

# The relationship between fine root demography and the soil environment in northern hardwood forests<sup>1</sup>

Ronald L. HENDRICK<sup>2</sup> & Kurt S. PREGITZER<sup>3</sup>, Department of Forestry, Michigan State University, East Lansing, Michigan 48824, U.S.A., e-mail: rhendric@uga.cc.uga.edu

**Abstract:** We used minirhizotrons to measure growing-season fine root dynamics at 0-30 and 50-100 cm depths in two northern hardwoods forests. Concomitant measurements of several soil and site environmental variables were also made. We then used regression models to quantify the relationships between these environmental variables and fine root demography. Generally, environmental factors had a moderate effect on broad, inherent phenological patterns of root activity and abundance. For example, both shallow fine root length density and potential evapotranspiration reached their maximum in mid-summer, but the relationship between the two was not strong at either site ( $R^2 = 0.12$ ). Deep root length density was not significantly related to any measured environmental factor. Periods of high water demand during which soil moisture was also abundant (*i.e.*, late spring and early summer) were related to increased shallow root production. Root length mortality was low at these times, but the correlation with soil moisture was statistically significant only in the shallow depth increment. Quantifying the relative importance of the environment on root growth in large field studies like ours is complicated by a number of factors. These include the difficulty of intensive sampling, interactive effects of environmental factors, and the uncertainty of encountering environmental conditions sufficiently severe to elicit a measurable root response during the study period.

**Keywords:** fine root length, production, mortality, soil temperature, moisture, water balance.

**Résumé:** Nous avons utilisé des minirhizotrons pour évaluer la dynamique des racines pendant la saison de croissance, à des profondeurs de 0 à 30 et de 50 à 100 cm. Plusieurs variables écologiques en ce qui a trait au sol et au site ont aussi été mesurées en concomitance. Nous avons ensuite utilisé des modèles de régression pour quantifier les relations unissant ces variables écologiques à la démographie des racines. En règle générale, les facteurs écologiques n'ont eu qu'un effet modéré sur les patrons de base du développement phénologique des racines, tant au chapitre de l'activité racinaire que de l'abondance des racines. Par exemple, la densité des racines superficielles ainsi que l'évapotranspiration potentielle ont atteint un maximum au milieu de l'été, mais la relation entre les deux variables demeure faible dans tous les sites ( $R^2 = 0,12$ ). En profondeur, la densité des racines n'est reliée de manière significative à aucun des paramètres de l'environnement que nous avons mesurés. Les périodes de demande accrue en eau, pendant lesquelles l'humidité du sol est élevée (c'est-à-dire à la fin du printemps et au début de l'été) sont associées à une production accrue de racines superficielles. La mortalité des racines est faible pendant ces périodes, mais la corrélation avec l'humidité du sol n'est statistiquement significative que dans la portion superficielle du sol. Dans les études d'envergure effectuées sur le terrain, de nombreux facteurs viennent ainsi compliquer les efforts de quantification de l'importance relative de l'environnement dans la croissance des racines. Ces facteurs réfèrent notamment à la difficulté d'effectuer un échantillonnage intensif, aux effets réciproques des facteurs écologiques et à l'incertitude quant aux possibilités de rencontrer des conditions suffisamment difficiles pour susciter une réaction des racines qui puisse être mesurée pendant la durée d'une étude.

**Mots-clés:** longueur, production, mortalité des racines, température du sol, humidité, bilan hydrique.

## Introduction

Soil temperature and moisture control both the timing and duration of root growth in forests. The onset of growth typically coincides with soil warming in the spring, while the over-winter cessation or reduction of root growth is associated with soil cooling (Kuhns *et al.*, 1985; Lyr & Hoffmann, 1967; Rogers, 1939; Teskey & Hinckley, 1981). Minimum cardinal root growth temperatures have been identified for a number of tree species, and range from 1 to more than 7°C (Kuhns *et al.*, 1985; Lyr & Hoffmann, 1967; Rogers, 1939; Teskey & Hinckley, 1981; Webb, 1976). Higher temperatures are often positively correlated with root growth (Bevington & Castle, 1985; Deans, 1979; Teskey & Hinckley, 1981). Lethal soil temperatures are rarely reached in forests and maximum cardinal tempera-

tures often exceed those occurring naturally (Lyr & Hoffmann, 1967). Indeed, there is good evidence to suggest that growing-season soil temperatures seldom limit root growth in forests.

Instead, periods of moisture deficit or abundance are often associated with root quiescence or growth, respectively. For example, root length growth in both white oak (*Quercus alba* L.) and black walnut (*Juglans nigra* L.) declined during summer and autumnal droughts, and increased after rain (Teskey & Hinckley, 1981; Kuhns *et al.*, 1985). Root growth in apple (Rogers, 1939) and Scots pine (*Pinus sylvestris* L., Bartsch, 1987) is also inhibited in dry soils. In a dry range ecosystem, root numbers increased in response to precipitation, and declined during intervening dry periods (Hansson, Aifen & Andren, 1994). Sitka spruce (*Picea sitchensis* L.) roots respond similarly to drought, and die progressively from the surface downward as the soil dries (Deans, 1979). There are few other direct reports of the effects of soil moisture on fine root mortality.

<sup>1</sup>Rec. 1996-01-23; acc. 1996-08-26.

<sup>2</sup>Author to whom correspondence should be addressed. Present address: D.B. Warnell School of Forest Resources, University of Georgia, Athens, Georgia 30602, U.S.A.

<sup>3</sup>Present address: School of Forestry and Wood Products, Michigan Technological University, Houghton, Michigan 49931, U.S.A.

There is a close relationship between root abundance and plant water balance in many forests (Nambiar, Bowen & Sands, 1979; Teskey & Hinckley, 1981). Therefore, it seems probable that root growth or mortality might also respond to high plant water demand, or to changes in soil water stored within the rooting profile. However, the effects of changes in ecosystem-level variables like precipitation (PPT), potential evapotranspiration (PET) and soil water content on fine root dynamics are seldom studied. This is unfortunate, because attempts to understand and model root system responses to environmental changes at large spatial scales (*i.e.*, the landscape or biome level) will necessarily have to rely on relatively coarse-grained measurements (like PET) instead of data collected with soil temperature or moisture sensors.

We have previously described the dynamics of the fine root system of two northern hardwoods forests (Hendrick & Pregitzer, 1992; 1993a,b; 1996). We suggested that higher turnover rates at the most southern of our two sites might be partially related to higher soil temperatures (Hendrick & Pregitzer, 1993a). However, we have not addressed those effects that the soil environment might have on the total amount of either root mortality or production. Our long-term goal has been to build predictive models of fine root dynamics as affected by the environment. Here we attempt to relate fine root length density, production and mortality during the growing season to changes in soil temperature and moisture and site water balance variables.

### Material and methods

The study sites are second-growth northern hardwoods forests located in Michigan's lower peninsula and are separated by a north-south distance of 80 km. We will refer to the study areas as the northern and southern sites throughout the paper. The woody vegetation is dominated in the overstory, understory and seedling layers by sugar maple (*Acer saccharum* Marsh.). Associated species include red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), American beech (*Fagus grandifolia* Ehrh.) and black cherry (*Prunus serotina* Ehrh.). At the time we collected the data reported here (1989-1990), the mean age of the overstory trees at the southern site was 78 ( $\pm 5$ ) years and 74 ( $\pm 11$ ) at the northern site. The herbaceous community is sparse and covers less than 3% of ground area at its seasonal peak in the spring. There is essentially no shrub community at either site. The soils are spodosols at both sites. Further site descriptions can be found in Hendrick & Pregitzer (1993b).

In June 1988, we installed 4 clear polybutyrate minirhizotrons (5 cm inside diameter  $\times$  2 m in length) at a 45° angle to the soil surface in each of three 30 m  $\times$  30 m replicate plots at each site. The minirhizotrons were inscribed with a series of numbered sampling frames along their length so that we could return to the same location and roots repeatedly (Hendrick & Pregitzer, 1992; 1993a,b). These frames were oriented upward during installation. We imaged each minirhizotron monthly during the growing season in 1989 and 1990. We imaged the southern site on 4/25, 6/7, 6/21, 7/18, 8/16, 9/16 and 10/14 in 1989 and on 4/25, 5/24, 6/18, 7/21, 8/18, 9/18 and 10/16 in 1990. The corresponding sampling dates at the northern site were 4/27,

6/11, 6/22, 7/18, 8/18, 9/16 and 10/14 in 1989 and 4/24, 5/23, 6/19, 7/22, 8/19, 9/18 and 10/16 in 1990.

We used an interactive PC-based image analysis system (MSU-ROOTS, Michigan State University, East Lansing, MI) to identify, measure and follow the fate of individual roots present in the minirhizotron images throughout the study period. (Further details of the image analysis process can be found in Hendrick & Pregitzer, 1992; 1993b). These data were then used to calculate mean daily root length density production (RLP) and mortality (RLM) for the periods between observation intervals. The units for both RLP and RLM are mm root length per cm<sup>2</sup> minirhizotron surface per day (mm cm<sup>-2</sup> day<sup>-1</sup>). These data were then used to calculate mean daily RLP and RLM for the calendar months May through September, which correspond to the period between canopy expansion and senescence at both sites. We also calculated root length density (RLD) in mm cm<sup>-2</sup> at each observation date. All roots that we observed were less than 2.0 mm in diameter. Greater than 99% were less than 1.0 mm and approximately 85% were less than 0.50 mm.

On each replicate plot, we installed soil temperature sensors (thermistors, Omnidata International, Ltd., Logan, Utah) at a depth of 15 cm, and moisture sensors at 15 and 75 cm (1 each per depth). Soil moisture data were converted from resistance (ohms) to matric potential from laboratory calibrations of resistance *versus* gravimetric moisture and from standard curves of gravimetric moisture and matric potential determined from pressure plate analyses. Field measurements were made every 30 minutes and averages were logged every three hours. We used daily means to calculate the monthly data reported here. The Thornthwaite equation (Thornthwaite & Mather, 1957) and our own measurements of soil water holding capacity were used to calculate monthly site water balance variables (to a depth of 1 m) at both sites. Those variables are PPT, PET, actual evapotranspiration (AET), available water (AW), water deficit (WD) and excess soil water (EW, more typically defined as leaching loss), all in cm mo<sup>-1</sup>. We use the term excess water instead of leaching loss because 1) we did not measure leaching loss *per se*, and 2) most of the soil water moving below 1 m is unlikely to be lost from the ecosystem because of deeper tree roots (Hendrick & Pregitzer, unpubl. data) and the depth to the water table (> 10 m). Monthly precipitation and temperature data came from the nearest NOAA stations at each site (< 20 km).

We used multiple linear regression to develop predictive models of root dynamics in response to changes in soil temperature, moisture and site water balance. Using a step-wise regression procedure, soil and site variables (mean monthly temperature and matric potential, and total monthly PPT, PET, AET, AW, WD and EW) were entered into the model if they were significant at an alpha of 0.15 or less. These variables were subsequently retained or removed in an iterative fashion as their significance changed as when other variables were added. Final, full models were considered meaningful and are reported here only if their significance level was 0.10 or less. We recognize the potential for collinearity in some of our site water balance variables because of computational and functional interdependence. This interrelatedness can complicate the calculation of regression coefficients and the identification of predictor

variables (Rawlings, 1988), and we have interpreted our results (below) accordingly. However, among the three primary variables that control site water balance, two (PPT and PET) are weakly and inversely correlated ( $r = -0.24$ ), and the third (soil water holding capacity) is unaffected by and unrelated to the other two.

We used RLD, RLP and RLM data from two depth increments (0-30 cm and 50-100 cm), designated as shallow and deep, in the regression models. We chose these two increments because we knew that they differ with respect to root phenology and survivorship, but the dynamics of roots that we have previously observed within each increment are similar (Hendrick & Pregitzer, 1992; 1993a;b; 1996). Moreover, these increments allowed us to bracket our soil moisture and temperature sensors (which were placed at 15 and 75 cm), while maximizing the number of the roots within the data base. For the regression analyses, data from 0-30 cm were paired with temperature and moisture data from 15 cm, and roots in the 50-100 cm increment were similarly paired with site data collected from moisture sensors located at 75 cm. We combined data from both years and results are presented for each site and depth combination.

**Results**

**SOIL TEMPERATURE AND MOISTURE AND SITE WATER BALANCE**

Soil temperatures at 15 cm followed fairly predictable seasonal patterns, some of which we have reported elsewhere (Hendrick & Pregitzer, 1993a,b). To summarize briefly, mean soil temperatures (with standard errors) from late April through mid-October at the southern site were 14.2 (4.3) and 14.6 (3.3)°C during 1989 and 1990, respectively. These were significantly greater than the corresponding values of 12.9 (3.5) and 12.9 (3.2)°C recorded at the northern site during the same time period ( $t$ -test,  $P < 0.0001$ ). Maximum monthly mean temperatures reached 19°C during July and August of 1989 at the southern site and 16°C during the same months at the northern site.

In general, matric potentials were relatively high at both sites and depths throughout the study period (Figure 1). During a summer drought in 1989, matric potentials at 15 cm reached a low of -0.65 MPa at the southern site and -0.85 MPa at the northern site. Mid-summer 1989 matric potential at 75 cm was similarly affected at the northern site but at no time was below -0.30 MPa. Matric potential at 75 cm at the southern site was unaffected by the 1989 drought (Figure 1). During 1990, matric potentials at both sites and depths remained above -0.10 MPa.

As in most temperate climates, AET and PET at both sites were greatest during mid-summer (Figure 2). PPT was highest in the spring during both 1989 and 1990. As stated previously, summer rainfall during 1989 was substantially less than in 1990, which led to measurable water deficits at both sites during July 1989. Available and excess water were greatest in the spring and early summer (Figure 2).

**ROOT LENGTH DENSITY, PRODUCTION AND MORTALITY**

Root length density in the 0-30 cm increment peaked in mid-summer at both sites and during both years (Figure 3). Root length density was least in both early spring and autumn (Figure 3). The seasonal changes were not dramatic

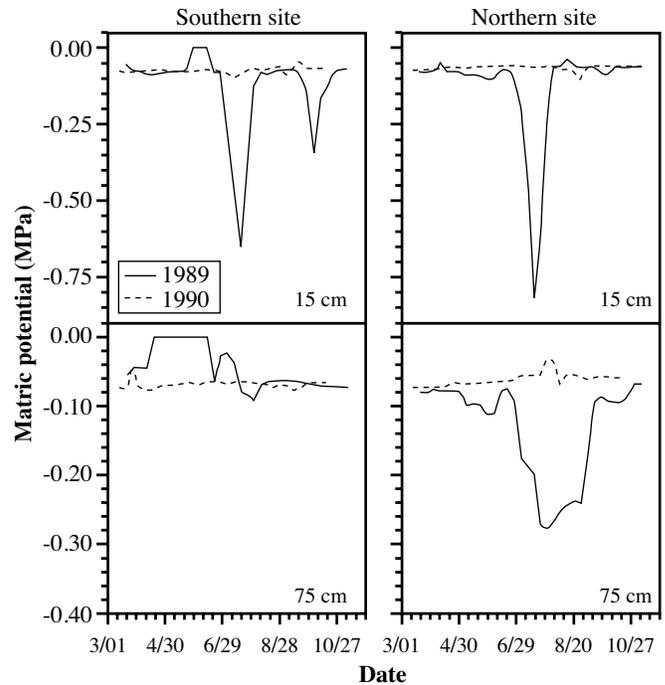


FIGURE 1. Average weekly soil matric potentials (MPa) at 15 and 75 cm during 1989 and 1990 ( $n = 3$ ).

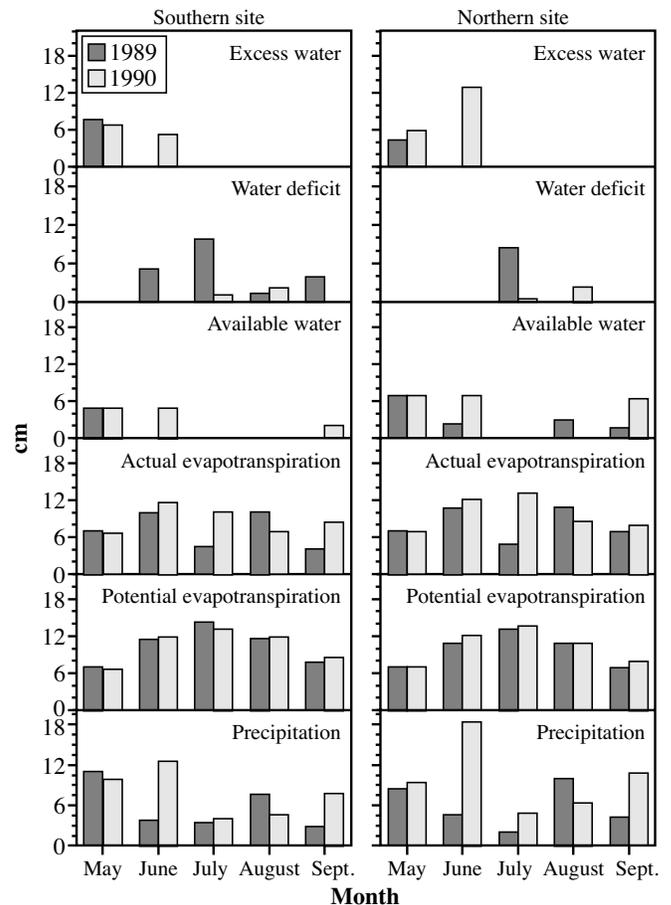


FIGURE 2. Site water balance variables for the 0-75 cm soil profile during 1989 and 1990 ( $n = 3$ ).

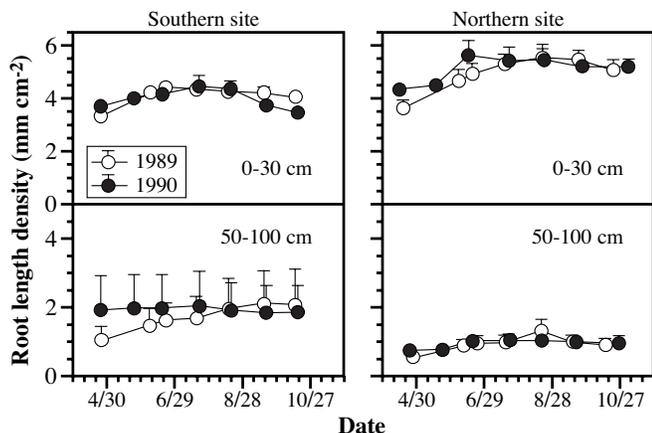


FIGURE 3. Mean fine root length densities (mm of root per cm<sup>2</sup> of minirhizotron viewing area, with standard errors) on each 1989 and 1990 sampling date (*n* = 3).

in the shallow increment, and were even less noticeable in the 50-100 cm increment. At both sites, RLD was significantly (positively) related only to PET (Table I). Only those roots in the 0-30 cm depth increment were affected and the model explained only a small proportion of seasonal variation in RLD (*R*<sup>2</sup> for both sites = 0.12). None of the soil or site variables appears to be strongly controlling seasonal patterns of RLD.

Within the 0-30 cm depth increment, RLP at both sites was greatest in the spring and early summer in both years (Figure 4). Conversely, RLP was more evenly distributed throughout the growing season in the 50-100 cm increment (Figure 4). Root length production was significantly affected by the soil environment at the shallower depth at both sites

TABLE I. Summary of regression equations relating minirhizotron root length density (RLD), production (RLP) and mortality (RLM) to site factors for each site and depth increment (data are pooled across years)

Site	Depth (cm)	Regression equation	Model <i>R</i> <sup>2</sup>	<i>p</i> > <i>F</i>
<b>ROOT LENGTH DENSITY (mm cm<sup>-2</sup>)</b>				
South	0-30	RLD = 3.53 + 0.06(PET)	0.12	0.07
South	50-100	n.s.		
North	0-30	RLD = 3.55 + 0.15(PET)	0.12	0.08
North	50-100	n.s.		
<b>ROOT LENGTH PRODUCTION (mm cm<sup>-2</sup> day)</b>				
South	0-30	RLP = 0.009 + 0.004(EW) - 0.005(AW) + 0.001(AET)	0.27	0.04
South	50-100	n.s.		
North	0-30	RLP = 0.016 + 0.002(EW)	0.32	0.001
North	50-100	n.s.		
<b>ROOT LENGTH MORTALITY (mm cm<sup>-2</sup> day)</b>				
South	0-30	RLM = 0.016 - 0.002(EW) - 0.002(AET) + 0.002(PPT)	0.52	0.004
South	50-100	n.s.		
North	0-30	n.s.		
North	50-100	n.s.		

AET: actual evapotranspiration (cm mo<sup>-1</sup>).

AW: available water (cm mo<sup>-1</sup>).

EW: excess water (cm mo<sup>-1</sup>).

PET: potential evapotranspiration (cm mo<sup>-1</sup>).

PPT: precipitation (cm mo<sup>-1</sup>).

n.s.: not significant.

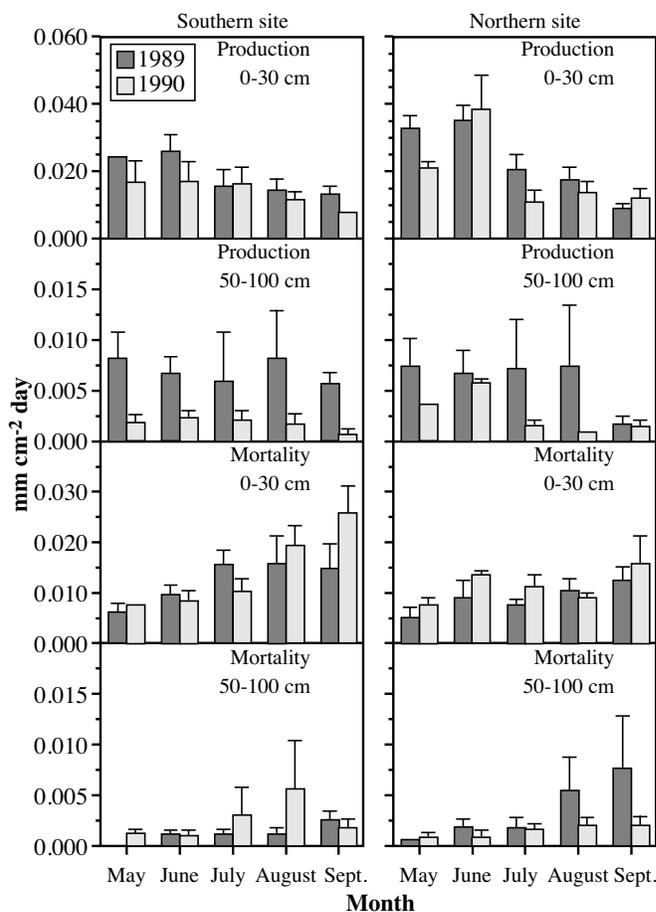


FIGURE 4. Mean daily fine root length density production and mortality (mm of root per cm<sup>2</sup> of minirhizotron viewing area per day, with standard errors) within the 0-30 and 50-100 cm soil profile during the 1989 and 1990 observation periods.

(Table I). The relationship between EW and shallow RLP was strongest at the northern site (*R*<sup>2</sup> = 0.32), while EW, AW and AET contributed equally to the model at the southern site (partial *R*<sup>2</sup>'s of 0.09, 0.11 and 0.08, respectively). As is true for RLD, the soil environmental factors that we measured appear to be exerting relatively little control over RLP at the 50-100 cm depth (Table I), where no variable met the minimum significance level for model inclusion (*P* < 0.15)

Unlike production, there was a tendency for mortality to be concentrated late in the growing season at both sites and during both years (Figure 4), although the total amount of RLM varied among both years and sites. Relationships between measured environmental factors and RLM were inconsistent. Mortality was significantly affected by the soil environment only within the shallow depth increment at the southern site (Table I). As was true for RLP, EW contributed most to the overall model, accounting for half of all explained variation (*R*<sup>2</sup> = 0.26). In contrast to the effect of EW on RLP, though, its effect on RLM was negative instead of positive (Table I).

## Discussion

Given the well-established facts that soil temperature and moisture can exert strong control over root activity, we

were surprised to find such weak relationships between RLD, RLP, RLM and the site variables that we measured. Although there are several statistically significant models for the 0-30 cm depth increment (Table I), none explains a sufficient proportion of total variation for us to find them acceptable as predictors of root abundance or activity. Moreover, both the beta and partial  $R^2$ -values of the environmental variables in the significant models are generally low, suggesting that these factors exert modest control over root activity at our sites. Nonetheless, the nature of the relationships between the site variables and root density and activity that we did detect do make some intuitive sense.

For example, there is a positive relationship between RLD and PET at both of our sites. Root absorbing area might be expected to increase with evapotranspiration potential, and root length should be closely related to root surface area within the narrow range of root diameters we studied. Similarly, the relationship between shallow RLM and EW and AET at the southern site suggests that root mortality is comparatively low when water supply and demand are both high (Table I). Indeed, RLM is greatest in autumn when plant water needs are minimal and the majority of roots produced in late spring and summer are dying (Hendrick & Pregitzer, 1993a). Further, EW is positively and significantly related to shallow RLP at both the northern and southern sites, suggesting that periods of relative water abundance stimulate root growth and production.

Soil water is also abundant during November and December at these sites, although we observe relatively little root growth after late fall and during the winter (Hendrick & Pregitzer, 1993b; 1996). The probable explanation for this apparent contradiction with the relationship between RLP and EW during the growing season is well documented, and relates to the interactive effects of soil moisture and temperature on root dynamics. As stated previously, root growth and soil moisture are positively correlated during much of the growing season (Bevington & Castle, 1985; Deans, 1979; Kuhns *et al.*, 1985; Lyr & Hoffmann, 1967). However, low soil temperatures most often limit root growth from autumn through early spring. For example, white oak root growth is most strongly controlled by soil temperature at temperatures less than 17°C and by soil moisture at higher temperatures (Teskey & Hinckley, 1981). Black walnut root growth is similarly regulated primarily by soil temperature during very cool periods, but is controlled by soil moisture during most of the growing season (Kuhns *et al.*, 1985). Similar interactions between moisture and temperature occur in apple (Rogers, 1939), Sitka spruce (Deans, 1979) and citrus (Bevington & Castle, 1985). At our study sites, soil temperatures at 15 cm can drop below 5°C by late October, cold enough to cause complete growth cessation in most temperate tree species (Lyr & Hoffmann, 1967), regardless of soil moisture availability.

The effects of AW and AET on RLP, and PPT on RLM, at the southern site (Table I) are difficult to interpret, as these variables indicate only the nature of their relationship with that portion of RLP or RLM left unexplained by EW (+ AET for the RLM model). The model for shallow RLP at the southern site indicates that the positive effect of EW on RLP is moderated to some extent by AW and

augmented by AET (Table I). There are similar seasonal patterns in RLP, AW and AET at the northern site, but no significant regression model incorporating these two variables. The positive relationship between PPT and shallow RLM at the southern site (after accounting for EW and AET) is difficult to reconcile with the site and mortality data (Figures 2 and 4). Such apparently counterintuitive relationships highlight both the interactive effects of the environmental variables and the limitations of predictive variables that lack complete independence. These are also likely explanations for the lack of a significant relationship between RLD and EW, even though this variable is related to both RLP and RLM.

Roots in the 50-100 cm depth increment seem to be little affected by the soil environment or the indices of plant water demand that we quantified. At no time did we find any statistically significant relationship between any site variable and either RLD, RLP or RLM in the 50-100 cm depth increment. It is difficult to compare the biological significance of these results to other forests because roots growing deeper than 20-30 cm are seldom studied. Black walnut root growth increased with soil temperature and then decreased and stopped as the soil dried (Kuhns *et al.*, 1985), but we did not observe any significant effects of either temperature or matric potential at either of our sites. Fernandez & Caldwell (1975) observed a relative increase in the growth of progressively deeper roots in three semi-desert shrubs species as the soil surface dried. At our sites, however, a high proportion of deep roots are produced coincident with the shallow roots (Figure 4, Hendrick & Pregitzer, 1996).

The modest relationships between root growth and mortality and the site variables we measured suggest that fine root activity at all depths is under strong internal control in these forests. In other words, there seems to be an inherent phenology to root growth and mortality that is phenomenologically, if not mechanistically, similar to canopy development and senescence. This seems to be especially true for roots growing within the 50-100 cm depth increment. Pronounced seasonality of root growth has been observed in many forest ecosystems, regardless of prevailing environmental conditions. For example, the considerable spring and early summer root growth that we observe at shallow depths is typical of northern hardwood forests throughout eastern North America (Hendrick & Pregitzer, 1993b; 1996; Fahey & Hughes, 1994; Burke & Raynal, 1994). The deeper roots seem to exhibit a life history similar to leaves, in that many live until the end of the growing season and are shed coincident with and after canopy senescence (Hendrick & Pregitzer, 1996). These data suggest that the soil environment modifies fine root dynamics to some degree, but that broad temporal patterns of fine root activity are regulated primarily by the taxon. There is increasing evidence that root longevity may be "programmed" to some extent (Lynch, 1995), or at least under limited environmental control. Merritt (1968) also suggested that gross patterns of root activity are primarily endogenously controlled and that the root and stem environments exert more modest control over the timing and amount of root growth. Teskey & Hinckley (1981) reached a similar conclusion for white oak.

There are other environmental factors that we did not measure, but which probably play some role in regulating root dynamics. We believe that N may be especially important. For example, spring root growth responds positively to increased soil temperature and abundant soil moisture in forests (Kuhns *et al.*, 1985; Teskey & Hinckley, 1981), but these factors stimulate microbial activity and N mineralization as well. Mineralization data from subsequent years at our sites indicate that 25% of total annual N mineralization occurs during spring and early summer (Donald Zak, pers. comm.), and root growth often increases in response to N and other nutrients (Drew, 1975; Drew & Saker, 1975; Eissenstat & Caldwell, 1988; Pregitzer, Hendrick & Fogel, 1993).

The potential for root responses to soil resources to vary across spatial scales, coupled with the non-uniform distribution of both roots and soil resources, may also have hindered our ability to detect strong relationships between site factors and fine root dynamics. Trees are able to exploit large volumes of soil, and localized changes in soil resources, or root responses to those changes, may have little effect on the dynamics of the root system as a whole. For example, efforts to make broad generalizations about the effects of soil N on fine root longevity have been complicated in part by the tendency for the effects to be positive at small (*i.e.*, soil patch) scales (Pregitzer, Hendrick & Fogel, 1993; Fahey & Hughes, 1994), but variable at larger (*i.e.*, whole-pot or stand) scales (Hendricks, Nadelhoffer & Aber, 1993; Pregitzer *et al.*, 1995).

Finally, it is possible that our sites were too favorable, and the fluctuations in site factors too small, to elicit a detectable response in either RLP or RLM. For example, root mortality is often unaffected until the soil is nearly devoid of water (Lyr & Hoffmann, 1967), but at no point did soil moisture decrease below -0.85 MPa at our sites. Similarly, root growth and soil temperature data from other temperate hardwood forests suggest that soil temperatures at our sites were probably never high enough to cause root mortality (Lyr & Hoffmann, 1967; Kuhns *et al.*, 1985; Teskey & Hinckley, 1981). Moreover, at the time of this study, foliar losses to insect, disease and weather were low at both sites. Consequently, the trees at our sites were probably well buffered against the relatively minor fluctuations in soil temperature, moisture and plant water demand that we observed. Tree responses to these changes may have more often been unmeasured physiological changes in uptake, respiration, etc. than increased or decreased root growth and mortality.

In summary, fine root length density, production and mortality do not appear to be strongly affected by soil moisture, temperature or site water balance in these two forests. Modest relationships between root activity and site variables occur near the soil surface, but roots growing at depths > 50 cm are largely unaffected by any of the site variables that we measured. Shallow root length density is related to PET at both site and periods of abundant moisture and high water demand appear to stimulate production and decrease root mortality. However, patterns and amounts of root activity at all depths appear to be under strong endogenous control.

## Acknowledgements

We thank N. MacDonald for providing most of the environmental data and A. Burton for reviewing the models and manuscript. Comments by T. Fahey, R. Ruess and K. Van Cleve improved the manuscript significantly. This research was supported by NSF grants DEB 9221003, 9203031 and the USDA Northern Studies Global Change Program.

## Literature cited

- Bartsch, N., 1987. Response of root systems of young *Pinus sylvestris* and *Picea abies* plants to water deficits and soil acidity. *Canadian Journal of Forest Research*, 17: 805-812.
- Bevington, K. B. & W. S. Castle, 1985. Annual root growth pattern of young citrus trees in relation to shoot growth, soil temperature, and soil water content. *Journal of the American Horticultural Society*, 110: 840-845.
- Burke, M. K. & D. J. Raynal, 1994. Fine root growth phenology, production and turnover in a northern hardwood forest ecosystem. *Plant and Soil*, 162: 135-146.
- Deans, J. D., 1979. Fluctuations of the soil environment and fine root growth in a young sitka spruce plantation. *Plant and Soil*, 52: 195-208.
- Drew, M. C., 1975. Comparison of the effects of localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot in barley. *Journal of Experimental Botany*, 26: 479-490.
- Drew, M. C. & L. R. Saker, 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. *Journal of Experimental Botany*, 26: 79-90.
- Eissenstat, D. M. & M. M. Caldwell, 1988. Seasonal timing of root growth in favorable microsites. *Ecology*, 69: 870-873.
- Fahey, T. J. & J. W. Hughes, 1994. Fine root dynamics in a northern hardwood forest ecosystem. *Hubbard Brook Experimental Forest, NH. Journal of Ecology*, 82: 533-548.
- Fernandez, O. A. & M. M. Caldwell, 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *Journal of Ecology*, 63: 703-714.
- Hansson, A. C., Z. Aifen & O. Andren, 1994. Fine root production and mortality in degraded semiarid rangeland in inner Mongolia, China. *Ambio*, 23:225-228.
- Hendrick, R. L. & K. S. Pregitzer, 1992. The demography of fine roots in a northern hardwood forest. *Ecology*, 73: 1094-1104.
- Hendrick, R. L. & K. S. Pregitzer, 1993a. Patterns of fine root mortality in two sugar maple forests. *Nature*, 361: 59-61.
- Hendrick, R. L. & K. S. Pregitzer, 1993b. The dynamics of fine root length, biomass and nitrogen content in two northern hardwood ecosystems. *Canadian Journal of Forest Research*, 23: 2507-2520.
- Hendrick, R. L. & K. S. Pregitzer, 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *Journal of Ecology*, 87: 167-176.
- Hendricks, J. J., K. J. Nadelhoffer & J. D. Aber, 1993. Assessing the role of fine roots in carbon and nutrient cycling. *Trends in Ecology and Evolution*, 8: 174-178.
- Kuhns, M. R., H. E. Garrett, R. O. Teskey & T. M. Hinckley, 1985. Root growth of black walnut trees related to soil temperature, soil water potential and leaf water potential. *Forest Science*, 31: 617-629.
- Lynch, J., 1995. Root architecture and plant productivity. *Plant*

- Physiology, 109: 7-13.
- Lyr, H. & G. Hoffmann, 1967. Growth rates and growth periodicity of tree roots. *International Review of Forest Research*, 2: 181-236.
- Merritt, C., 1968. Effect of environment and heredity on the root-growth patterns of red pine. *Ecology*, 49: 34-40.
- Nambiar, E. K. S., G. D. Bowen & R. Sands, 1979. Root regeneration and plant water status of *Pinus radiata* D. Don seedlings transplanted to different soil temperatures. *Journal of Experimental Botany*, 30: 1119-1131.
- Pregitzer, K. S., R. L. Hendrick & R. Fogel, 1993. The demography of fine roots in response to patches of water and nitrogen. *New Phytologist*, 125: 575-58147.
- Pregitzer, K. S., D. R. Zak, P. S. Curtis, M. E. Kubiske, J. A. Teeri & C. S. Vogel, 1995. Atmospheric CO<sub>2</sub>, soil nitrogen and turnover of fine roots. *New Phytologist*, 129: 579-585.
- Rawlings, J. O., 1988. *Applied Regression Analysis*. Wadsworth and Brooks, Pacific Grove, California.
- Rogers, W. S., 1939. Root Studies VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. *Journal of Pomology and Horticultural Science*, 17: 99-130.
- Teskey, R. O. & T. M. Hinckley, 1981. Influence of temperature and water potential on root growth of white oak. *Physiologia Plantarum*, 52: 362-369.
- Thornwaite, C. W. & J. R. Mather, 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Laboratory of Climatology, Drexel Institute of Technology, Publications in Climatology, Volume 10, Centerton, New Jersey.
- Webb, D. P., 1976. Root growth in *Acer saccharum* Marsh. seedlings: Effects of light intensity and photoperiod on root elongation rates. *Botanical Gazette*, 137: 211-217.