to those for leaf area growth (Robson, 1959; Meredith & Stehman, 1991).

Cohort analysis (Hendrick & Pregitzer, 1993*a*) was used as another method of quantifying the influence of the four treatments on the survivorship of fine roots. The cohort of fine roots produced prior to 21 July was followed until harvest of the experiment to determine cumulative percentage survival as an indication of root turnover rate. Treatment effects were determined by pairwise comparisons of all four treatment combinations using a Gehan–Wilcoxon nonparametrics test appropriate for survivorship data in which not all individuals senesce during the experiment (Pyke & Thompson, 1986).

The experiment was terminated after 158 d growth on 16 October 1992, and all above- and belowground plant components were harvested. Total tree leaf area was measured using a LICOR LI-3000 leaf-area meter. The entire rooting volume was excavated by hand. Coarse roots were hand-sorted in the field. Fine roots were recovered by passing the entire volume of soil through a 2 mm screen in the field, freezing bulk soil, and hand-sorting fine roots in the laboratory. Above- and belowground tissues were dried at 70 °C, weighed, and ground for C and N analysis.

Tissue concentrations of C and N for the various plant parts were determined using a Carlo Erba CHN analyzer. Data were analyzed using split-plot analysis of variance, in which plant organs were treated as sub-units within experimental chambers (whole units) following transformation $2 \sin^{-1} (\sqrt{x})$ for proportional data. Tissue C/N values were analyzed similarly following cube-root transformation.

RESULTS

The CO_2 by fertility interaction effect was significant in leaf area mean ($P = 0{\cdot}036$). Both CO_2 and fertility effects were significant in the linear variable ($P = 0{\cdot}014$ and $< 0{\cdot}001$, respectively) and fertility was significant in the quadratic variable ($P < 0{\cdot}001$). Translation: leaves grew faster at elevated CO_2–high N and these trees displayed significantly more leaf area than the other treatments (Fig. 1*a*); the other treatments did not differ in cumulative leaf area.

For root length production (Fig. 1*b*), CO_2 treatment effects were significant in the mean variable, an indication that greater root length occurred at elevated CO_2 ($P = 0{\cdot}012$). Soil N effects were significant in the linear variable, an indication that the rate of fine root extension was greater at high N ($P = 0{\cdot}007$). Thus, high N resulted in a more rapid rate of fine root production (significantly steeper linear effect) at both ambient and elevated CO_2 (Fig.

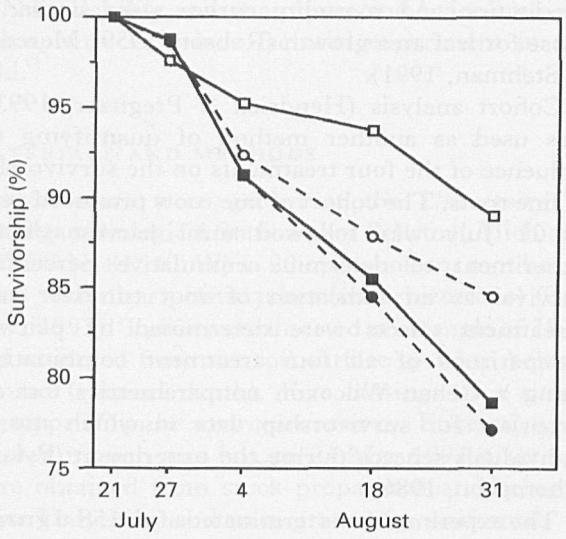

Figure 2. Survivorship of a cohort of fine roots (< 0·5 mm diam.), produced prior to 21 July, of *Populus* trees that were grown in ambient (squares) and twice ambient (circles) atmospheric CO_2 at low (open symbols) and high (closed symbols) soil N.

1*b*). This is why the form of the root length production functions in Fig. 1*b* appear to be controlled primarily by soil N availability.

Nitrogen effects on root mortality were significant in the mean ($P = 0{\cdot}011$) and linear ($P < 0{\cdot}001$) variables, and both CO_2 and fertility were significant in the quadratic variable, which indicates the rate of change in mortality ($P = 0{\cdot}046$ and 0·004, respectively). Thus, rates of fine root mortality were greater at elevated CO_2 for trees growing in both high and low soil N (significantly steeper linear effect, Fig. 1*c*). Rates of increase in fine root mortality (quadratic effect, Fig. 1*c*) were also greater at high N under both ambient and elevated atmospheric CO_2. Notice that at both high and low soil N, fine root mortality was roughly twice as great for trees growing under elevated CO_2 than ambient (Fig. 1*c*).

An analysis of cohort survivorship indicated that CO_2 level affected survivorship in low fertility ($P = 0{\cdot}0001$), but not high fertility ($P = 0{\cdot}356$). Survivorship differed with fertility at both ambient ($P = 0{\cdot}035$) and elevated ($P = 0{\cdot}005$) CO_2. This analysis confirms that fine root mortality was proportionally higher with high fertility, and with elevated CO_2 at low fertility (Fig. 2). The CO_2 effect on root mortality at high soil N (Fig. 1) was apparently due primarily to greater root production. Thus, soil N had a greater effect on fine root demography than did atmospheric CO_2.

Results from the final harvest showed a significant response in total tree biomass to elevated CO_2 at both high and low N (Table 1). Proportional treatment response to elevated CO_2 was greater at high N, i.e. a 26 % increase in final plant weight at low N and a 51 % increase at high N. Soil N had a pronounced effect on the morphological balance of carbon to leaves vs. fine roots, while atmospheric CO_2 appeared to have little effect (Table 1). Soil N apparently had a very significant impact on carbon allocation to fine roots in this experiment. We are currently attempting to quantify relative changes in carbon allocation to roots by linking measurements of specific root length with changes in root length over time.

Input of plant litter with a greater C/N ratio is often cited as a factor that might dampen CO_2-induced increases in carbon assimilation by forests. Increased microbial immobilization of N is the mechanism that would drive such a negative feedback at the ecosystem level (Pastor & Post, 1988;

Table 1. *Biomass (g) of* Populus *trees grown in ambient and twice ambient (elevated) atmospheric CO_2 concentrations and two levels of soil N availability. Values are the sum of 5 trees per experimental unit. Means (S) within a row followed by different letters are significantly different* (P < 0·05) *as indicated by a two-way analysis of variance*

	Low N		High N	
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
Total biomass	298·2 (43·1) c	374·4 (49·0) b	381·6 (28·8) b	562·8 (27·9) a
Leaves	48·1 (6·5) c	60·1 (8·7) b	65·4 (6·8) b	97·4 (5·3) a
Stems	52·7 (8·8) c	64·2 (10·5) b	69·8 (4·9) b	108·6 (7·1) a
Cuttings	26·7 (5·2) a	30·4 (4·6) a	30·5 (14·3) a	36·5 (4·3) a
Coarse roots (> 0·5 mm diam.)	150·1 (25·0) c	192·5 (23·5) b	199·9 (7·5) b	293·1 (19·7) a
Fine roots (< 0·5 mm diam.)	20·6 (4·5) b	27·2 (7·8) a	16·0 (2·8) b	27·2 (4·2) a
Total roots	170·7 (24·3) c	219·7 (27·4) b	215·9 (6·5) b	320·2 (20·5) a
Root/shoot	1·70 (0·13) a	1·78 (0·10) a	1·60 (0·13) b	1·56 (0·11) b
Coarse root/stem	2·86 (0·27) a	3·03 (0·29) a	2·88 (0·24) a	2·70 (0·19) a
Fine root/leaf	0·44 (0·12) a	0·45 (0·10) a	0·24 (0·03) b	0·28 (0·04) b

Table 2. *Mean (S) C and N concentrations (mg g^{-1}) and C/N ratio of* Populus *trees and tree organs grown in ambient and twice ambient (elevated) atmospheric CO_2 concentrations and two levels of N availability. Values of the same parameter within a column (other than 'whole tree') or row followed by different letters are significantly different*

	Low N			High N		
	Ambient CO_2	Elevated CO_2	%Δ	Ambient CO_2	Elevated CO_2	%Δ
Whole tree						
C	4·609 (0·024) a	4·634 (0·024) a	+0·5	4·596 (0·027) a	4·649 (0·023) a	+1·2
N	0·087 (0·015) a	0·072 (0·012) a	−17·2	0·151 (0·007) b	0·148 (0·006) b	−2·0
C/N	54·08 (8·57) a	66·19 (10·41) a	+22·4	30·52 (1·66) b	31·43 (1·33) b	+3·0
Leaves						
C	4·658 (0·065) bc	4·675 (0·039) bc	+0·4	4·694 (0·025) bc	4·760 (0·026) bc	+1·4
N	0·194 (0·040) b	0·144 (0·026) c	−25·9	0·321 (0·027) a	0·339 (0·023) a	+5·5
C/N	25·01 (5·93) d	33·38 (5·88) d	+33·5	14·68 (1·12) a	14·09 (0·95) a	−4·0
Stems						
C	4·942 (0·026) a	4·952 (0·009) a	+0·2	4·925 (0·021) a	4·951 (0·011) a	+0·5
N	0·089 (0·007) d	0·081 (0·008) d	−9·6	0·115 (0·005) b	0·121 (0·007) b	+5·2
C/N	55·85 (4·53) b	61·96 (6·11) b	+10·9	43·04 (2·02) c	41·18 (2·44) c	−4·3
Cuttings						
C	4·802 (0·047) b	4·780 (0·040) b	−0·5	4·798 (0·037) b	4·776 (0·033) b	−0·5
N	0·059 (0·007) a	0·050 (0·007) a	−15·2	0·100 (0·002) bc	0·099 (0·012) c	−1·6
C/N	82·76 (10·36) a	97·42 (13·86) a	+17·7	47·96 (1·37) b	49·12 (6·44) b	+2·4
Coarse roots (> 0·5 mm)						
C	4·483 (0·051) cd	4·524 (0·034) cd	+0·9	4·441 (0·067) cd	4·517 (0·041) cd	+1·7
N	0·058 (0·012) a	0·049 (0·014) a	−16·8	0·113 (0·008) bc	0·099 (0·008) c	−12·7
C/N	79·06 (15·03) a	97·03 (22·19) a	+22·7	39·46 (2·78) b	46·01 (3·36) b	+16·6
Fine roots (< 0·5 mm)						
C	4·428 (0·091) d	4·542 (0·089) d	+2·6	4·550 (0·084) d	4·459 (0·267) d	−2·0
N	0·089 (0·008) d	0·082 (0·013) d	−8·1	0·160 (0·007) e	0·145 (0·011) e	−9·0
C/N	50·36 (5·67) c	56·79 (8·27) c	+12·8	28·55 (1·42) d	30·78 (1·74) d	+7·8

Vitousek, 1991; van de Geijn & van Veen, 1993; Zak *et al.*, 1993). In our study, N availability played a much greater role in determining plant and plant organ C/N ratios than did atmospheric CO_2. There were no treatment effects on plant C concentration, and no CO_2 effects in plant N concentration or C/N ratio. Thus, within a fertility level, C/N ratios did not differ statistically among CO_2 treatments (Table 2). In contrast, fertility effects were significant for whole-tree N and C/N, with plants from low nitrogen chambers having higher C/N than those from high nitrogen, as would be expected. These data must be interpreted with some caution since both atmospheric CO_2 and soil N availability might alter the timing of dormancy, retranslocation of N, and tissue senescence (Curtis & Teeri, 1992). Whole-tree C/N ratios are probably the best indication of how tissue quality varies in this experiment, and Table 2 shows a negligible CO_2-induced increase in whole-tree C/N at either level of N. The prevailing assumption that C/N ratios of plant litter will increase under elevated atmospheric CO_2 did not hold in this experiment, particularly at high soil N. Soil N availability played the dominant role in regulating tissue quality. Ecosystem-level feedback links between the carbon and nitrogen cycles thus become a critical aspect of predicting how ecosystems will respond to elevated atmospheric CO_2, and ultimately, how much carbon they will store (Pastor & Post, 1988; van de Geijn & van Veen, 1993; Zak *et al.*, 1993).

DISCUSSION

Several important conclusions can be drawn from this experiment. First, elevated atmospheric CO_2 increased the rate of fine root growth and mortality at both low and high N availability. Inputs of carbon to soil from fine root turnover roughly doubled at both levels of N availability. A central question identified by Bazzaz (1990) was: do CO_2-enriched plants merely grow faster, or does the nature of the plant itself change? Our results clearly demonstrate that fine root growth rates increase and lifespans decrease due to elevated CO_2, with little change in litter quality, at both high and low N availability. The demography of these plant modules was fundamentally altered by a doubling of atmospheric CO_2, particularly at low N availability. In contrast, leaf growth was less responsive to elevated CO_2 at low N availability, both in this study and others (Norby *et al.*, 1992; Zak *et al.*, 1993).

A second conclusion is that estimates of carbon return to the soil made by destructively harvesting fine root biomass could be extremely misleading. One need only compare our fine root treatment responses in Table 1 with those in Figures 1*b* and 1*c* to imagine just how misleading static estimates of fine root biomass can be. For example, notice in Table 1 that there are no significant differences in the standing crop of fine roots between the low and high N treatments at elevated CO_2 (27·2 vs. 27·2 g biomass). However, Figures 1*b* and 1*c* clearly demonstrate that both fine root production and mortality differ among these treatments. The dynamic nature of fine root production and mortality is difficult, if not impossible, to accurately estimate from static measurements of plant biomass.

It is not surprising that there is debate in the literature about the effect of elevated CO_2 on root/shoot ratios (Stulen & den Hertog, 1993). In our experiment, root/shoot ratios would provide a very poor estimate of carbon returned to the soil via the death of fine roots. This is probably true for most perennial plants. Fine root turnover may account for some of the carbon that is missing from comparisons of rates of photosynthesis and estimates of net assimilation made by destructively harvesting plants.

A third conclusion is that soil N availability plays a major role in the allocation of carbon to fine roots, both in terms of new root growth and rates of root mortality. Soil N availability played a critical role in determining the form of the fine root production and mortality functions in Figure 1 and the ratios of fine root to leaf biomass in Table 1. In addition, fine roots died at a faster rate (i.e. exhibited a shorter lifespan) when soil N was more available, regardless of the partial pressure of atmospheric CO_2. Similar studies with a variety of tree species, studies of mature trees, and the quantification of mycorrhizal C inputs to soil are now necessary to determine how universal our results might be. Nonetheless, it is clear that soil N availability will play a key role in determining the flux of carbon to the soil from the death of fine roots as the partial pressure of CO_2 in the Earth's atmosphere increases. We speculate that this is particularly true in temperate deciduous forests based on our recent research (Hendrick & Pregitzer, 1992, 1993*a*, *b*; Pregitzer, Hendrick & Fogel, 1993). And finally, since the flux of carbon from fine roots and mycorrhizas to soil represents a significant transfer of plant carbon to the soil in a majority of the Earth's forests (Vogt, Grier & Vogt, 1986; Hendrick & Pregitzer, 1993*b*), it appears likely that elevated CO_2 will fuel greater microbial activity in the soil. As pointed out by others (Pastor & Post, 1988; Schimel, 1990; Vitousek, 1991; van de Geijn & van Veen, 1993; Zak *et al.*, 1993), this could have a fundamental, and as yet unresolved, effect on soil N availability and the cycling and storage of C in terrestrial ecosystems.

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