Effects of altered water regimes on forest root systems

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SUMMARY

How ecosystems adapt to climate changes depends in part on how individual trees allocate resources to their components. A review of research using tree seedlings provides some support for the hypothesis that some tree species respond to exposure to drought with increases in root:shoot ratios but little change in total root biomass. Limited research on mature trees over moderately long time periods (2–10 yr), has given mixed results with some studies also providing evidence for increases in root:shoot ratios. The Throughfall Displacement Experiment (TDE) was designed to simulate both an increase and a decrease of 33% in water inputs to a mature deciduous forest over a number of years. Belowground research on TDE was designed to examine four hypothesized responses to long-term decreases in water availability; (1) increases in fine-root biomass, (2) increases in fine root:foliage ratio, (3) altered rates of fine-root turnover (FRT), and (4) depth of rooting. Minirhizotron root elongation data from 1994 to 1998 were examined to evaluate the first three hypotheses. Differences across treatments in net fine-root production (using minirhizotron root elongation observations as indices of biomass production) were small and not significant. Periods of lower root production in the dry treatment were compensated for by higher growth during favorable periods. Although not statistically significant, both the highest production (20 to 60% higher) and mortality (18 to 34% higher) rates were found in the wet treatment, resulting in the highest index of FRT. After 5 yr, a clear picture of stand fine-root-system response to drought exposure has yet to emerge in this forest ecosystem. Our results provide little support for either an increase in net fine-root production or a shift towards an increasing root:shoot ratio with long-term drought exposure. One possible explanation for higher FRT rates in the wet treatment could be a positive relationship between FRT and nitrogen and other nutrient availability, as treatments have apparently resulted in increased immobilization of nutrients in the forest floor litter under drier conditions. Such hypotheses point to the continued need to study the interactions of water stress, nutrient availability and carbon-fixation efficiency in future long-term studies.

Key words: global climate, drought, root growth, fine-root turnover (FRT), root mortality, upland oaks, carbon allocation.

INTRODUCTION

The Intergovernmental Panel on Climate Change (IPCC) concluded that climate has changed over the past century and is expected to continue to change (Houghton *et al.*, 1996). Increases in the levels of greenhouse gases in the atmosphere are predicted to cause an additional 1.0–3.5°C increase in average global surface temperatures by the year 2100 (Kattenberg *et al.*, 1996). These temperature increases should modify global hydrologic budgets, leading to increased winter precipitation at high latitudes, with more hot days and fewer cold days (Rind *et al.*, 1990; Kattenberg *et al.*, 1996). The response of forests to decreased water availability is considered to be a key issue in climate change scenarios (Wigley *et al.*, 1984). Concerns regarding effects on vegetation have been amplified because rates of change are expected to occur more rapidly than past successional processes and species dispersal rates (Solomon, 1986; Pastor & Post, 1988; Davis, 1989; Overpeck *et al.*, 1991).

The ability of ecosystems – and individual components thereof – to survive and adapt to changes in climate will depend in part on how individual trees

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Table 1. *Summary of seedling irrigation studies with respect to the effects of absence of irrigation (vs irrigation) on increases in root biomass, root:shoot ratio and rooting depth*

Study	Species	Root biomass	Root:shoot	Root depth
Torreano & Morris (1998)	*Pinus taeda*	ns	ns	Yes
Osunubi & Davies (1981)	*Quercus robur*	Yes	–	YES
	Betula pendula	ns	ns	ns
Bongarten & Teskey (1987)	*Pinus taeda*	ns	YES	–
Tomlinson & Anderson (1998)	*Quercus rubra*	ns	YES	–
Pallardy & Rhoads (1993)	*Juglans nigra*	ns	YES	–
	Quercus stellata	ns		–
	Quercus alba	ns		–
	Acer saccharum	ns		–

ns, no significant difference; Yes, trend showing increase; YES, statistically significant increase; –, no data available.

allocate resources to their various plant components. Aboveground forest productivity will certainly depend in part on the allocation of carbon (C) belowground. The way in which plants balance resources between photosynthetic organs, supporting stems and branches, reproductive organs and root systems is a complex process that plant physiologists have long been struggling to understand. It has been well documented that tree species adapted to dry climatic regimes generally have higher root:shoot ratios (R:S) and deeper root systems than species that are more suited to mesic climatic regimes (van Buijtenen *et al.*, 1976; Caldwell & Richards, 1986; Bongarten & Teskey, 1987; Pallardy & Rhoads, 1993). Kozlowski *et al.* (1991) list 10 references that document the successful avoidance of water stress by some deep-rooted tree species able to use subsurface sources of water.

Such evidence has probably contributed to the general concept that trees frequently respond to dry conditions by altering R:S ratios and by increasing rooting depth (Kozlowski *et al.*, 1991). Several hypotheses have arisen from this general concept concerning the effects of long-term decreases in water availability: (1) increases in fine-root biomass, root length density and gross and net root elongation; (2) increases in R:S, especially the fine-root biomass:foliar biomass ratio; (3) altered rates of FRT; (4) increased depth of rooting and/or density of fine roots at greater depths.

The first objective of this manuscript is to review evidence in the literature that pertains to these hypotheses with regard to tree species. The second objective is to present results from one long-term study that pertains to hypotheses 1–3.

What scientific evidence exists that indicates that exposure to increasingly dry moisture regimes results in trees allocating a higher percentage of their resources to their root systems? At least one gradient study indicates that, within a single tree species, the ratio of fine-root biomass:aboveground biomass is considerably greater under xeric conditions than under mesic conditions (Comeau & Kimmins, 1989). Another such gradient study, however, found no significant difference in living fine-root biomass across three sites exhibiting a natural gradient of soil water availability (Santantonio & Hermann, 1985). In fact, in this study, living fine-root biomass was lowest at the driest site, whereas FRT rates were highest at this site.

It is quite well established that tree root elongation declines as soil water potential decreases across the range -0.3 to -1.2 MPa and that it virtually ceases close to or before the latter point (Larson, 1980; Teskey & Hinckley, 1981; Kuhns *et al.*, 1985; Torreano & Morris, 1998; J. D. Joslin *et al.*, unpublished). But what impact does exposure to water stress have on fine-root growth in portions of the rooting zone that are less dry or during subsequent periods when soil is rewetted? Several studies indicate that, when trees experience moisture stress in one part of the rooting zone, root growth increases in areas where water is still available, usually at greater depths (Dickman *et al.*, 1996; Hendrick & Pregitzer, 1996; Torreano & Morris, 1998; Table 1). Osunubi & Davies (1981) found this to be the case for seedlings of a deep-rooted tree species (English oak, *Quercus robur*), but not for a shallow-rooted species (silver birch, *Betula pendula*).

In irrigation studies, prior exposure to water stress has yielded various plant responses. In Bongarten & Teskey (1987), loblolly pine (*Pinus taeda*) seedlings previously exposed to drought developed higher R:S ratios than nonexposed seedlings (Table 1). Tomlinson & Anderson (1998) found that, in northern red oak (*Quercus rubra*) seedlings subjected to moderate water stress, the sink strength of the belowground plant parts increased. By contrast, Pallardy & Rhoads (1993) reported that prior exposure to drought had no effect on the subsequent root growth of seedlings of four different tree species. Similarly, Torreano & Morris (1998) found reduced root growth and no change in R:S ratios in loblolly pine seedlings receiving the lowest level of irrigation.

Gower *et al.* (1992) found that the percentage of net primary productivity (NPP) allocated belowground over a 2-yr period was significantly higher in nonirrigated Douglas-fir (*Pseudotsuga menziesii*)

Table 2. *Summary of long-term, stand-level irrigation studies with respect to the effects of absence of irrigation (vs irrigation) on increases in root biomass, root:shoot ratio and rooting depth*

Study (duration of study)	Dominant species	Root biomass	Root:shoot	Root depth
DeVisser *et al.* (1994) (3–4 yr)	*Picea abies*	Yes	Yes	–
	Pseudotsuga menziesii	Yes	ns	–
	Picea abies	Yes	Yes	–
Bredemeier *et al.* (1998) (3 yr)	*Picea abies*	ns	ns	–
Devakumar *et al.* (1999) (10 yr)	*Hevea brasiliensis*	ns	YES	NO
Gower *et al.* (1992) (2 yr)	*Pseudotsuga menziesii*	YES	YES	–
Dickman *et al.* (1996) (4 yr)	*Populus deltoides* (hybrid)	ns	–	YES

ns, no significant difference; Yes, trend showing increase; YES, statistically significant increase; NO, statistically significant decrease; –, no data available.

stands than in irrigated stands (Table 2). Similarly, R:S ratios were more than two-fold higher in a nonirrigated rubber tree (*Hevea brasiliensis*) plantation than in an irrigated one, after 10 yr of dry season irrigation (Devakumar *et al.*, 1999). Further support for R:S shifts comes from long-term irrigation studies on coniferous forests as part of the EXMAN (Experimental manipulation of forest ecoytems) project in Europe (Devisser *et al.*, 1994). In three of these studies, irrigation treatments over 3–4 yr diminished net root production relative to nonirrigated treatments, while irrigation increased aboveground biomass production. By contrast, Bredemeier *et al.* (1998) observed no effect of prior artificial exposure to drought on subsequent Norway spruce (*Picea abies*) stand root production.

For predictions of the long-term response of forests to climate changes, all of the studies mentioned are limited when extrapolating results to mature deciduous forests. Gradient studies are subject to confounding by genetic differences in the trees growing at the various sites, as well as other uncontrolled site differences. The extrapolation of results from short-term studies on seedlings under artificial conditions to long-term effects on 'natural', mature forests, obviously requires considerable caution. Even stand-irrigation results are often based on relatively short-term responses.

Our confidence in predicting forest responses to climate change are greatly limited by the lack of long-term ecosystem-level studies. Practical limitations are obvious barriers to such research. Such studies as, the EXMAN Project, where inputs of water and nutrients were controlled in five stands for 3 or 4 yr (Beier & Rasmussen, 1993; Devisser *et al.*, 1994), the long-term irrigation research of Devakumar *et al.* (1999) on rubber tree plantations and the research of Gower *et al.* (1992), have begun to shed light on the effects of varying the supply of water on forest growth responses, above and below-ground (Table 2). Even in the context of global climate change, the 2–4-yr length of the Gower *et al.* (1992) and Devisser *et al.* (1994) studies might be considered relatively short-term!

These long-term studies were conducted on conifer forests of the western USA or on tropical evergreen species. Root-growth strategies for coniferous tree species are often quite distinct from those for deciduous angiosperms tree species (Bauhs & Messier, 1999). The oak–hickory and northern hardwood forests of the north temperate zone have been identified as sensitive plant communities that are likely to show early responses to climate change. The upland oak-dominated forest found on the Walker Branch Watershed (Oak Ridge, TN, USA) is a good example of one of these critical and commercially valuable vegetation zones. The Through-fall Displacement Experiment (TDE) on this watershed has the specific goals of looking at the long-term effects of both decreasing and increasing water inputs to the forest floor on a mature deciduous forest in the warm temperate zone. This 1.92-ha field manipulation experiment is examining both aboveground and belowground changes, looking not only at alterations in tree growth, mortality and C allocation, but also at the morphological and physiological mechanisms behind such changes.

Belowground research as part of the TDE is focused on the four hypotheses mentioned previously, by comparing fine-root responses across the three treatments. To date, data from minirhizotrons, root coring, soil pits and root ingrowth cores have been collected over a 5-yr period. Net changes in absolute values for fine-root biomass, root length density, root:shoot ratios and root distribution will not be available until repeated coring and excavation are carried out after the fifth year. However, in the meantime, 5 yr of minirhizotron observations on

root elongation across the treatments are being used as indicators of the treatment effects on fine-root production, ratios of fine-root production:foliar production and FRT rates. This paper presents results from this extensive period of minirhizotron data collection and relate them to three of the four hypotheses introduced earlier – alterations in (1) root production, both gross and net, (2) root:shoot ratios and (3) rates of FRT. Evidence pertaining to hypothesis 4 (changes in rooting depth) is currently lacking. The results presented will be restricted to root elongation occurring in the area of greatest treatment effect (as evidenced by the monitoring of soil water potential) and of greatest rooting density, that is the upper 30 cm of the soil profile on the upper slope of the experimental plots. Greater root response variability in minirhizotron observations, coupled with smaller treatment differences in both soil water potentials and fine-root responses at lower depths, make the results from the upper 30 cm the most interesting.

MATERIALS AND METHODS

Study site

All the belowground research reported here was conducted as part of the TDE, which is located on the Walker Branch Watershed in Oak Ridge, Tennessee, USA. At the beginning of the study, the overstory of the site was dominated by chestnut oak (*Quercus prinus* L.), white oak (*Quercus alba* L.), black gum (*Nyssa sylvatica* Marsh.) and red maple (*Acer rubrum* L.) (Table 3). The understory was dominated by red maple, dogwood (*Cornus florida* L.) and black gum with 29, 19 and 14% of sapling basal area, respectively. Initial stand basal area averaged 21 m² ha⁻¹, with each treatment plot nearly identical. Mean leaf area index averaged 6.3 m² m⁻² over the first 4 yr of the study. The study site lies on a southeast-facing slope with uniform residual soils that are cherty, infertile and permeable. The soils are classified as Typic Paleudults by the US system of soil classification. Soil water content at field capacity

ranges from 22% to 36%, depending on horizon. At 'wilting point' (-1.5 MPa), soil water contents varied between 8–12% (Hanson *et al.*, 1995, 1998). Mean annual precipitation is 1358 mm and mean temperature is 14.1 °C. Soil temperature at 10-cm depth regularly fluctuates from an average low of 1 °C in January to a high of 26 °C in July–August; lows during the growing season occur in early April and average 9 °C. Further details on the TDE site, climate, soils and vegetation are available in Hanson *et al.* (1995, 1998).

The TDE experimental system is designed to maintain multi-year changes in soil water potential similar to those which might occur as a result of global climate change. Treatments simulate both a 33% increase (wet treatment) and a 33% decrease (dry treatment) in water inputs, relative to control (ambient treatment). The reduction of throughfall by 33% was used because the soil water reductions expected would be similar to that experienced during a 1980's drought in the southeastern USA (Cook *et al.*, 1988), that resulted in increased mortality of tree saplings and reduced growth of vegetation (Jones *et al.*, 1993). These treatments were generated by passively collecting and diverting 33% of throughfall from the dry plot to the wet plot through a system of trough-like collectors and pipes. The wet, dry and ambient treatments each encompass an area of 0.64 ha (80×80 m). No statistically significant differences in soil temperature were observed among treatments. Additional details on daily climate and the experimental design and performance of the TDE system are available in Hanson *et al.* (1995, 1998).

Minirhizotrons

Minirhizotron tubes (30) were installed in the TDE site between February and March 1994. In each of the three TDE treatment plots, 10 tubes were installed, five along the upper slope (at approx. 340 m elevation) and five along the lower slope (at approx. 330 m elevation). The tubes were installed pointing upslope at a 45° angle to the slope to a vertical depth of 90 cm; however, because of the

Table 3. *Overstory composition: total basal area by species and treatment plot for trees > 0.1 m diameter at breast height at the beginning of the study* (*March 1994*) (*adapted from Hanson* et al., *1998*)

| | Total basal area by treatment plot (m² ha⁻¹) (% of total) | | | |
Species	Wet	Ambient	Dry	Entire area
Quercus prinus	5.6 (26%)	3.3 (16%)	7.7 (36%)	5.5 (26%)
Quercus alba	6.5 (30%)	4.9 (24%)	1.9 (9%)	4.4 (21%)
Nyssa sylvatica	1.9 (9%)	3.8 (19%)	2.9 (14%)	2.9 (14%)
Acer rubrum	2.4 (11%)	2.3 (11%)	2.5 (12%)	2.4 (11%)
Quercus spp.	2.1 (10%)	1.4 (7%)	1.7 (8%)	1.8 (9%)
Liriodendron tulipifera	1.3 (6%)	1.4 (7%)	2.3 (11%)	1.6 (8%)
Other species	1.7 (8%)	2.9 (14%)	2.2 (11%)	2.3 (11%)
Total	21.6	20.1	21.2	21.0

high rock content, the maximum depth achieved for most tubes was between 60 and 90 cm. The minirhizotron tubes (5.7 cm in diameter and 130 cm long) were etched with a single set of 130 equally spaced grids (Hendrick & Pregitzer, 1992). Only data from the upper 30 cm of the soil profiles on the upper slope tubes are presented in this paper.

Video imaging of roots, using a Circon color agricultural camera (Circon Inc., Santa Barbara, CA, USA), was conducted during the growing seasons 1994–98. In each year, imaging began in April before bud break and continued biweekly throughout October, with all root activity on the etched face of the tube recorded along with depth information. With the exception of 1995, 13–15 observation periods were recorded each year. Video images were digitized using PC based MSU-ROOTS software (Michigan State University Instructional Media Center; Enslin *et al.*, 1994) to measure root length production and to track the changes in the condition of fine roots over the duration of the study. All roots were categorized as new since the last sampling date, previously existing and still alive, dead, or missing. If a root became 'missing' before being categorized as dead, and did not reappear at a future photographic session, it was considered dead from the time of disappearance.

Fine-root production and mortality measurements were made as described by Hendrick & Pregitzer (1993). Such minirhizotron measurements of fine-root elongation and mortality do not provide direct measurements of total fine-root-biomass production or mortality; however, they do serve as excellent indices of such production and mortality across treatments. Root production (elongation) for a given time interval was considered to be the length of new roots in each set of five minirhizotrons per plot, present on a given sample date, that were not present on the previous sample date. Further details on minirhizotron installation and data collection can be found in Joslin & Wolfe (1998, 1999).

Fine-root turnover

Fine-root turnover refers to the process by which roots are produced, die and decompose. It has been defined as the ratio of annual fine-root production to either the maximum or minimum belowground standing crop of fine roots (Dahlman & Kucera, 1965; Gill & Jackson, 2000). Although this ratio provides an index of the rate at which new roots are being produced to replace those which are dying, we prefer a definition that acknowledges that the rate of turnover is really the average rate for all three processes involved – production, mortality and decomposition (Joslin & Henderson, 1982, 1987; Santantonio & Hermann, 1985). While it is commonly assumed that ecosystems are near equilibrium with regard to the rates of these three processes, so

that there is no net long-term change in the biomass of roots over time, this is clearly not the case in some ecosystems, particularly aggrading ones, or for certain time intervals. Hence, while the ratio of one of these processes, such as root production, to the standing crop is sometimes used as an index of turnover rate, the ideal measure would be one that employs the average of all three rates. Here we use the sum of root elongation (an index of production) and of root mortality as an index of turnover rate, since we have no data for this site on root decomposition rate, and since the initial standing fine-root biomass did not differ significantly across treatment plots or slope position (Joslin & Wolfe, 1999). It should be noted that because minirhizotron elongation and mortality measurements cannot be accurately converted into root biomass production estimates (e.g. in units of kg ha^{-1} yr^{-1}), these measurements cannot provide absolute turnover figures. Instead these measures are used as an index of FRT, for comparison purposes across treatments.

Soil water measurements

Soil water content was measured across the entire study area using an 8×8-m grid system of time domain reflectometers (TDR; Soil Moisture Equipment Corp., Santa Barbara, CA, USA: Hanson *et al.*, 1998). Soil-water measurements were conducted biweekly during the growing season and monthly during the dormant season, beginning in August 1992. Raw volumetric soil-water-content data from TDR measurements were corrected for mean coarse fraction of soil at a given location (Hanson *et al.*, 1998). Soil-water-content measurements were converted to soil water potential using soil water retention curves developed from representative samples from the A, AE and EB horizons. Curves were developed from gravimetric measurements of soil water content and psychrometric measures of soil water potential. Thermocouple psychrometers (SC-10, Decagon Devices, Inc., Pullman, Washington, DC, USA) were calibrated with a graded series of NaCl solutions before each use and these soil temperature readings were used in the conversion of TDR measurements into soil-water-potential values. Soil-water-potential conversions using the retention curve for the AE horizon were used for the 0–35 cm depth interval, as this horizon occupied 75% of the upper 35 cm of the profile and was considered most representative of this depth interval.

Foliar production and phenology

Fallen leaves and other aboveground litter (i.e. twigs, seeds, etc.) were collected from 49 baskets (0.53×0.38 m $= 0.20$ m^{-2}) per treatment, located near the central 49 (7 rows $\times$ 7 columns) grid
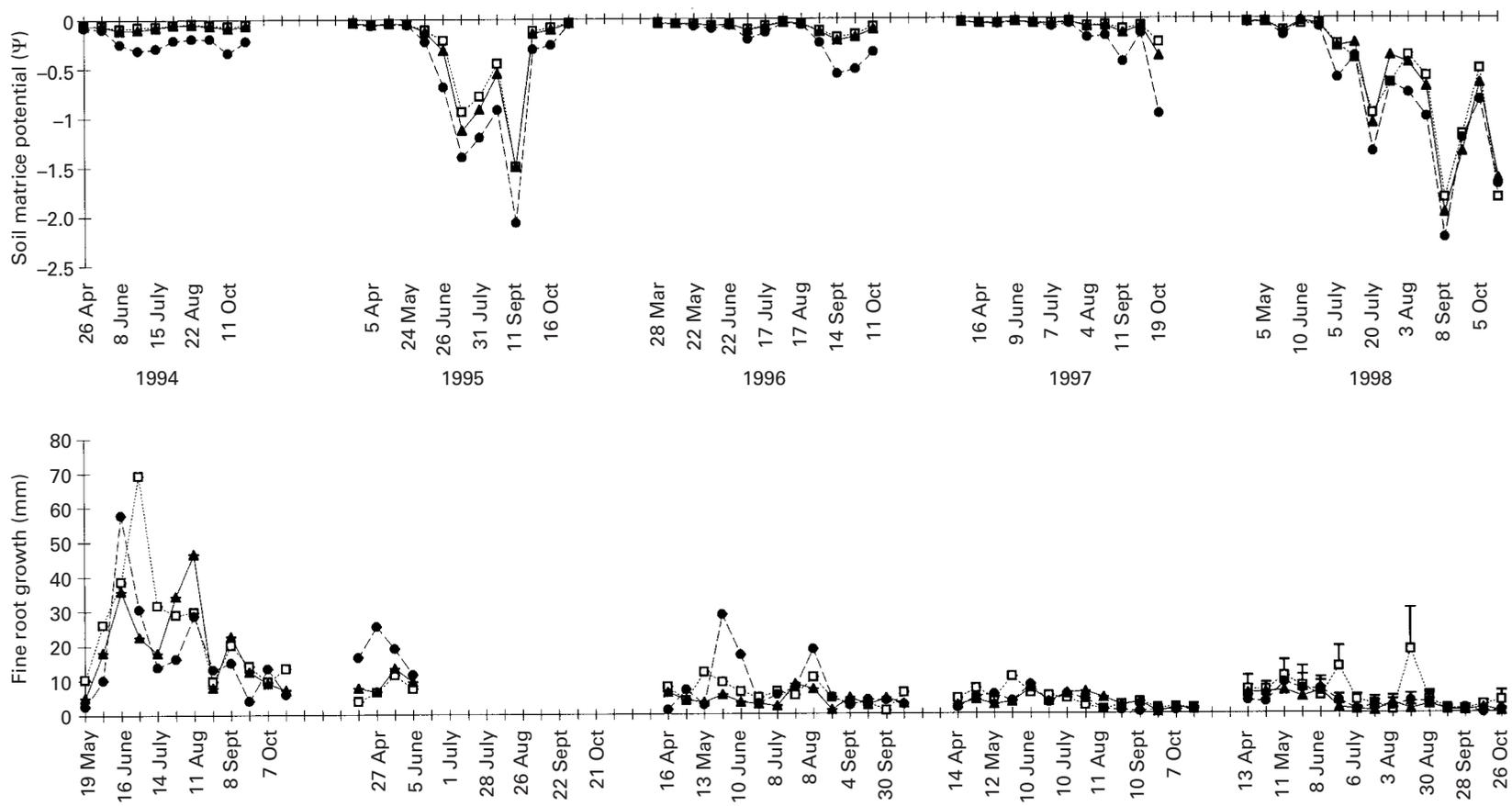
Fig. 1. Periodic root elongation intensity (mean net elongation per tube per 14-d interval) observed at minirhizotron faces in the upper 30 cm of the soil profiles on the upper slope position over the five growing seasons by treatment, juxtaposed with soil matric water potential for the upper 35 cm of the upper slope by treatment for the corresponding period. Standard errors of the mean are given for 1998 root elongation as an illustration of variability in the biweekly data. Treatments: open squares, wet (33% increase in water input relative to control); closed triangles, ambient (control); closed circles, dry (33% decrease in water input relative to control).

intersections of each of the three treatment blocks of the TDE. Litter collections were made periodically throughout each of the 5 yr (typically mid-May, late-Aug, and biweekly during the period 1 Oct–1 Dec of each year). Litter samples were oven-dried at 70°C, sorted into foliar and nonfoliar components and the total mass determined. Litter production was then converted to a ground area (g m^{-2}) basis.

Statistical analyses and data presentation

For the purposes of data presentation and statistical analysis, the primary experimental unit used was the summed response for each individual minirhizotron tube, across the appropriate depth and time interval. Since this study focuses on the upper 30 cm of the soil profiles on the upper slope, summed data from each of these tubes on root production, root mortality and net root production were analyzed. Thus, whether annual or 5-yr comparisons between treatments are being presented, they are based on summed data from five minirhizotron tubes per treatment. Statistical comparisons are restricted to annual and 5-yr treatment differences. Minirhizotron data were collected almost entirely during the growing season (Apr–Oct) as already mentioned. During the summer of 1996, video equipment failure occurred in late June which resulted in a 'data gap' for the remainder of that growing season; consequently no data are available from this period. As most of this period of missing data corresponded with the most severe drought of the research period (Fig. 1) and our data indicate minimal root growth occurring below –0.6 MPa water potential, we believe that very little root growth occurred in any of the treatments during the majority of this period. Mortality certainly occurred during this time, but we obviously have no data to report. The 5-yr totals for fine-root production and mortality do not include data from this period nor from any winter period. Checks for the occurrence of winter period root elongation, from January and March 1998 minirhizotron measurements, revealed that this winter period accounted for <5% of the annual total.

Data collected during the first year (1994), immediately following minirhizotron installation, strongly suggest that excessive root proliferation occurred during this year as a result of root pruning effects and soil disturbance impacts on nutrient availability (Fig. 1). This effect and its probable causes have been thoroughly described in Joslin & Wolfe (1999). Whereas the magnitude of minirhizotron measures of root growth appears to have been amplified during this period, there is no evidence for any treatment-related biases. The data from this first year appear to correctly reflect, across the three treatments, the phenology of fine-root production and mortality, as well as the relative quantity of organic matter involved in these pro-

cesses. Hence raw data from this first year are presented and analyzed along with data from the subsequent 4 yr.

Statistical tests for the main effects of treatment on an annual basis were conducted for each year using analysis of estimated coefficients based on response curves (Gurevitch & Chester, 1986; Meredith & Stehman, 1991). Polynomial response functions were fitted to 13 repeated measures of each experimental unit using orthogonal contrasts. The estimated coefficients of these functions were then treated as primary data and analyzed using univariate ANOVA, with the GLM procedure of SAS (SAS Institute, 1989). Statistical tests for differences between treatments for the entire 5-yr period were conducted using univariate ANOVA on summed data across the appropriate tubes within a treatment and the appropriate depth interval. ANCOVA was applied to annual stand foliar production values, using the 1993 data as the covariate. Main effects of year and treatment were evaluated with significance determined from *P*-values <0.10.

RESULTS

Patterns of fine-root production and mortality over five years

Fig. 1 juxtaposes fluctuations in soil water potential and fine-root elongation at biweekly intervals across the 5 yr of minirhizotron observation. As already discussed in the Materials and Methods section and in Joslin & Wolfe (1999), the magnitude of all responses during the first year (1994) are amplified across all three treatments. One trend that is apparent in several growing seasons (predominantly 1994, 1996 and 1998) is that early summer growth tends to last longer in the wet treatment than the ambient or dry, and that mid-summer growth spurts are more likely in the wet treatment. Whereas differences in soil water potential are small between treatments, soil drying generally occurs sooner and is more severe in the dry and ambient treatments. Previous studies with white oak indicate that root elongation rate begins to decline markedly at soil water potentials between −0.4 and −0.8 MPa and virtually ceases at *c*. −1.2 MPa (Larson & Whitmore, 1970; Teskey & Hinckley, 1981; Kuhns *et al.*, 1985). Our results with this mix of upland hardwood species generally agree with this conclusion (Fig. 1; J. D. Joslin *et al.*, unpublished). It is noteworthy that root elongation rate differences among treatments often begin to occur as soil water potentials reach −0.5 MPa in the dry treatment before the other treatments. Also few differences occur among treatments in late August, September or October, as a lull in root growth in these upland hardwood species seems to occur at this time of year regardless of moisture conditions (Teskey & Hinckley, 1981;
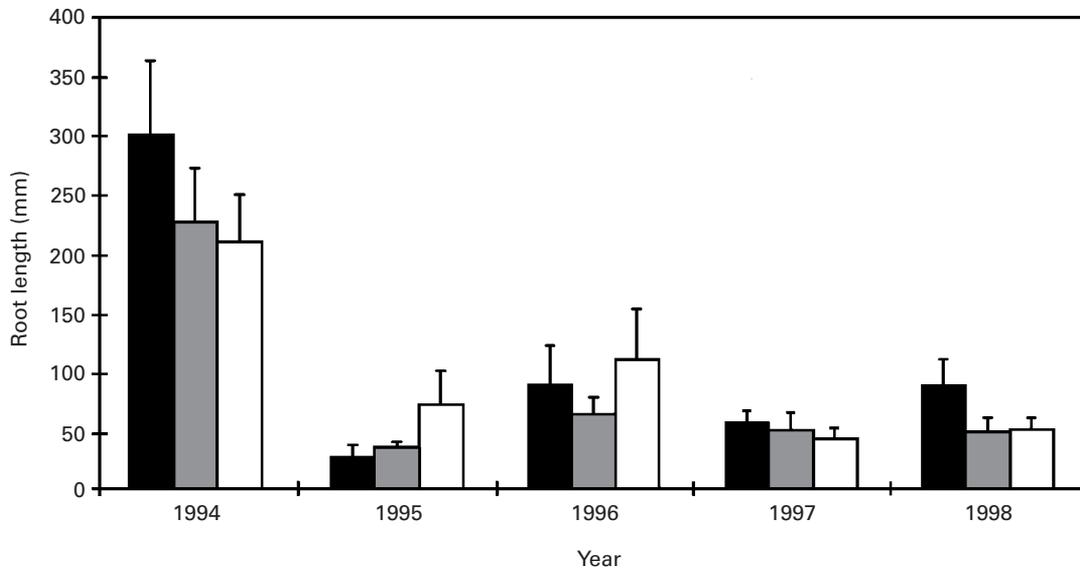
Fig. 2. Mean annual gross root growth (elongation) by treatment for each of the 5 yr (1994–98). Gross growth = mean of sums of new root elongation measurements over a particular growing season for all five minirhizotron tubes within a treatment. Error bars indicate SE of the mean. Treatment differences were not significantly different in any year. Treatments: closed columns, wet (33% increase in water input relative to control); grey columns, ambient (control); open columns, dry (33% decrease in water input relative to control).
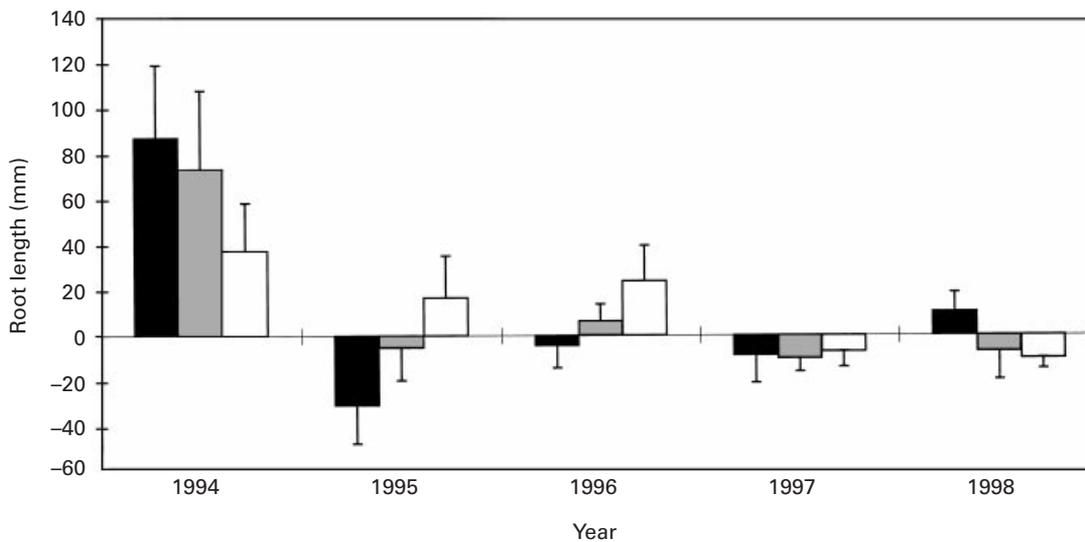

Fig. 3. Mean annual net root growth (elongation) by treatment for each of the 5 yr (1994–98). Net growth = gross growth minus mortality. Error bars indicate SE of the mean. Treatment differences were significant ($P < 0.1$) only during 1 yr, 1996. Treatments: closed columns, wet (33% increase in water input relative to control); grey columns, ambient (control); open columns, dry (33% decrease in water input relative to control).

McClaugherty *et al.*, 1982; Kuhns *et al.*, 1985; Joslin & Henderson, 1987; Hendrick & Pregitzer, 1996).

Gross and net root production for the entire 5-yr period are depicted in Figs 2 and 3. This depiction highlights how fine-root growth (both gross and net) in trees in the dry treatment, after their root growth was reduced relative to the other treatments during the first growing season (1994), subsequently exceeded that in the other two treatments during the following 2 yr. The higher level of gross fine-root production in the dry compared with the other two treatments was marginally significant ($P < 0.10$) only during 1996 (Joslin & Wolfe, 1998). In the fourth and fifth years, gross production was comparable across all treatments. As noted previously, the 1998 pattern was similar to 1994, with the dry treatment lagging behind the other two as an apparent result of an earlier mid-season drought in the dry treatment. The wet treatment August peak in 1998 appears to be the result of an outlier, though determination of outliers is difficult with a highly
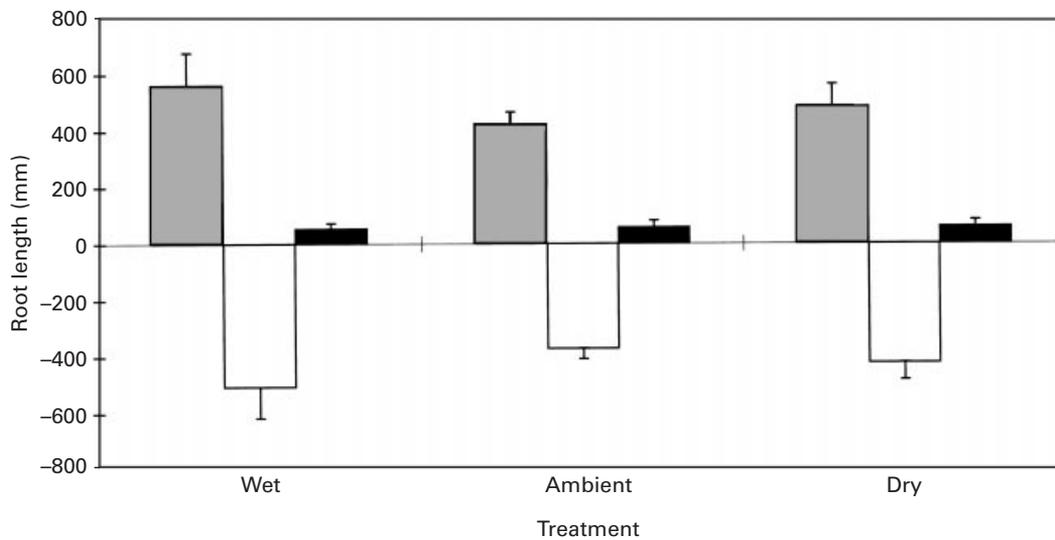
Fig. 4. Summation of 5 yr of gross root growth (grey columns), root mortality (open columns) and net root growth (closed columns) by treatment. Each value represents the mean of summed root length data for five minirhizotron tubes. Error bars indicate SE of the mean. No treatment differences are statistically significant.
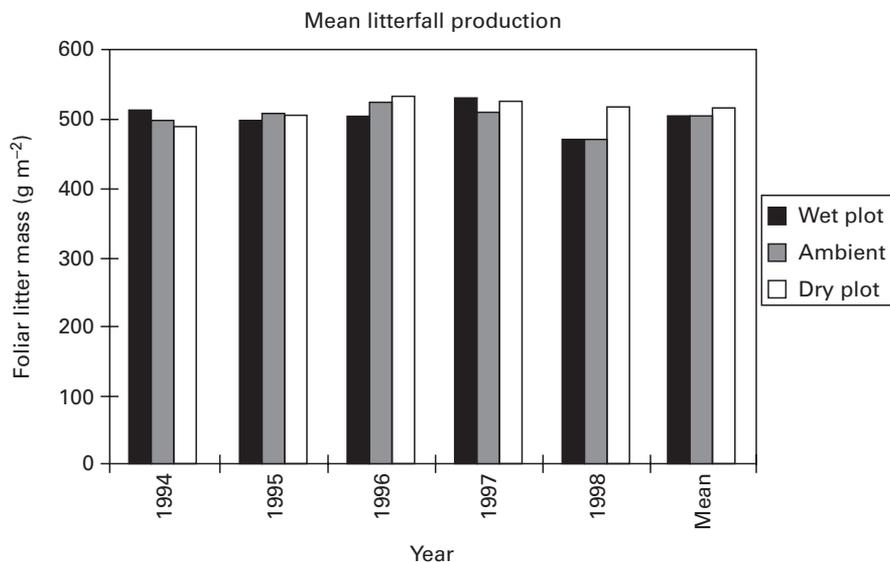
Fig. 5. Annual stand litterfall production (covariate adjusted means) by year and treatment, using the 1993 data as the covariate. ANCOVA for treatment main effects revealed no statistically significant treatment effects for any year, nor any differences between years.

spatially and temporally variable parameter such as root growth, and with our relatively small number of minirhizotron tubes. Despite periods of drought during 1995 and 1998, fine-root production was apparently able to compensate with sufficient growth during more favorable periods.

Five-year totals of fine-root production, mortality and turnover

Fig. 4 depicts the summation, across all 5 yr, of gross fine-root production, fine-root mortality and net fine-root production (the difference between the first two values). Whereas differences are small in gross

root production, the highest rate was found in the wet treatment, closely followed by the dry treatment. Although treatment differences were not significant, the highest mortality was also found in the wet treatment; in fact, mortality was 20% and 60% higher in the wet treatment than in the dry and ambient treatments, respectively. This combination of higher mortality and higher production rates in the wet treatment resulted in comparable amounts of net root production across the three treatments. Mortality in all treatments occurred at a relatively steady rate throughout each growing season, with no apparent relationship to soil water potential or soil temperature.

Using the average of root production and root mortality as an index of root turnover (as described in the Materials and Methods section) the combination of higher root production and higher mortality in the wet treatment resulted in indices of FRT that were 18% and 34% higher than in the dry and ambient treatments, respectively (Table 4). Treatment differences again were not statistically significant. The high rate of FRT in the wet treatment coincides with the fact that this treatment also had the highest rate of leaf litter decomposition (Todd & Hanson, 1999).

Foliar production and fine root : foliage ratio

Annual stand-level foliar biomass production (as indexed by litterfall) has not been significantly affected by either the throughfall treatments during any of the 5 yr or by interannual differences in weather. Annual production of aboveground litterfall at the stand level (Fig. 5) has been nearly constant at approx. 500 g m^{-2} yr^{-1}. Whereas the annual increment of coarse root, bole and tree branch production (i.e. woody increment) has not been significantly affected by the TDE treatments to date, statistically significant (P <0.05) inter-annual differences in wood production have been observed (Hanson *et al.*, 1998; P. J. Hanson & D. E. Todd, pers. comm.). Because there have been no statistically significant effects of the water regime treatments on either foliar biomass (Fig. 5) or on the long-term net increment in fine-root biomass (as indexed by net root elongation measures in minirhizotrons; Fig. 4), we cannot conclude from these data that there has been any significant treatment effect on fine root : foliage ratio over this 5-yr period.

DISCUSSION

One of the most interesting findings from these observation of root elongation over 5 yr, is the apparent resilience of this forest ecosystem in ostensibly maintaining a relatively constant fine root mass over the long-term (i.e. net root length production is not significantly different from zero for any treatment), despite seeming short-term declines during certain periods, particularly in the dry treatment. This resilience, most evident in the dry treatment, is dependent on the ability of the stand to respond opportunistically with spurts of root growth during periods of high soil moisture and moderate temperature. The results of our research indicate that, in this ecosystem, the major pulse of root elongation is apparently genetically programmed to occur in late spring and early summer, a pattern similar to that in many deciduous forests in much of the temperate zone (Joslin, 1983; Hendrick & Pregitzer, 1996; J. D. Joslin *et al.*, unpublished). At the same time, they also seem to indicate that root growth can be increased, in an apparent compensatory response, following periods of net reduction in fine-root biomass.

After 5 yr, these results do not give a clear picture of root system response to drought exposure in this forest ecosystem. Net fine-root growth was significantly higher (P <0.10) during 1996 in the dry treatment, a response that could be interpreted as a whole-stand adaptation to the reduced water inputs and higher water stress experienced during the previous 2 yr (Joslin & Wolfe, 1998). Conversely, this response could be interpreted as simply an 'equilibration response', with the dry stand restoring its previous level of fine-root biomass.

The absence of either higher net fine-root production or higher R:S ratios in the dry treatment compared with other treatments is not consistent with some of the literature (Tables 1, 2). As noted previously, several studies on seedlings (Osunubi & Davies, 1981, English oak; Bongarten & Teskey, 1987; Tomlinson & Anderson, 1998) support the concept of a shift towards increased fine-root growth with increasing drought exposure. Similarly, at least three long-term irrigation studies on plantations or forests provide support for root responses of a similar nature and/or a shift in R:S ratio (Gower *et al.*, 1992; Devisser *et al.*, 1994; Devakumar *et al.*, 1999). The results of Devakumar *et al.* (1999), showing a decrease in R:S ratio with irrigation, are particularly convincing evidence for the particular species studied, since the study was conducted over a 10-yr period. However, the results of certain experiments with contrasting results indicate, perhaps, that such a response may be highly species-specific (Osunubi & Davies, 1981; Pallardy & Rhoads, 1993).

In our study, the possibility that root systems are tapping supplies of water deep in the soil profile during dry periods has not been eliminated. Although a very high bulk density (bulk density = approx. 1.75 g cm^{-3}) argillic horizon appears to restrict root growth to the upper 90 cm, there remains the possibility that some roots have penetrated this barrier. The lack of strong or highly significant responses to the water treatments might, in part, be a result of reduced treatment effects caused by this phenomenon. This question is currently being investigated. A second reason for the lack of statistically significant results is the relatively high variability in growth rates observed between minirhizotrons, coupled with the relatively low number of tubes (n = 5) per treatment, and slope position. Such reductions in statistical power are largely the result of the high labor requirements of measuring root growth and the natural variability in root distribution and responses; two factors that have consistently plagued root research since its inception. The Devisser *et al.* (1994) study closely examined fine-root biomass responses at three of five

Table 4. *Indices of fine-root turnover (FRT) by treatment for the entire five-year period*

	Treatment		
	Wet	Ambient	Dry
FRT index	1070 (221)	796 (75)	908 (136)

FRT index equals mean values, for all five minirhizotron tubes within a treatment, for summed root elongation plus summed root mortality. SE of the mean in parentheses. Treatment differences are not statistically significant.

sites. Whereas more available water resulted in lower fine-root biomass relative to the drier treatment (control), the differences were rather small and not statistically significant. Positive aboveground responses to irrigation in their study, however, resulted in a decrease in R:S ratio with increasing water availability. Our results, however, lend little support, at least at this site across this range of water stress, to the hypothesis of a shift towards an increase in the fine-root biomass:foliar biomass ratio with increasing drought exposure.

The results of our study indicate a higher index of FRT in the wet treatment than in the ambient and dry treatments (Table 4). Again treatment differences were not statistically different. The wet treatment had the highest gross fine-root production over 5 yr of treatment; it also had the highest fine-root mortality rate. In a review on root turnover, Gill & Jackson (2000) found that globally there was a positive correlation between mean annual precipitation and FRT ($r = +0.57$), but that the relationship was not statistically significant. By contrast, Ewel & Gholz (1991) predicted no change in FRT with decreasing moisture availability in slash pine (*Pinus elliottii*) stands. Similarly, Santantonio & Hermann (1985) and Pregitzer *et al*. (1993) found greater average fine-root longevity (i.e. lower turnover rates) under moist conditions than under dry conditions.

These conflicting results can perhaps be explained by the different experimental designs and conditions. The Santantonio & Hermann (1985) experiment deals with a water availability gradient across three Douglas-fir-dominated stands. Genetic differences in the Douglas-fir stock are certain to have occurred at these three separate sites where tree species have had millenia to adapt genetically to site conditions. Such a genetically evolved difference in tree root-growth pattern is clearly different from a short-term adaptive response of an existing stand to a changing water regime. The Pregitzer *et al*. (1993) study, by contrast, examined the rate of FRT in isolated irrigated microsites within a stand over a relatively short time period. In such a study, root longevity in a small part of a root system exposed to portions of the soil environment with unique characteristics, is

likely to be quite different from the response of an entire root system to changes introduced uniformly across the stand and its soil profile over a long time span.

Fine-root mortality, across 5 yr of our study showed no seasonal pattern during the 6-month growing season, remaining fairly constant throughout the period. These results are consistent with those reported in Edwards & Norby (1999), even though artificial temperature manipulations did increase mortality rates across temperature treatments in that study. Such lack of seasonality in mortality is somewhat paradoxical since there is support for shorter root life spans in trees as soil temperatures increase (Hendrick & Pregitzer, 1993; Pregitzer *et al*., 1997, 2000). Gill & Jackson (2000) also noted that one might expect higher root mortality rates during periods of high soil temperatures since root respiration rates, nutrient mineralization rates, and pathogen and herbivore levels all increase with soil temperature. Although our results do not support such a seasonal pattern, the frequent occurrence of reductions of soil moisture during the periods of highest soil temperature are likely to introduce a confounding variable. Our results also do not support an increase in root mortality during leaf senescence in this upland oak forest, in contrast to other studies on northern hardwood forests (McClaugherty *et al*., 1982; Hendrick & Pregitzer, 1992, 1996).

Perhaps greater insight into possible causes of higher rates of root turnover in our wet treatment can be gained from studies that demonstrate that root turnover rates are positively related to the availability of nitrogen (N) in an ecosystem. The throughfall treatments in our study are having a statistically significant impact on the accumulation of foliar litter on the forest floor, such that litter layers are thickest on the dry site and thinnest on the wet site (Todd & Hanson, 1999). This is clearly a result of a positive relationship between wetness of the forest floor and litter decomposition rate. An unexpected result of this litter accumulation is increased immobilization of N and other nutrients in the thicker forest floor layers on the drier sites, probably resulting in its reduced availability for root uptake. Evidence of lower nutrient availability in soil solution nutrient concentrations on the dry site compared with the wet site has recently appeared (D. W. Johnson, pers. comm.). Although this hypothesis is speculative at this point, Eissenstat *et al*. (2000) note that increasing N concentrations in fine roots reduce longevity, which he attributes, in part, to increasing respiration costs with higher N levels, as reported by both Reich *et al*. (1998) and Pregitzer *et al*. (1998). Nadelhoffer *et al*. (1985) and Nadelhoffer (2000) have also found that root turnover rates are positively correlated with soil N availability across a number of studies. Eissenstat *et al*. (2000) further

propose that the benefits accrued from maintaining roots with short life spans are reduced when nutrients are in short supply.

High rates of FRT should result in greater volumes of soil being explored, or at least the same volumes being 're-explored' with higher frequency, and sites of high nutrient availability being 'tapped'. Whereas such exploration would appear to come at a greater cost to trees in terms of C utilization for the construction of new roots, the trees on the wetter site also have greater annual rates of C fixation and so can perhaps 'afford' the C expenditure. These hypotheses point to the continued need to study the interactions of water stress, nutrient availability and C fixation efficiency in future studies.

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