Mountains and Sevier Desert detachments) to high angle, may then be controlled by lateral variations in thermal and mechanical properties of a layered crust[10–16]. ☐

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Patterns of fine root mortality in two sugar maple forests

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MUCH of the carbon assimilated by plants is allocated to fine root production[1–5], and the amount of carbon and nutrients subsequently returned to the soil from fine root turnover equals or surpasses that returned through leaf litter in many forests[6–9]. Unfortunately, limitations in traditional methods of studying roots have prevented us from thoroughly understanding the dynamic nature of fine root mortality in most forests, and better measurements of fine root longevity are needed to quantify and model more accurately ecosystem carbon and nutrient budgets[8–11]. We used minirhizotrons[12,13] to follow the mortality of contemporaneous fine root cohorts in two sugar maple (*Acer saccharum* Marsh.) forests located 80 km apart (north–south) during 1989 and 1990. We report here that roots in the northern forest consistently lived the longest, principally owing to greater rates of mortality early in the life of roots at the southern site. Differences in site factors suggest that warmer soil temperatures seem to be associated with the more rapid death of roots at the southern site.

During the 1989 and 1990 growing seasons, we used a microvideo camera[12,13] to record monthly images of fine root cohorts growing along the exterior surfaces of 12 minirhizotrons (clear plastic tubes) located in each forest. Fine root cohorts were comprised of all living roots ≤1.5 mm in diameter (pooled across the 12 minirhizotrons[14]) that were produced during the intervals between sampling dates. We used a microcomputer software program (ROOTS[12,15]) to identify and measure the length of individual roots within contemporaneous cohorts at each site, and subsequently to follow their fate by repeatedly measuring the same roots at each sampling date.

Because there are no appreciable differences among the sites in soil organic matter content, exchangeable Ca, Mg, Al or K[16], N mineralization, growing season soil moisture content, canopy leaf area, litterfall mass or N[17,18], we hypothesized that fine root length would be lost at similar rates in both forests. Instead, we found large differences in fine root lifespans (Fig. 1). Analyses of survival distributions of contemporaneous cohorts showed that roots at the northern site consistently lived longer on average than roots born during the same periods at the southern site (Geham-Mantel[19] test, $\alpha = 0.05$). The only exceptions were in July (no site difference) and September (greater longevity at the southern site) of 1989. The longer lifespan of roots in the northern forest was due to significantly lower first-season mortality rates (Fig. 2). New roots were lost 64% faster at the southern forest (0.41 versus 0.25% per day at the northern forest, $P < 0.01$), but overwinter and second-year mortality rates were not significantly different ($P > 0.5$; 0.14 versus 0.12% per day at the northern forest).

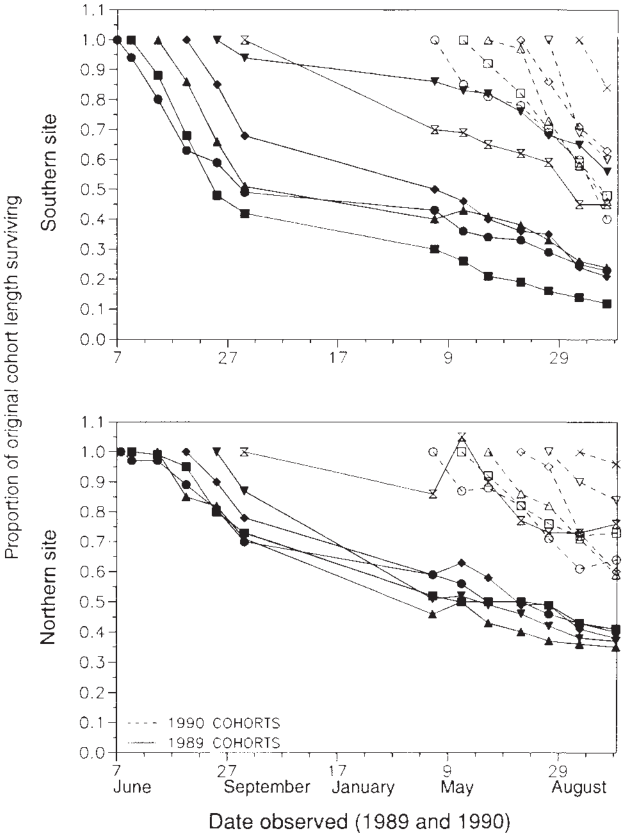

FIG. 1 Root length survival curves for root cohorts during 1989 and 1990. Survival times were significantly greater at the northern site for all but the July (no difference) and October (southern site greater) 1989 cohorts. Cohorts were comprised of all new roots present along a 1.8-cm-wide transect on the minirhizotron surface that were produced between successive sample dates in the upper 30 cm of the soil. The data were pooled from the 12 minirhizotrons in each forest. Cohort sizes ranged from 26 to 245 roots, with a mean and standard deviation of 87 and 50, respectively. Each root was identified and numbered by the ROOTS image analysis program we developed, and was remeasured and classified as live or dead at each sampling date. Significant differences in length survival were tested using a Gehan–Mantel test for the censored data[19] at an α of 0.05.

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The good fits of the first growing season mortality regressions (Fig. 2) were due to very similar patterns of mortality for all cohorts at each site (Fig. 1). These results were unexpected, because several studies have shown seasonal variation in forest ecosystem fine root biomass turnover[2,3,20–22], which is often believed to reflect variable root mortality rates. But the dynamics of root length and root biomass production and mortality are similar within both forests (R.L.H. and K.S.P., manuscript in preparation) and our results suggest that temporal differences in biomass 'turnover' may be due to temporal variation in root production, not in root mortality, in ecosystems like those we studied.

Low overwinter fine root mortality, relative to growing season mortality, might be due to low maintenance respiration rates under cold soil temperatures[23–25], but it is unclear why roots produced in the 1989 growing season should continue to die at a slower rate during the 1990 growing season. Survival of these roots may have been enhanced by greater lignification and/or suberization of cortical or epidermal cells, or perhaps they were located in resource-rich microsites. Low branch orders of roots can also live longer than higher order roots[26]. Our study was not designed to address these possibilities, but they deserve further investigation.

Both forests we studied are similar in structure, composition and site quality (Table 1 and refs 14–16). Thus, site differences in these factors cannot be invoked as obvious explanations[1,3,9] for the site differences in mortality rates and survival distributions. But it is possible that warmer soil temperatures contribute in part to greater fine root mortality rates in the southern forest (Table 1). Late-spring and summer soil temperatures at 15-cm depth were 2–4 °C warmer at the southern site in both 1989 and 1990 (Fig. 3), and soil temperatures were significantly warmer at the southern site from late April to mid-October during both years (paired t-test; $P<0.001$) by an average of about 1.5 °C. Soil temperature was not controlled in our study, and so the evidence linking temperature and root mortality is circumstantial. But previous studies have demonstrated increased root respiration rates and faster root turnover associated with higher soil temperature[23–25], and we believe that higher soil temperatures at the southern forest act in part to accelerate maintenance costs and mortality rates throughout the entire system of fine, absorbing roots. Soil organisms, which would be more active in the warmer soil, can also shorten root longevity[27].

TABLE 1 Stand, soil and climatic characteristics of the study sites

General stand characteristics	Southern forest	Northern forest
Latitude	43°40′	44°23′
Longitude	86°09′	85°50′
Above-ground biomass (Mg ha^{-1})	234	275
Overstory age (yr)	78 (3)	74 (6)
Basal area (m^2 ha^{-1})	30 (1.2)	30 (1.6)
Sugar maple basal area (%)	75 (8)	83 (3)
Canopy height (m)	24 (1)	28 (1)
Leaf area index (m^2 m^{-2})		
1989	7.9 (0.2)	7.1 (0.5)
1990	7.7 (0.2)	7.8 (0.3)
Mean annual air temperature (°C)	7.6	5.8
Mean annual precipitation (mm)	850	810
Mean spring-fall soil temperature (°C at 15 cm)		
26/4/89–17/10/89	14.2 (4.3)	12.9 (3.5)
30/4/90–16/10/90	14.6 (3.3)	12.9 (3.2)
Soil variables (A + E Horizons)		
pH (1:1 water)	4.66 (0.046)	4.66 (0.27)
Bulk density (g cm^{-3})	1.27 (0.07)	1.27 (0.04)
Nitrogen (kg ha^{-1})	1,408 (100)	1,125 (398)
N mineralization (mg kg^{-1} yr^{-1})	134.4	100.8
Phosphorus (kg ha^{-1})	156 (18)	191 (58)
Organic matter (Mg ha^{-1})	41.7 (3.3)	45.7 (13.6)

Values are averages across plots, with s.e.m. in parentheses where shown.

The relationship between soil temperature and root longevity needs to be more firmly established, and rates of fine root mortality may not be as predictable in other ecosystems as they are in the forests we studied. Nonetheless, our findings highlight the need for a better understanding of the processes controlling fine root inputs of carbon and nutrients to the soil. For example, below-ground resource allocation is driven by nitrogen or water availability[28,29] in many forest ecosystem models. In others,

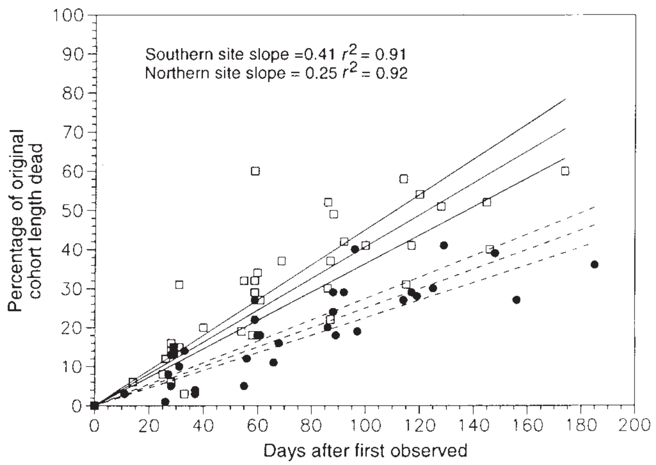

FIG. 2 Regressions of length mortality data against the number of days a cohort had been under observation during its first growing season, with the line forced through the origin. The slope (mortality rate) of the sourthern site was significantly greater than the northern site. There were no site differences in over-winter and second-year mortality rates (regressions not shown). Data were pooled across all 1989 and 1990 cohorts. Differences among the two forests were tested by comparing regression slopes at an α of 0.05. 95% confidence intervals shown.

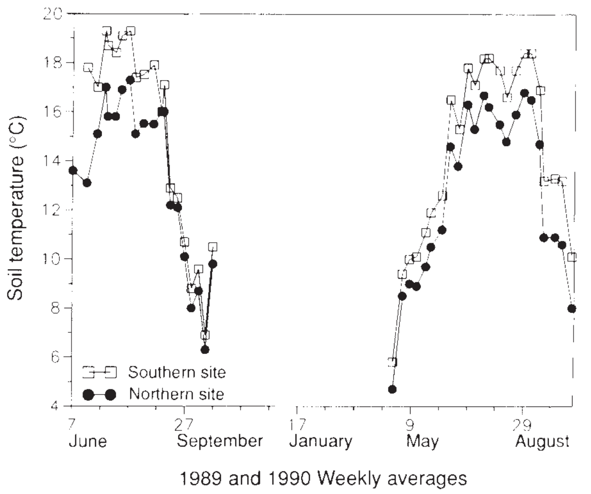

FIG. 3 Weekly averages of soil temperatures at 15-cm depth in both forests. Paired t-tests of site differences in weekly averages (derived from the mean of three temperature sensors in each forest) showed that temperatures from 26/4/89 to 17/10/89 and 30/4/90 to 16/10/90 were significantly higher in the southern forest ($P<0.001$). Data were collected every 30 min with an Omnidata monitoring system (Omnidata International, Logan, Utah, USA).

carbon and nutrient budgets allow for greater C costs through increased root respiration in warmer soils[10,29,30] associated with seasonal or climatic increases in temperature. But none of these models or any others that we are aware of make allowance for possible differences in root turnover rates within an ecosystem type, nor are root turnover rates intrinsically linked to soil temperature. We do not wish to imply that current models are flawed in their construction. Instead, they reflect how little is known of the demographic processes (such as root mortality) that control below-ground carbon and nutrient cycling, and the relationship between root demography and the soil environment. Given the importance of fine roots in terrestrial carbon and nutrient budgets[1-10], the need for more and better data on fine root dynamics is apparent. Even if soil temperature is generally found to have a minimal influence on root mortality, the fact that rates of fine root turnover can vary substantially among virtually identical ecosystems needs to be reconciled with current knowledge and models of below-ground processes that do not account for this phenomenon. ☐

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Increase in C3 plant water-use efficiency and biomass over Glacial to present CO_2 concentrations

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ATMOSPHERIC CO_2 concentration was 160 to 200 μmol mol^{-1} during the Last Glacial Maximum (LGM; about 18,000 years ago)[1], rose to about 275 μmol mol^{-1} 10,000 years ago[2,3], and has increased to about 350 μmol mol^{-1} since 1800 (ref. 4). Here we present data indicating that this increase in CO_2 has enhanced biospheric carbon fixation and altered species abundances by increasing the water-use efficiency of biomass production of C_3 plants, the bulk of the Earth's vegetation. We grew oats (*Avena sativa*), wild mustard (*Brassica kaber*) and wheat (*Triticum aestivum* cv. Seri M82 and Yaqui 54), all C3 annuals, and selected C4 grasses along daytime gradients of Glacial to present atmospheric CO_2 concentrations in a 38-m-long chamber. We calculated parameters related to leaf photosynthesis and water-use efficiency from stable carbon isotope ratios ($^{13}C/^{12}C$) of whole leaves. Leaf water-use efficiency and above-ground biomass/plant of C3 species increased linearly and nearly proportionally with increasing CO_2 concentrations. Direct effects of increasing CO_2 on plants must be considered when modelling the global carbon cycle and effects of climate change on vegetation.

The shoots of plants grown in the 38-m chamber were enclosed by a transparent cover through which air was moved in one direction. Photosynthesis by enclosed plants progressively depleted the CO_2 concentration ($[CO_2]$) and increased the $^{13}C/^{12}C$ of air (B.D.M. *et al.*, manuscript in preparation) as it moved the 38 m from the air intake to outlet of the chamber. The $\delta^{13}C$ values (see Fig. 1 legend) of leaves of C3 species and of concurrently grown C4 grasses, grassbur (*Cenchrus incertus*), crabgrass (*Digitaria ciliaris*) and Gaspé yellow flint maize (*Zea mays*), were linearly correlated with $[CO_2]$ (Fig. 1). The difference between the $\delta^{13}C$ of atmospheric CO_2 and leaf carbon of maize (and certain other C4 species) is conservative across environments[5] and did not vary significantly with $[CO_2]$ (B.D.M. *et al.*, manuscript in preparation), enabling us to use the $\delta^{13}C$ of C4 leaves as a proxy for the $\delta^{13}C$ of chamber air[6].

Leaf intercellular $[CO_2]$ (c_i), calculated from leaf $\delta^{13}C$ values, increased linearly and nearly proportionally (by the same ratio) with higher ambient $[CO_2]$ (c_a) in each C3 species. As a result, intercellular $[CO_2]$ was a constant but different fraction of c_a in oats ($c_i/c_a = 0.70$) and mustard ($c_i/c_a = 0.65$) grown at mean $[CO_2]$ from 330 to 160 μmol mol^{-1} (Fig. 2). The c_i/c_a of wheat cultivars increased only slightly from 0.63 and 0.66 at 225 μmol mol^{-1} to 0.66 and 0.69 at 350 μmol mol^{-1} for Yaqui 54 and Seri M82, respectively. A similar result has been reported[7] in young wheat plants exposed to CO_2 partial pressures between 120 and 500 μbar. Others have demonstrated that coordination of stomatal and mesophyll functions minimizes variation in c_i/c_a to similar values in C3 species[8], but this is the first demonstration of such for C3 plants grown over a $[CO_2]$ range characteristic of Last Glacial Maximum (LGM)-to-present atmospheric concentrations. Intrinsic water-use efficiency, defined as the ratio of leaf photosynthesis or net assimilation (A) to stomatal conductance to water vapour (g), increased by the same (oats and mustard) or nearly the same (wheat) relative amount as did $[CO_2]$, a consequence of conservative c_i/c_a in these C3 species (Fig. 3).

Leaf assimilation should have increased substantially at the higher c_i that accompanied increasing $[CO_2]$, unless photosynthetic capacity (the relationship of A to c_i) declined. The positive linear relationship of A to c_i at subambient $[CO_2]$ that is typical of C3 species did not differ between oat plants grown at extremes of the $[CO_2]$ gradient[9]. We estimate from that relationship that with a constant c_i/c_a of 0.70, net assimilation of oat leaves would have increased ~40% with the 75 μmol mol^{-1} rise in $[CO_2]$ since 1800. That the increase in leaf c_i was correlated with greater plant carbon gain is evidenced by the positive linear relationships between c_i and aboveground biomass per plant of all C3s studied (Fig. 4).

Climate[10], and particularly site water balance[11], largely control the structure and productivity of vegetation. This control is determined in part by plant water-use efficiency (WUE), biomass produced per unit transpiration. Our results imply that WUE of C3 plants may have increased by 27% over the past 200 years