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Fine Root Production, Demography and Turnover in Northern Hardwood Forests

presented by

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Kurt S. Pregitzer
Major professor

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FINE ROOT PRODUCTION, DEMOGRAPHY AND TURNOVER IN NORTHERN HARDWOOD FORESTS

By

Ronald L. Hendrick

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ABSTRACT

FINE ROOT PRODUCTION, DEMOGRAPHY AND TURNOVER IN NORTHERN HARDWOOD FORESTS

By

Ronald L. Hendrick

Data were collected from two sugar maple (Acer saccharum Marsh.) forests in 1989 and 1990. Direct observations of fine root production, development and mortality were used in conjunction with physical harvests of fine root biomass and nitrogen content to measure root growth and death, and to estimate the amount of carbon and nitrogen allocated to fine root production and subsequently returned to the soil via fine root turnover.

Analyses of cumulative survival distributions of contemporaneous 1989 and 1990 cohorts revealed that roots at the northern site consistently lived longer on average than roots born during the same periods of time at the southern site. The longer lifespan of roots in the northern forest was due to significantly lower first-season mortality rates; new roots were lost 64% faster at the southern forest (0.41 vs. 0.25 $\%\cdot day^{-1}$, $p < .01$.). Overwinter and second-year morality rates were not significantly different ($p > 0.5$; 0.14 vs. 0.12 $\%\cdot day^{-1}$) among the sites. Patterns of fine root mortality at each site were the same for roots produced at all times of the year, and our results suggest that

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temporal differences in biomass "turnover" may be due to temporal variation in root production, not in root mortality.

Greater than 50% of annual length production occurred before mid-summer in both ecosystems, while the period of greatest mortality was from late summer through winter. About 1/3 of annual fine root production and mortality occurred simultaneously, with little observable change in total root length. Total fine root length observable in the minirhizotrons peaked in mid-summer in both ecosystems.

Annual production values of approximately 8000 and 7300 $kg \cdot ha \cdot yr^{-1}$ were calculated at the Southern and Northern sites, respectively, representing about 60% of total NPP in both forests. Corresponding biomass mortality (i.e. turnover) values were 6700 and 4800 $kg \cdot ha \cdot yr^{-1}$, and total nitrogen returns to the soil from fine root mortality were 72 $kg \cdot ha \cdot yr^{-1}$ at the Southern site and 54 $kg \cdot ha \cdot yr^{-1}$ at the Northern site. Fine roots dominated total biomass and N litter inputs to the soil in both ecosystems, accounting for over 55% of total biomass and nearly 50% of total N returns. In both ecosystems, roots <0.5 mm comprised the bulk of fine root biomass and N pools, and the contribution of these roots to northern hardwood ecosystem carbon and nitrogen budgets has probably been underestimated in the past.

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I am indebted to the other members of my guidance committee, Drs. Donald Dickmann, Robert Fogel, G. Philip Robertson and Alvin Smucker, for their continuing advice and assistance. Dr. Smucker was instrumental in exposing me to minirhizotron technology and applications, and Dr. Fogel taught me a great deal about roots and mycorrhizae while in the field and at the Soil Biotron. Dr. Carl Ramm willingly provided considerable statistical help and advice, for which I am grateful. Drs. Donald Hall and Katherine Gross helped guide me into the demography literature early in my studies, and I thank them both. I would also like to express my gratitude to my friend Dr. Phu Nguyen for his advice, encouragement and willingness to assist me whenever I asked.

Melissa Moss deserves a special thanks for her tireless efforts while digitizing minirhizotron images and sorting root samples. Andy Burton was instrumental in helping collect minirhizotron images and root samples, and was responsible for much of the laboratory work getting done properly and in a timely fashion. Bill Enslin wrote the ROOTS program, and without ROOTS this work would not have been possible. Several undergraduate laboratory assistants helped in numerous ways, including Leslie Jagger, Lynn Hanninen, Lori Grimm, Chiu Kwan Yu, Beth Palik and Wendy Williams. I would also like to thank my colleagues Andy Burton, Zhijun Liu and Brian Palik for their friendship, advice and ability to carry on intellectually stimulating discussions over a wide range topics.

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INTRODUCTION

Until the late 1970's, little was known about the role of fine roots in the carbon and nutrient economies of forest ecosystems. The paper of Harris et al. (1977) from a Liriodendron tulipifera L. forest was probably the first English-language report that specifically addressed fine root production and mortality (i.e. turnover) in an ecosystem context. Subsequent papers, many from coniferous forests, soon followed (e.g. Cox et al. 1978, Fogel and Hunt 1979, Grier et al. 1981, Keyes and Grier 1981, McClaugherty et al. 1982, Persson 1978, 1979), and fine root and mycorrhizal production and turnover have now been studied in several deciduous and coniferous forests worldwide (e.g. Aber et al. 1985, Fogel and Hunt 1983, Gholz et al. 1986, Gower et al. 1992, Hendrick and Pregitzer 1992, Joslin and Henderson 1987, Nadelhoffer et al. 1985, Powell and Day 1991, Santantonio 1982, Vogt et al. 1982).

A consensus has emerged from these and other studies that fine roots play a dominant role in the carbon and nutrient budgets of most forests. Greater than one-half of annual NPP is allocated belowground in many forests, and nutrient fluxes to the soil from fine root mortality can be greater than those from aboveground litterfall (Arthur and Fahey 1992, Cox et al. 1978, Fogel and Hunt 1979, Harris et al. 1977, Grier et al. 1981, Joslin and Henderson 1987, Keyes

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and Grier 1981, Vogt et al. 1986). However, many aspects of fine root dynamics are still poorly understood. For example, we know very little about fine root longevity (or fine root life-history in general), even though measuring longevity is key to quantifying carbon and nutrient fluxes to and from fine roots. Given our poor understanding of fine root longevity, it is not surprising that there is considerable disagreement over the effects of soil resources on rates of fine root turnover (i.e. Aber et al. 1985, Gower et al. 1992, Keyes and Grier 1981, Nadelhoffer et al. 1985).

Compounding these problems has been our inability to measure the magnitude of concurrent fine root production and mortality (Joslin and Henderson 1987, Kurz and Kimmins 1987, Santantonio and Grace 1987). Because a physical sample of roots can be destructively assayed only once, production and mortality can be measured neither directly nor independently, but must be inferred from changes in live and/or dead fine root pool sizes. A high degree of spatial variability in fine root biomass further exacerbates the difficulties in measuring temporal variation in mass, and hence root production and mortality. Small temporal changes in root mass may be masked by random spatial variation introduced by the heterogeneous nature of fine root distribution, and the need to collect subsequent samples from different locations in the soil.

Close examination of these methodological difficulties leaves little doubt that the destructive, discontinuous methods typically used to study fine root dynamics are largely responsible for our inability to make significant new advances in our knowledge of fine roots (Fogel 1990, Hendrick and Pregitzer 1992, Santantonio and Grace 1987, Vogt et al. 1989). In contrast to traditional physical sampling schemes, minirhizotrons offer the ability to study fine roots in-situ in a non-destructive fashion. Because the same roots can be monitored over extended periods of time, spatial variability in fine root distribution becomes fixed, and temporal dynamics can be measured directly and more accurately (Atkinson 1985, Hendrick and Pregitzer 1992). The small size of minirhizotrons, and the portability of the video systems used to collect minirhizotron images, make them ideal tools for field studies in remote, natural ecosystems. Minirhizotrons have already been used in several natural and managed plant communities (Beyrouty et al. 1987, Cheng et al. 1990, Eissenstat and Caldwell 1988, Hendrick and Pregitzer 1992, Upchurch and Ritchie 1983), and their continued use in root research seems likely.

Minirhizotrons, however, suffer from limitations of their own. The heterogeneous distribution of fine roots that has long plagued destructive approaches can also lead to high minirhizotron-to-minirhizotron variability in root

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distribution. Coefficients of variation range up to as much as several hundred percent (Merrill et al. 1987, Upchurch and Ritchie 1983, Upchurch 1987), and can make treatment effects difficult to detect. Extracting data from minirhizotron images has historically been a laborious, time consuming process, although more automated methods of analyzing minirhizotrons images are forthcoming (Smucker et al. 1987). And, although there has been some success in converting root length densities measured with minirhizotrons to root biomass (Upchurch and Ritchie 1983, Upchurch 1987), it is doubtful that minirhizotrons or other direct observation techniques will replace destructive sampling as a means to measure standing root biomass or nutrient content.

The research reported in this dissertation is the result of an attempt to: 1) more fully describe and quantify the life-history and development of fine roots from their time of birth until death, and 2) link direct observations of root birth, growth and death with physical measurements of root biomass and nutrient content to quantify carbon and nutrient allocation to fine roots, and C and N returns to the soil from fine root mortality. Secondary objectives of this project were to increase the efficacy of minirhizotrons as a means of measuring fine root dynamics, and to facilitate the extraction and analysis of data from minirhizotron images.

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The conceptual basis for this research lies in the premise that a better knowledge of fine root demography (i.e. the birth, development and death of individual fine roots and root cohorts) is needed before we can make significant advances in understanding the role of fine roots in ecosystem processes. Demographic studies of leaves (Bazzaz and Harper 1977, Hartnett and Bazzaz 1985, Maillette 1982a), buds (Maillette 1982b), meristems (Porter 1983a,b) and clonal ramets (Dickerman and Wetzel 1985) have proven useful in research on aboveground plant parts, but this approach has yet to be taken belowground, at least on a large scale. The overall goal of this research, then, was to study fine root demography at the ecosystem scale, and subsequently use this information to quantify the role of fine roots in the C and N cycles of Northern Hardwoods forests by linking modern video technology with traditional ecosystem science methodologies.

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Chapter I

THE DEMOGRAPHY OF FINE ROOTS IN A NORTHERN HARDWOOD FOREST

Abstract

The production, development and mortality of fine roots in a northern hardwood forest dominated by sugar maple (Acer saccharum Marsh.) was monitored for one year using minirhizotrons. Roots were divided into two strata based upon their depth in the soil, <30 cm and >30 cm. Cohort analyses of roots produced in the spring of 1989 revealed that while almost 50% of fine roots at both depths survived after 346 days, the number of white roots in each cohort declined very rapidly. Virtually all roots had turned brown after 346 days. The probability of a surviving white root turning brown was much greater than the probability that it would die at all times of the year, and the bulk of root mortality was accounted for by brown roots. Analysis of root length production and mortality showed that total annual length mortality at the <30 cm depth was 76% of the initial standing crop and 110% at >30 cm depth. Fine root production and mortality occurred simultaneously throughout the year, and production was slightly greater than mortality at both depths. Total root length peaked in the summer at both depths, and overwinter production and mortality was rather low.

Production of white and brown root length indicated that roots near the soil surface were undergoing much more rapid rates of browning than deep roots. Loss of root length between sampling dates was largely due to roots that died and rapidly decayed or otherwise disappeared.

Introduction

We have learned much about the contribution of roots to the carbon and nutrient economy of forest ecosystems. For example, greater than one-half of annual net primary production is allocated belowground in some forests (Fogel 1985; Harris et al. 1977; Grier et al. 1981; Keyes and Grier 1981). Fine (small diameter and/or non-woody) root mortality can represent a substantial carbon and nutrient input into the soil (Joslin and Henderson 1987; Cox et al. 1978). The quantity of N added to the soil by root mortality is from 18 to 58% greater than that added by aboveground litterfall in some ecosystems (Vogt et al. 1986). Mycorrhizae may also account for a substantial portion of total belowground production (Fogel 1985).

The importance of understanding and quantifying the processes influencing fine root dynamics (production, longevity and mortality) has been recognized for some time (Joslin and Henderson 1982, 1987; Kurz and Kimmins 1987; McClaugherty et al. 1982; Nadelhoffer et al. 1985; Persson 1978). Unfortunately, traditional sampling procedures do not permit the simultaneous measurement of fine root production, death and disappearance (Santantonio and Grace 1987; Kurz and Kimmins 1987). Despite numerous computational approaches that have been devised to

compensate for this difficulty (McClaugherty et al. 1982; Joslin and Henderson 1982; Santantonio 1979), the destructive nature of repeated soil coring renders the direct measurement of these processes impossible. Additional problems with destructive sampling include differentiating between temporal differences in root standing crops and artifacts of sampling variability (Singh et al. 1984), and separating live and dead roots (Fogel 1983, 1990).

Our incomplete understanding of fine root turnover is due in part to our inability to quantify the demographic processes underlying root dynamics. For example, we have a poor understanding of fine root longevity, or how longevity is influenced by the soil environment. Estimates of fine root lifespans in forests range from less than one to greater than eight years, depending on the size, species and mycorrhizal status of the roots (Harris et al. 1977; Joslin and Henderson 1987; Grier et al. 1981; Keyes and Grier 1981; Persson 1978, 1979, 1980; Santantonio 1979; Trappe and Fogel 1977).

A more complete knowledge of fine root demography could contribute to our understanding of several ecosystem processes. The proportion of white roots that brown before dying, versus those that die while still white, could affect the quality of litter returned to the soil via root

turnover. We have previously documented substantial differences in the N concentrations of white and brown fine roots in sugar maple (Acer saccharum L.) (Goldfarb et al. 1990). In that study we found that the N concentration in brown roots averaged only about 60% that of white roots throughout the growing season. If white (often presumptuously called "unsuberized") roots are those most important in nutrient and water uptake (but see Atkinson 1983, 1985), then the rate and extent that roots age and brown is also of considerable significance to canopy processes like photosynthesis and transpiration.

Rhizotrons can be used to study root demography in situ, and to measure rates of root production and mortality directly. This is more desirable than infering these rates from estimates of biomass change. If the same roots and soil space are monitored over time, temporal changes in root dynamics are not confounded by random spatial variability at each sampling date. Instead, spatial variability becomes more or less fixed (Atkinson 1985). Minirhizotrons are useful for observational studies of roots in both natural and managed ecosystems because of their small size and accessibility. Several investigators have recently used minirhizotrons to study root turnover in a variety of agronomic and natural ecosystems (e.g. Beyrouty et al. 1987; Cheng et al. 1990; Eissenstat and Caldwell 1988; Upchurch and Ritchie 1983). To our knowledge there are no

minirhizotron data from forests in the literature. The use of minirhizotrons to study fine root production, development and mortality (i.e. demography) should provide new insights into the cycling of carbon and nutrients belowground.

The objectives of this research were to quantify several demographic and life history traits of fine roots in a deciduous forest, including their development and fate, as well as the production and decline of white and brown root length over time. For the purpose of this study, we arbitrarily defined a fine root as any root less than 2.0 mm in diameter. We were especially interested in the demography of non-woody roots less than 1.0 mm in diameter. Our belief is that a demographic approach to data collection and analysis, coupled with minirhizotrons, can be used to answer several simple but important questions. These include: how long do fine roots live? To what extent are root production and mortality continuous in time? What are the typical stages of development in fine roots from production to mortality? The conceptual framework on which our questions were formulated is presented in Figure 1.

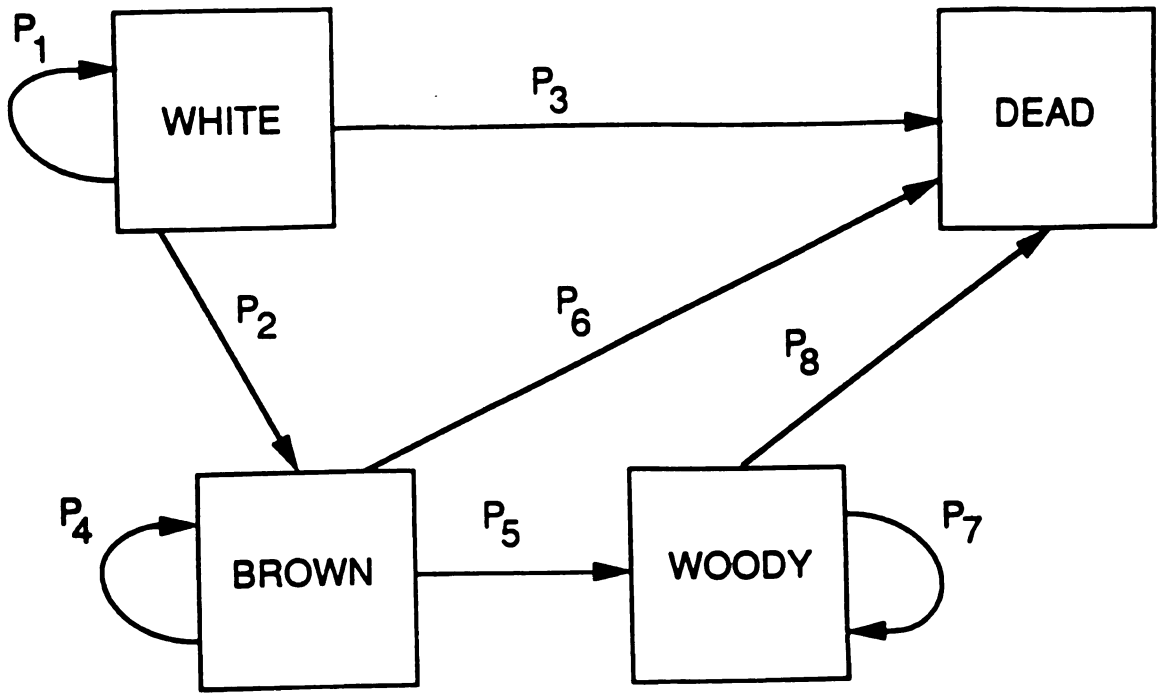

Figure 1.1 Life cycle diagram for the fine roots of trees. P_i's are the probabilities of a root following a particular path from one stage of development to another during some time interval t.

Methods

Study Site and Minirhizotrons

Our study site is a hardwood forest located in the northern lower peninsula of Michigan (Manistee County, 40° 42′ N, 85° 43′ W), USA. The forest is a second growth stand dominated by sugar maple (Acer saccharum L., Table 1). The overstory species, including their basal and leaf areas, are listed in Table 1. Three 30 m by 30 m plots were established at the site in 1987, selected so that a maximum degree of homogeneity existed among them with respect to physiography, soils and vegetation (Burton et al. 1992). The herbaceous community is depauperate, with an average cover value of less than 3%. There are virtually no shrubs. The soil is a Typic Haplorthod of the Blue Lake and Kalkaska series. A number of stand and environmental variables were monitored on each plot throughout the 1989 growing season. Percent canopy foliation was determined periodically from prior to bud break in the spring until after 100% leaf fall in the autumn. Gravimetric soil moisture content was determined monthly at 15 and 75 cm depths. Soil temperature at 15 cm was recorded weekly with an Omnidata Easylogger (Omnidata International, Logan UT).

Table 1.1 Stand, soil and climatic characteristics of the study site. Values are averages across plots, with standard errors of the mean in parentheses where shown.

General Stand Characteristics

Aboveground biomass ($Mg \cdot ha^{-1}$)	275
Overstory Age (yrs)	74 (11)
Canopy Height (m)	28 (1)
Budbreak (1989)	May 9
100% Canopy Foliation (1989)	May 23
50% Leaf Fall (1989)	Oct 17
100% Leaf Fall (1989)	Oct 30

Soil Variables (A+E Horizons)

pH (1:1 Water)	4.66(.27)
Bulk Density ($g \cdot cm^{-3}$)	1.27(.04)
Nitrogen ($kg \cdot ha^{-1}$)	1125(398)
Phosphorus ($kg \cdot ha^{-1}$)	191(58)
Organic Matter ($Mg \cdot ha^{-1}$)	45.7(13.6)

Climatic Variables

30 Yr. Mean Annual Air Temperature (^{o}C)	5.8
1989 Mean Annual Air temperature (^{o}C)	4.7
Annual Precipitation (cm, 30 yr mean)	81
Growing degree Days (>5.6 ^{o}C)	1944

Stand Composition

	Basal Area ($m^2 \cdot ha^{-1}$)	% Total	Leaf Area ($m^2 \cdot m^{-2}$)	% Total
Acer saccharum	24.93 (0.50)	82.6	5.34 (0.34)	75.4
Acer rubrum	2.40 (0.74)	8.0	0.42 (0.13)	5.9
Prunus serotina	1.48 (1.07)	4.9	0.10 (0.05)	1.4
Quercus rubra	1.35 (0.68)	4.5	0.95 (0.24)	13.4
Fagus grandifolia	0.03 (0.03)	0.1	0.14 (0.06)	2.0
Total	30.19 (1.64)	100.0	7.08 (0.54)	100.0

In June 1988, 4 minirhizotrons (2 m long x 5.08 cm inside diameter) were permanently installed in each plot at a 45^{o} angle to the soil surface, and to a depth of 165 cm along their length (= 110 cm in vertical depth). The portion of the minirhizotron extending above the soil surface was painted and capped with a rubber stopper to prevent light and rainfall from entering. Numbered image frames were scribed onto the exterior surface of each minirhizotron prior to installation so that we could return to the same location within the minirhizotrons at all sampling dates. A total of 130 frames were scribed, one every 1.2 cm (Figure 2). The image frames were oriented vertically during installation. All minirhizotron images were collected on VHS videotape with a Circon Microvideo 9011 Color Agricultural Camera (Circon Co., Santa Barbara CA). The camera is attached to a pole and jig assembly that is used to control the depth and orientation of the camera lens in the minirhizotron (Figure 2). Each minirhizotron was imaged throughout the 1989 growing season, and imaging was resumed in the spring of 1990 after snowmelt. The data presented in this report were collected on 4/27, 6/11, 6/22, 7/18, 8/18, 9/16 and 10/14 in 1989, and on 4/24 and 5/23 in 1990.

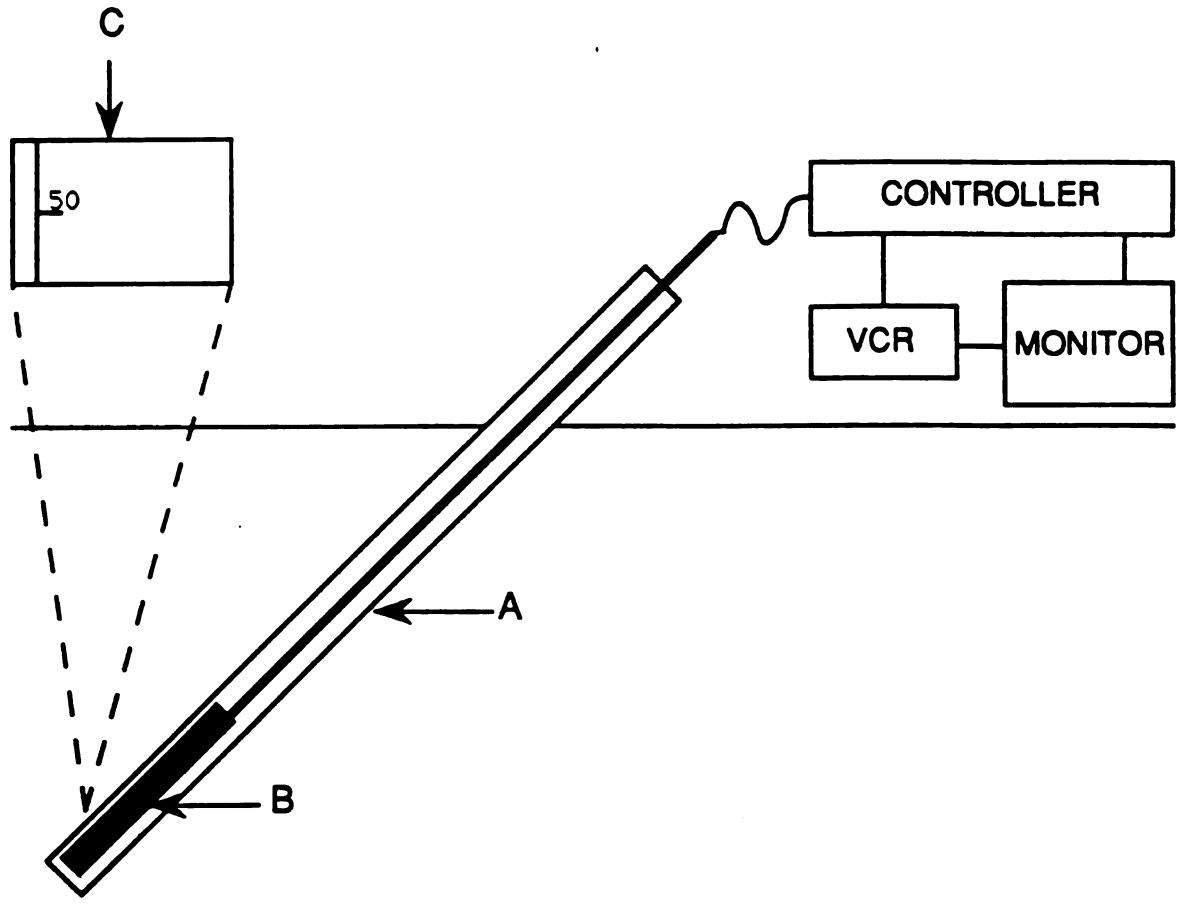

Figure 1.2 Diagram of the minirhizotron, scribing and camera system used to collect images. Components of the camera and image recording system are labelled. Item A is the minirhizotron itself, installed at a 45^{o} angle to the soil surface. Component B is the camera, which records an image 1.8 cm wide by 1.2 cm in height. A blow-up of image frame 50 is depicted in C, showing a scribed longitudinal line along the left edge of the image and a small numbered cross-hatch on this line. When filming, the longitudinal line was aligned immediately adjacent to the left edge of the image (as seen in the monitor), and the cross hatch was centered in the image using a reference mark on the monitor.

Image Analysis

An interactive PC-based software program (ROOTS) that we have developed was used to analyze the minirhizotron video images. A TARGA (Truevision Inc., Indianapolis IN) video board was used in conjunction with ROOTS to digitize the images from VHS tape, project them onto a computer monitor and temporarily save them on-screen for processing. The length and diameter of all roots present in each image was traced using a mouse, and the measurements were automatically calculated and written to a database file (dBASE III+, Ashton-Tate, Torrance, CA) by ROOTS. The tracings of each root were permanently saved by ROOTS on a separate disk file. An identification code was assigned to each root and written to the database. The code number was derived from the order in which a root was traced within an image (1, 2, 3, etc.); the frame (1-130), minirhizotron (1-4) and plot (1-3) in which it was located; and the date on which it was imaged (A-I). The same code (except for the collection date) was used for each root during the analysis of subsequent images. We were able to identify the same roots at subsequent dates by using ROOTS to recall and overlay the tracings and identification numbers from an image at time t-1 when analyzing time t images. Complete records were kept for each root throughout its development, even after it died and/or disappeared.

Each root was assigned a development stage code after it had been traced. Roots were classified as "new" if they first appeared in an image as white in color, and "white" at subsequent dates if they remained white or cream in color. Roots that turned, or first appeared as, tan to brown in color were classified as "brown". Those that turned black were classified as "dead". As roots decayed and disappeared, or disappeared without first moving into a "dead" state, they were classified as "missing".

When all the images from a given date had been analyzed, the database records were compiled by minirhizotron and plot. After images from all dates had been processed, the records for the entire year were combined. The final database for each plot was a time series of lengths, diameters and development stages for each root in all four minirhizotrons.

Fine Root Life History, Longevity and Dynamics

A cohort of roots produced between April 27 and June 11, 1989 was selected from each of two depths, (<30 cm, 194 roots and >30 cm, 140 roots), to study fine root development and life history. All roots (summed across plots) produced in this interval and still alive at the time of the June 11 observation were included in the cohorts. The mean root diameter for each cohort was determined, as were the frequency distributions (by diameter class) for root numbers

and root length. The development of the cohorts was followed for a period of 346 days (June 11, 1989 to May 23, 1990). The number of white roots moving into the brown, dead or missing stages was determined for each time period, as was the number of brown roots moving into the dead, missing or woody stages. Brown roots were observed for evidence of secondary vascular or cork cambial growth when determining woody status.

The total number of roots alive at the end of each interval was used to calculate percent survival of the original cohort. Means and standard deviations were derived using a formula (Cochran 1977) for estimating proportions from cluster samples (cohorts) with unequal numbers of elements (roots). Differences in final survival were tested using a simple t-test (alpha = .01, Steel and Torrie 1980). The probability of a root following any of the pathways depicted in Figure 2 (remaining in stage i or moving to stage j) was calculated by dividing the number of roots remaining in i or moving to j during t to t+1 by the number in state i at time t.

To calculate periodic and annual root production and mortality, the white, brown and total (white + brown) root lengths present on April 27, 1989 (time t = 0) were summed for each plot by depth (<30 and >30 cm). Production and loss of root length was followed for the next 363 days,

until April 24, 1990. The production of new white and brown root length was calculated for the intervals t to t+1 by summing the lengths of white and brown roots present at time t+1 that were not present at time t, and adding the length growth of existing roots. (All roots are white when first produced, and brown root "production" during a given interval actually reflects the browning of new white roots during the same period).

Mortality was calculated by summing the length of roots that moved into the dead or missing class during the same period, plus the length of any roots that first appeared in a dead state at time t+1. Percent production and mortality estimates for the interval t to t+1 were calculated by dividing the production and loss of white, brown and total root length during the interval by the initial (April 27, 1989) standing crop. The mean and standard deviation of each estimate was calculated using the method described above for percent survival (Cochran 1977).

Results

Root Life History and Longevity

The average diameters of the <30 and >30 cm depth cohorts were 0.42 mm ($\pm$0.18) and 0.49 mm ($\pm$0.21), respectively. The average diameter of the shallow cohort was less than that of

the deeper roots (t test alpha = .01), although the range of diameters was similar for both cohorts: 0.18 - 1.55 mm for the shallow cohort and 0.19 - 1.46 mm for the deep cohort. The distribution of root length and numbers among diameter classes was somewhat different between the cohorts (Figures 3 and 4). While 80% of root numbers and 76% of root length in the shallow cohort was comprised of roots less than 0.50 mm diameter, the corresponding values for deeper roots were only 64% and 56%. It is unlikely that many roots from herbaceous species were included in the cohorts, due to the very sparse ground layer in this stand (<3% total ground coverage). Given the preponderance of sugar maple in the overstory (83% BA and 75% of LAI), most of the roots we observed probably belonged to this species.

The decline in numbers of live roots was greatest early in the year at both depths (Figure 5). The mean 346 day survival for roots at <30 cm depth was 47.4($\pm$6.8)%, greater than that of 40.0($\pm$5.5)% for roots >30 cm deep (t-test, alpha = .01). Most mortality was attributable to roots that became missing before appearing dead. Of the 103 roots in the shallow cohort that died, only one passed into a dead stage before decaying or otherwise disappearing. At >30 cm, eight of the 84 roots that died first occurred as dead, rather than missing, roots.

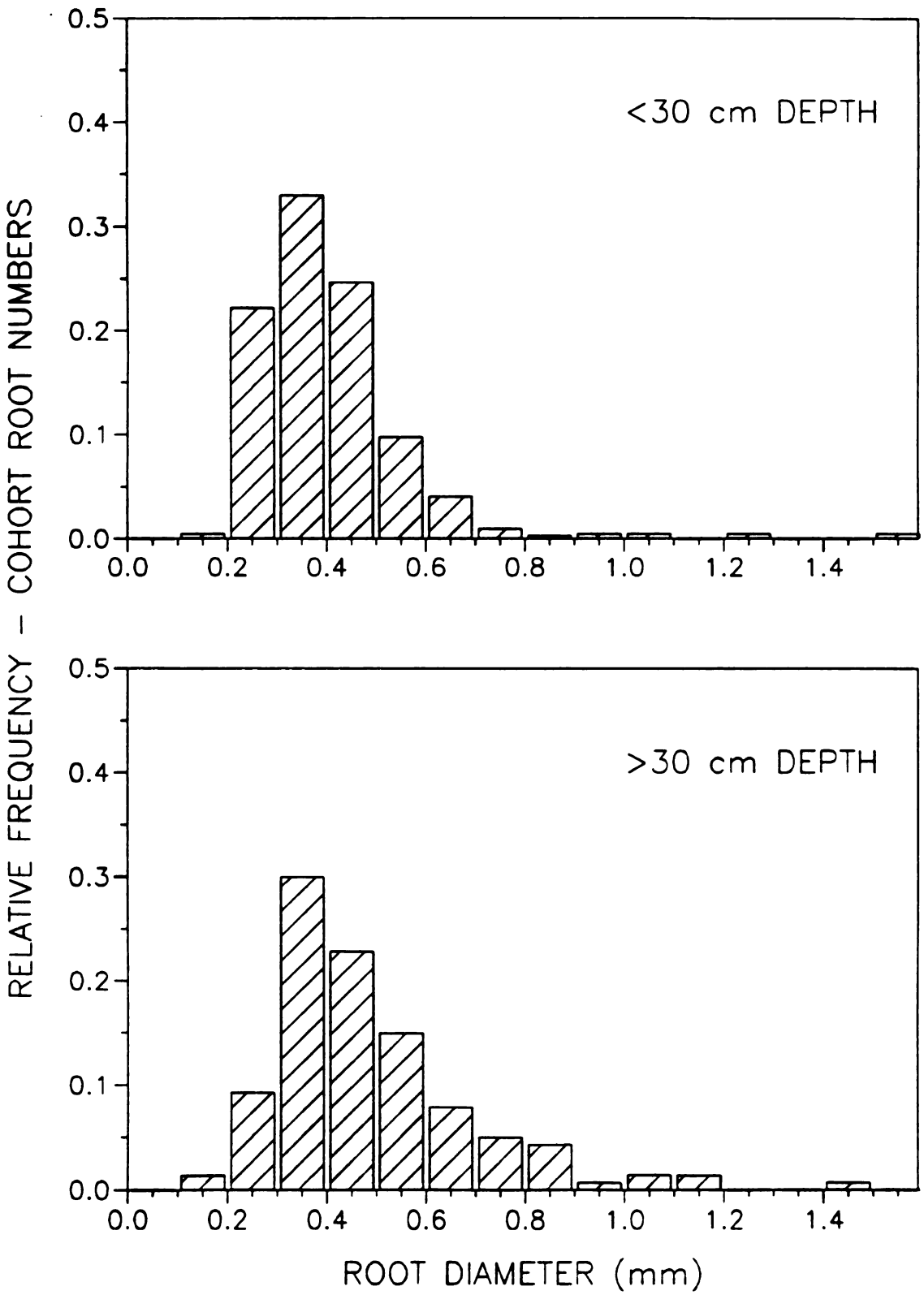

Figure 1.3 Initial distribution of root numbers among diameter classes for the <30 and >30 cm depth cohorts produced between April 27 and June 11, 1989.

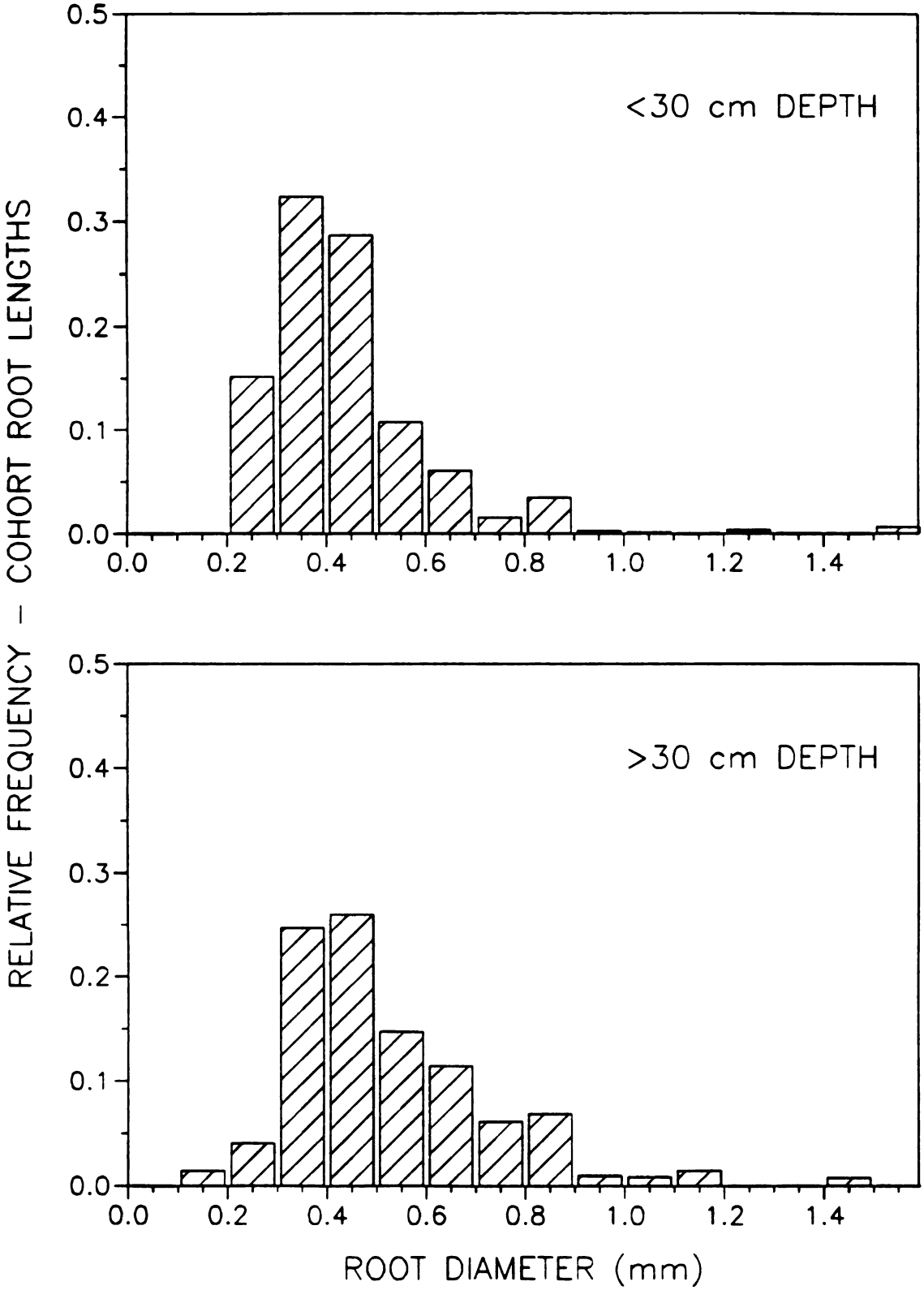

Figure 1.4 Initial root length distributions among diameter classes for the <30 and >30 cm depth cohorts produced between April 27 and June 11, 1989.

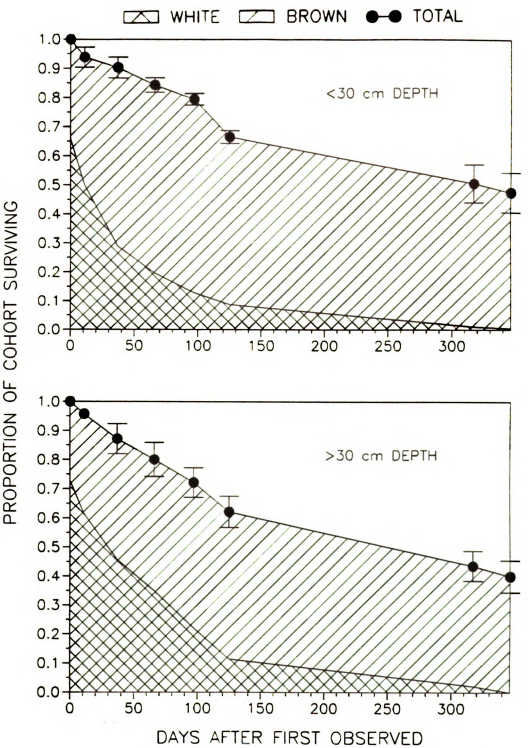

Figure 1.5 Percent survival, with standard deviations, of original root cohorts at <30 and >30 cm depths. The proportion the remaining cohort comprised of white and brown surviving roots is also shown. The period of observation covers 346 days between June 11, 1989 and May 23, 1990.

The portion of the surviving cohort consisting of white and brown roots changed considerably over time. Initially, both cohorts were comprised primarily of white roots (128 of 194 roots <30 cm depth and 102 of 140 roots > 30 cm depth). However, the portion of the cohorts comprised of white roots dropped rather dramatically (Figure 5). By the end of summer (125 days after the first observation), roughly 10% of the roots were still white in both cohorts. After 346 days, no white roots remained in the deep cohort, while only one of the roots from the shallow cohort remained white in color.

The stage transition probabilities presented in Table 2 show that white roots were most likely to remain in that state between observation periods, rather than move to some other stage. The chance of a white root dying (P_3) was low throughout the entire observation period. The probability of a white root turning brown (P_2) was considerably greater than the probability of it dying (P_3) during all time periods, regardless of depth. Browning probabilities were greater for shallow roots during most of the growing season (Table 2). Periods with high browning probabilities in the shallow roots generally correspond to periods of low soil moisture and high soil temperature at 15 cm (Figure 6). Brown root mortality probabilities (P_6) were greater for deep roots during the summer, but were similar at both depths from fall through spring. Brown root mortality was

Table 1.2 Transition probabilities for roots in various stages of development. P_1, P_2 and P_3 are the probabilities of a white root remaining white, turning brown or dying during a given time interval, respectively. P_4 and P_6 refer to the probability of a brown root remaining alive and brown or dying, respectively. The stage transitions are depicted graphically in Figure 1.

<30 CM DEPTH

TIME PERIOD	P_1	P_2	P_3	P_4	P_6
JUN 11 - JUN 22	0.76	0.17	0.07	0.95	0.05
JUN 22 - JUL 18	0.58	0.39	0.03	0.95	0.05
JUL 18 - AUG 16	0.68	0.32	0.00	0.92	0.08
AUG 18 - SEP 16	0.66	0.32	0.03	0.95	0.06
SEP 16 - OCT 14	0.68	0.28	0.04	0.81	0.19
OCT 14 - APR 24	0.12	0.82	0.06	0.74	0.26
APR 24 - MAY 23	0.50	0.50	0.00	0.93	0.07

>30 CM DEPTH

TIME PERIOD	P_1	P_2	P_3	P_4	P_6
JUN 11 - JUN 22	0.84	0.10	0.06	0.97	0.03
JUN 22 - JUL 18	0.74	0.21	0.05	0.88	0.12
JUL 18 - AUG 16	0.77	0.19	0.05	0.88	0.12
AUG 18 - SEP 16	0.63	0.27	0.10	0.90	0.10
SEP 16 - OCT 14	0.52	0.45	0.03	0.81	0.19
OCT 14 - APR 24	0.19	0.68	0.13	0.66	0.34
APR 24 - MAY 23	0.00	1.00	0.00	0.91	0.09

greatest between Sept. 16 and Oct. 14 at both depths (Table 2), a period in which considerable leaf fall occurred (Table 1). The overwinter mortality probabilities were low for white and brown roots at both depths. We did not observe any roots in either cohort that developed obvious signs of secondary growth during the 346 days the two cohorts were followed.

Root Production and Mortality (Turnover)

Considerable root length was produced in the spring and early summer of 1989 at both depths (Table 3), but very little occurred from fall through winter. Root length production at the <30 cm depth was about evenly distributed among white and brown roots from June 11 onward, except during the period from July 18 to August 18, when there was considerably more white root length produced. Soil moisture increased rather substantially during this period (Figure 6). White length production was high for deep roots until the end of summer, and then rapidly dropped off. There was a considerable increase in the production of white root length from July 18 to August 18 at >30 cm, just as there was in the shallow roots. However, there was not a corresponding increase in soil moisture at the 75 cm depth (Figure 6). Other than during the first time period, brown length production was spaced rather evenly throughout the year at >30 cm. The annual production of white root length

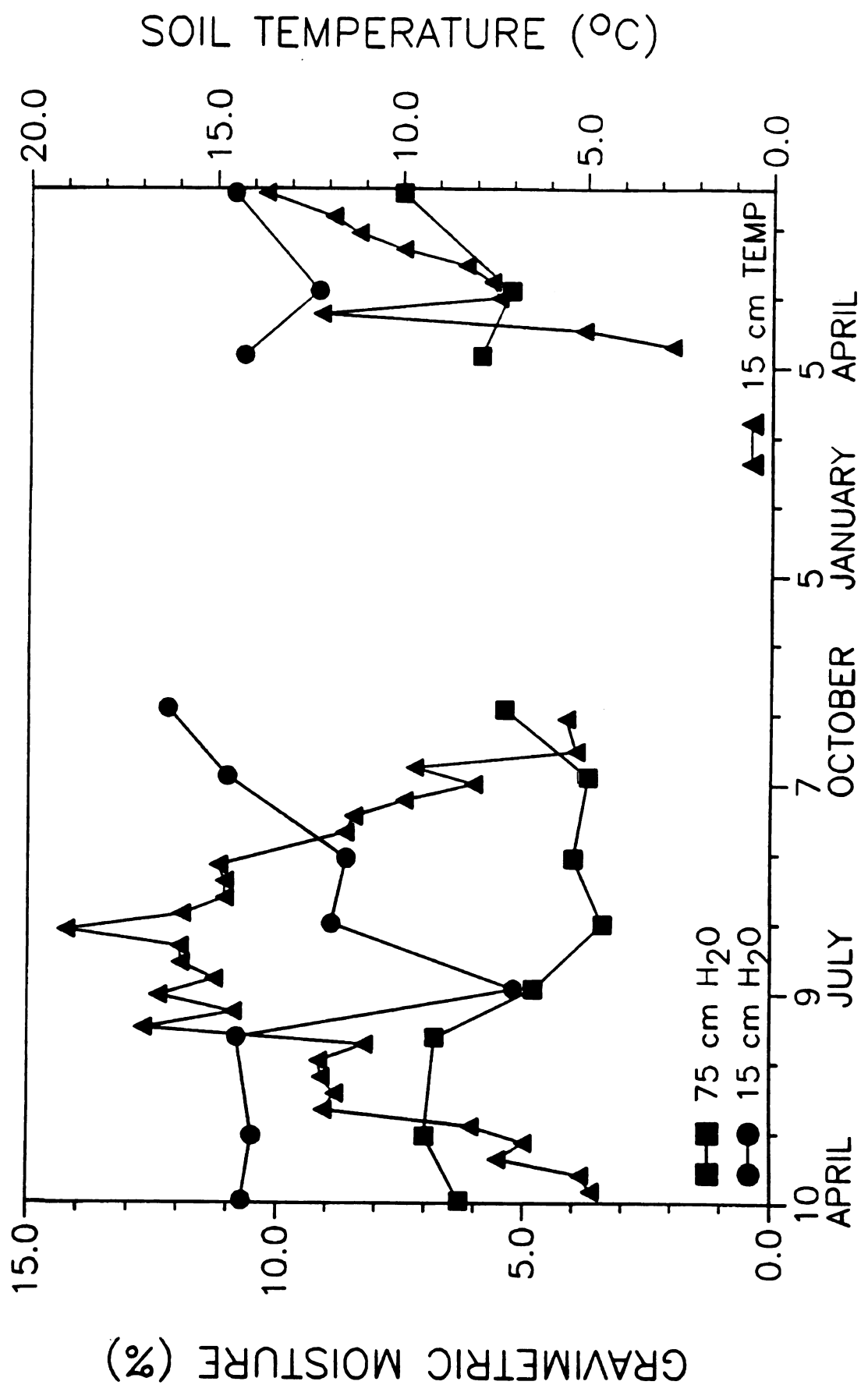

Figure 6. Average soil moisture (15 and 75 cm depths) and soil temperature (15 cm depth) during the 1989 and early 1900 growing seasons. Values are plot averages.

Table 1.3 Periodic root length production and mortality for total, white and brown root length. Values are expressed as a percentage of the April 27, 1989 live root standing crop (plot mean) at both <30 and >30-cm depths. Standard deviations are in parentheses.

<30 CM DEPTH

TIME PERIOD	WHITE ROOT PRODUCTION	BROWN ROOT PRODUCTION	TOTAL PRODUCTION	WHITE ROOT MORTALITY	BROWN ROOT MORTALITY	TOTAL MORTALITY
4/27 - 6/11	27.9 (1.2)	12.0 (1.8)	40.0 (2.9)	3.9 (1.4)	4.6 (1.3)	8.5 (2.0)
6/11 - 6/22	5.8 (1.4)	8.6 (0.5)	14.4 (1.9)	1.8 (1.0)	2.6 (1.9)	4.4 (2.8)
6/22 - 7/18	8.9 (4.4)	5.0 (2.2)	13.9 (2.3)	0.8 (0.3)	3.0 (0.8)	3.8 (0.5)
7/18 - 8/16	12.8 (4.0)	5.2 (1.5)	18.0 (3.9)	1.8 (1.0)	6.9 (0.5)	8.7 (0.5)
8/18 - 9/16	5.6 (1.6)	4.0 (1.4)	9.6 (1.4)	2.6 (1.0)	6.8 (1.1)	9.4 (2.1)
9/16 - 10/14	2.4 (1.1)	1.6 (0.7)	4.0 (1.7)	0.7 (0.2)	12.0 (0.5)	12.7 (0.3)
10/14 - 4/24	2.6 (1.3)	4.9 (2.3)	7.6 (3.5)	3.1 (2.3)	25.3 (3.2)	28.4 (5.0)
AVG ANNUAL	66.1 (9.6)	41.3 (7.6)	107.5 (5.9)	14.7 (4.4)	61.2 (5.1)	75.9 (8.5)

>30 CM DEPTH

TIME PERIOD	WHITE ROOT PRODUCTION	BROWN ROOT PRODUCTION	TOTAL PRODUCTION	WHITE ROOT MORTALITY	BROWN ROOT MORTALITY	TOTAL MORTALITY
4/27 - 6/11	39.8 (6.1)	17.1 (2.9)	56.8 (8.3)	3.7 (2.0)	1.5 (0.9)	5.2 (2.9)
6/11 - 6/22	12.6 (2.6)	3.3 (1.3)	15.8 (3.1)	1.8 (0.8)	4.5 (4.6)	6.3 (5.4)
6/22 - 7/18	10.6 (4.1)	2.2 (1.7)	12.9 (4.8)	5.0 (3.2)	7.2 (4.9)	12.3 (8.1)
7/18 - 8/16	27.1 (26)	4.0 (1.7)	31.1 (25)	2.2 (1.5)	5.1 (1.8)	7.3 (0.9)
8/18 - 9/16	3.7 (2.3)	1.7 (1.5)	5.4 (2.2)	19.1 (15)	9.5 (4.6)	28.6 (19)
9/16 - 10/14	4.4 (1.6)	1.6 (0.5)	5.9 (1.7)	2.2 (1.1)	15.6 (5.6)	17.8 (6.4)
10/14 - 4/24	2.5 (1.8)	5.9 (1.9)	8.5 (3.1)	5.0 (2.3)	27.4 (6.5)	32.4 (8.4)
AVG ANNUAL	100.7 (33)	35.7 (1.7)	136.4 (31)	39.0 (20)	70.9 (25)	109.8 (43)

was about 50% greater than brown length production at <30 cm, but was more than twice brown length production at the greater depth (Table 4). As noted above (see Methods), all roots are white when first produced, and high rates of brown root "production" during a given interval actually reflect a rapid browning of new roots during the same period. The greater proportional production of white root length deeper in the soil thus reflects a less rapid rate of browning at greater depths.

Total shallow root mortality was more evenly distributed throughout the year than was production, but increased gradually from summer through fall (Table 3). There was generally more total mortality at depths >30 cm, especially towards the end of the growing season. The majority of total root mortality at both depths was due to the loss of brown root length (Tables 3 and 4). Overwinter length loss was minimal at both depths (Table 3, Figure 7). Root length peaked on August 18, 111 days after the first observation. The decline from summer through fall was greater for deep roots than shallow roots (Figure 7). Annual production was greater than annual mortality at both depths (Table 4), resulting in a net increase in total root length.

Table 1.4 Initial root length standing crops, and the production and mortality of total, white and brown root length from April 27, 1989 to April 24, 1990 at <30 and >30 cm depths. Lengths are plot averages in cm, with standard errors of the mean in parentheses. (TOTAL length production and mortality includes roots that first appeared in a dead state, and thus the sum of WHITE and BROWN production and mortality does not always equal the TOTAL.)

<30 CM DEPTH

	TOTAL	WHITE	BROWN
Standing Crop	93.4 (6.0)	29.5 (9.9)	63.9 (5.8)
Production	106.4 (10.9)	61.6 (11.8)	43.1 (7.1)
Mortality	76.5 (11.5)	12.1 (4.9)	62.6 (7.2)

>30 CM DEPTH

	TOTAL	WHITE	BROWN
Standing Crop	57.1 (6.2)	31.8 (15.2)	25.3 (2.7)
Production	85.3 (10.3)	57.3 (13.6)	25.8 (3.2)
Mortality	69.8 (19.3)	20.5 (9.2)	47.1 (10.7)

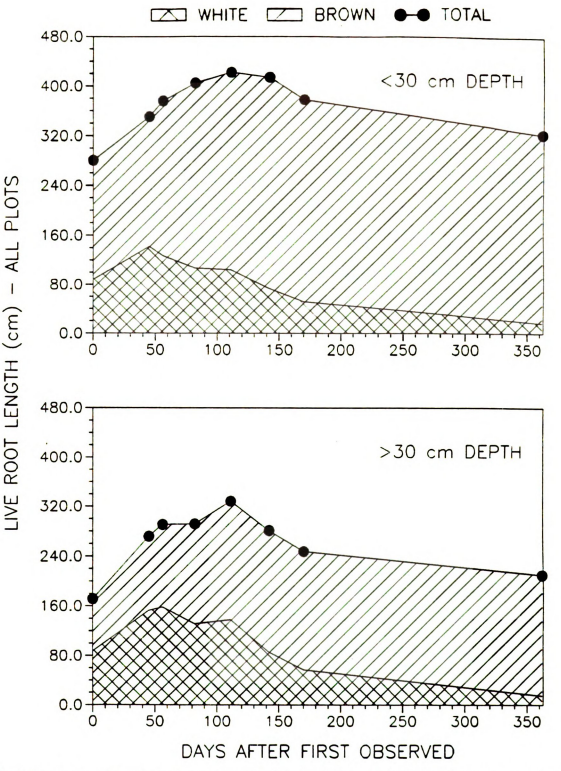

Figure 1.7 Temporal changes in total, white and brown root lengths (cm) at <30 and >30 cm depth, summed across all plots. The period of observation covers 363 days, from April 27 ,1989 to April 24, 1990.

Discussion

The distribution of root numbers and lengths suggests that the shallow root system is, on average, comprised of thinner (possibly longer) roots than the deep root system. Silberbush and Barber (1983) suggested that a morphological strategy favoring long, thin roots may be more effective with respect to resource capture than one consisting of shorter, thicker roots. In both cohorts most roots were less than 0.5 mm in diameter, and most of the root length consisted of roots of similar size.

White roots in the forest we studied are more likely to turn brown than die at all times of the year (Figure 4). The result is a rapid "loss" of white root length and numbers from the cohorts, while total length and numbers change more gradually. Our results also show that the fine roots of deciduous trees can remain white considerably longer than those of coniferous trees (Bartsch 1987). It is difficult to place any functional significance on these results because of our lack of understanding regarding physiological differences between white and brown roots. Cortical browning is temporally but not causally associated with the process of suberization, and roots may be partially suberized long before they turn brown (Richards and Considine 1981; Johnson-Flanagan and Owens 1985). The ability of "suberized" roots to absorb water to some extent

apparently exists (Kramer and Bullock 1966, Chung and Kramer 1975, Atkinson 1983, 1985), but more sophisticated experiments are needed for a greater understanding of development and age associated changes in root function. Only then can we link root form and function to aboveground processes. The effects of root aging on carbon and nutrient cycling belowground also cannot be ignored. We have previously shown that sugar maple roots in this forest lose about 40% of their N concentration upon browning (Goldfarb et al. 1990). The fact that most fine root mortality is attributable to the loss of brown roots suggests that development-stage differences in root mortality probably have a significant impact on the quality of litter returned below ground.

The cohort survival data show that fine roots are capable of relatively long-term survival. Few other estimates of root longevity in deciduous forests are available in the literature. However, if we assume that the lifespans of fine roots are normally distributed, then one half of the time required for the fine root pool to turnover once should roughly equal the mean fine root lifespan. Under these assumptions, the data of Nadlehoffer et al. (1985) yield a mean lifespan of slightly more than 6 months for roots <3.0 mm in a Wisconsin sugar maple stand (turnover time = 0.94 yr). Visual inspection of the data of McClaugherty et al. (1982) shows that the mass of roots <0.5 mm lost to

mortality each year in a mixed hardwood stand in Massachusetts was around 100% of the standing crop, equal to an average fine root lifespan of about 6 months. Using data from our study, the 76% annual length mortality of roots <30 cm in depth equates with a mean lifespan of 0.65 years, or 8 months. The corresponding value for roots >30 cm in depth is 0.46 years, or 5.5 months. It appears from Figure 5 that the mean lifespan of roots produced in the spring is closer to 10 months (= time to 50% survival). Apparently there are differences in the mean longevity of roots produced at different times of the year. To more accurately measure fine root longevity it will be necessary to follow multiple cohorts of roots produced at various times of the year until all individuals have succumbed to mortality, an avenue we are continuing to pursue.

In the shallow root system, most root production occurred prior to August 18. Virtually no new root length was produced from late fall through spring. White, brown and total root mortality was spread rather evenly throughout the year, other than a small peak between September 16 and October 14 (Table 3). The data show that deep root production was high through August, and declined considerably thereafter. Conversely, almost half of total root length was lost late in the year (Aug. 16 - Oct. 14), when leaf senescence and the majority of leaf fall took place (Table 1). The fall peak in shallow root mortality

also coincided with the period of greatest leaf senescence (Tables 1 and 3). There is apparently some degree of temporal synchrony between leaf senescence and root mortality, although we have no physiological data to suggest a causal link between the two processes. While our data permit little more than speculation at this point, the possibility that fine root longevity is under strong endogenous control deserves further study.

The seasonal trends in total live root length we observed are in general agreement with patterns of fine root biomass estimated from other North American deciduous forests. Joslin and Henderson (1987) and McClaugherty et al. (1982) measured late summer peaks for fine root biomass, as we did for root length (Figure 7). We observed a substantial loss of root length during late summer and autumn at both depths, but minor overwinter losses of root length and numbers. Joslin and Henderson (1987) and McClaugherty et al. (1982) also observed a substantial autumnal decline in fine root biomass. They and Nadelhoffer et al. (1985) all reported minimal losses of root biomass during the winter months as well.

Considerable production occurred throughout the growing season at both depths (Table 2). Likewise, substantial amounts of root length were lost at both depths from spring through late fall. These data confirm the statements of

others (e.g. Fairley and Alexander 1985; Fogel 1985; Joslin and Henderson 1987; Persson 1979) that estimates of fine root production and turnover that do not accurately account for concurrent production and mortality are potentially in error. Substantial amounts of fine root production and turnover do occur simultaneously, at least in the system we studied, and temporal separation of these processes should not be assumed in other ecosystems. Had we calculated root length production based on the maximum difference in length standing crops (sensu the min-max method of McClaugherty et al. 1982), our estimates for annual production would have been 53 and 90% of the April 27 shallow and deep root length standing crops, respectively. These numbers are considerably less than the corresponding values of 107 and 136% we derived from direct observations of length growth and production (Table 2).

A rather unexpected finding was the apparent rapid decay of dead roots, as evidenced from the number and length of roots that passed into the missing stage without first becoming obviously dead. This phenomenon has been observed by others working with rhizotrons of various types (R. Fogel, personal communication), and the mechanisms responsible need to be identified. Movement of the minirhizotrons between videotaping is unlikely because there should have been a simultaneous disappearance of substantial numbers of roots within a minirhizotron image, something we did not observe.

The necessity that we use ROOTS to overlay the tracing of a root from time t-1 on its image at time t for our cohort analyses revealed that temporal differences in camera placement were generally much less than 0.5 mm.

Herbivory is an alternative explanation, but the available literature would suggest that it is unlikely. Although many groups of soil arthropods contain bacteria and fungal feeders (Anderson and Ineson 1983; Richards 1987), little importance has generally been ascribed to the invertebrate fauna of forest soils as major consumers of live root tissue (Ausmus et al. 1978; Fogel 1983, 1985; Magnussen and Schlenius 1980). We see very little evidence of herbivory in the form of partially eaten roots or fecal deposits on the minirhizotrons. It must be acknowledged, however, that knowledge of the composition and feeding biology of the soil fauna is rather incomplete in most forest ecosystems, including the one we studied.

Rapid decomposition after death seems to be the most likely explanation for the disappearance of fine roots, although one somewhat difficult to defend if published estimates of root decomposition are used as the benchmark by which minirhizotron observations are to be compared (McClaugherty et al. 1984; Fahey et al. 1988; Joslin and Henderson 1987). Present estimates of decomposition rates are considerably slower than those we observed in the minirhizotrons, and

resolving the two poses some difficulty. It is likely that litterbag studies underestimate rates of decay to some extent, as removing roots from the soil for washing, drying and weighing severely disturbs the rhizosphere and rhizoplane communities. The effect of litterbag mesh size must be considered (Fogel 1990; McClaugherty et al. 1984), as small openings can restrict the entry of various detritus-feeding invertebrates. Most of the roots we observed were less than 0.50 mm in diameter, and the difficulty of recovering these small roots from the soil may result in litter samples that are biased towards larger, more recalcitrant roots. It is also possible that the readily available carbon supply (live and dead roots) on the minirhizotron surface might stimulate rates of root decay by attracting and supporting greater numbers of decomposers than are found in non-rhizotron soil. In any event, the rapid disappearance of roots from minirhizotrons deserves further study. It is necessary that the discrepancy between the rapid disappearance of roots from rhizotrons and the rather slow decomposition rates reported by those using buried bags be resolved. If the minirhizotrons give a more accurate picture of the process of root decomposition than buried bags, the ramifications for estimates of carbon and nutrient cycling rates are considerable.

It is possible that the growth or development of the roots we observed could have been altered in some way due to the

presence of the minirhizotrons. The minirhizotron is a rather inert surface, and may eliminate some biotic factor (either adverse or beneficial) with which roots must contend when growing through the soil. Ease of growth may also be facilitated along the minirhizotron surface. However, the general agreement of trends in our data with those derived from destructive harvests suggests that any effect of the minirhizotron is probably small. The fact that we were able to observe and quantify phenomena that were previously thought to occur (like the simultaneous production and mortality of fine roots) suggests that minirhizotrons can be of considerable use when addressing certain questions concerned with root dynamics. By linking direct observations of fine root demography with simultaneous measurements of root biomass, nutrient content and the soil environment, a better understanding of the role of roots in ecosystem processes should be possible.

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Chapter II

SPATIAL VARIATION IN TREE ROOT DISTRIBUTION AND GROWTH ASSOCIATED WITH MINIRHIZOTRONS

Abstract

Four minirhizotrons were installed in each of three replicate plots in a deciduous forest dominated by Acer saccharum Marsh. The length growth of tree roots along the surface of the minirhizotrons was measured for a period of one year, and the resulting data were analyzed in nested, averaged and pooled arrangements. The analyses of nested data showed that spatial variation in root growth and abundance among minirhizotrons within plots was greater than variation among plots. Averaging data from minirhizotrons within plots prior to analysis reduced variation about plot means, but extensive intraplot variation invalidates this approach on statistical grounds. Both nested and averaged data failed to account for the contribution of individual roots to the mean, and root production rates were consequently overestimated. Pooling the data from the four minirhizotrons reduced variation about the means, and resulted in a more representative estimate of root production rates. The analysis of composited data can be used to incorporate small scale variation into a single replicate sample in those circumstances where the activity

of the root systems of plant communities is the object of study.

Introduction

Recent advances in microvideo technology have made minirhizotrons popular research tools in both agronomic (e.g. Cheng et al., 1990; Hansson and Andren, 1987; Keng, 1988; Upchurch and Ritchie 1983) and natural plant communities (e.g Eissenstat and Caldwell, 1988; Hendrick and Pregitzer 1992). During these and other research efforts, several analytical and statistical problems with minirhizotron data have been identified. High minirhizotron-to-minirhizotron (i.e. spatial) variability in root density and distribution has proven to be especially problematic. Coefficients of variation range to as high as several hundred percent (Merrill et al., 1987; Upchurch and Ritchie, 1983; Upchurch 1987), often making treatment effects (if any) difficult to detect. Quantifying and controlling spatial variation is necessary to properly execute minirhizotron experiments focused on root systems at the level of the plant community or ecosystem, but information on the extent of variation among minirhizotrons at various levels within the hierarchy of an experimental design is generally lacking.

Individual minirhizotrons are often the sampling units upon which measurements of roots are made, and several minirhizotrons are typically nested within replicate experimental units, usually a field plot or greenhouse pot

(e.g. Beyrouty et al., 1987; Box and Johnson, 1987; Cheng et al. 1990). Alternatively, minirhizotrons are sometimes treated as experimental units, with measurements of root numbers or length made along several different transects (sampling units) within the minirhizotron (Eissenstat and Caldwell, 1988; Gregory, 1979; Meyer and Barrs, 1985; Sanders and Brown 1978). Rarely, however, has the full extent of among-sampling unit and among-experimental unit variability in the data been reported. Instead, sampling unit averages are the typical data upon which statistical analyses are made.

As an alternative to analyzing sampling unit averages as primary data, a few investigators have performed statistical analyses on composited data from multiple minirhizotrons (sampling units) within replicate experimental plots (Hendrick and Pregitzer 1992) or from multiple transects (sampling units) within replicate minirhizotrons (Hansson and Andren 1987). Pooling minirhizotron data incorporates spatial variation in root abundance and activity into a single aggregate sample. Multiple samples within experimental units are commonly pooled in studies of soil and plant characteristics, but the assumptions and implications of this practice in minirhizotron research have not been discussed.

Our objectives in this paper are: 1) to more fully describe the extent of spatial variation in tree root system attributes; 2) to discuss the impact of analyzing the same minirhizotron data under different experimental arrangements; and 3) to suggest some ways to better control spatial variability through analytical means. We have extensive minirhizotron data on individual tree roots from multiple minirhizotrons (sample units) within replicated plots (experimental units), and hence the ability to analyze minirhizotron data in a variety of experimental arrangements.

Methods

Our study site is a second growth northern hardwoods stand dominated by sugar maple (Acer saccharum Marsh), and is located in the northern lower peninsula of Michigan (Manistee County, 40° 42′ N, 85° 43′ W), USA. The soil is a Typic Haplorthod of the Blue Lake and Kalkaska series. Three 30 m by 30 m analogous plots were established at the site in 1987 (Burton et al. 1991). In June of 1988, 4 randomly located minirhizotrons (2 m long x 5.08 cm inside diameter) were permanently installed in each plot at a 45° angle to the soil surface, and to a depth of 165 cm along their length (110 cm in vertical depth). The portion of the minirhizotron extending above the soil surface was painted and capped with a rubber stopper to prevent rainfall and

light from entering. Numbered image frames were scribed onto the exterior surface of each minirhizotron prior to installation so that we could return to the same location within the minirhizotrons at all sampling dates. A total of 130 frames were scribed, one every 1.2 cm. The image frames were oriented vertically during installation. Minirhizotron images were collected on VHS videotape with a Circon Microvideo 9011 Color Agricultural Camera (Circon Co., Santa Barbara CA). Each minirhizotron was imaged throughout the 1989 growing season, and imaging was resumed in the spring of 1990 after snowmelt. The data presented in this report were collected on 27/4, 11/6, 22/6, 18/7, 18/8, 16/9 and 14/10 in 1989, and on 24/4 and 23/5 in 1990.

An interactive PC-based software program (ROOTS) that we have developed was used to analyze the minirhizotron video images. A TARGA (Truevision Inc., Indianapolis IN) video board was used in conjunction with ROOTS to digitize the images from VHS tape, project them onto a computer monitor and temporarily save them on-screen for processing. The length of all roots present in each image was traced using a mouse and written to a database file (dBASE III+, Ashton-Tate, Torrance, CA) by ROOTS. Individual roots are defined here as root segments present and visible within the minirhizotron images. The tracings of each root were permanently saved by ROOTS on a separate file. Each root was classified as live or dead based upon its appearance.

Dead roots were distinguished from live roots by one or more of the following characteristics: very dark brown or black color, partial decay of the existing root and/or the appearance and growth of fungal mycelia around the root. Roots that completely decayed and disappeared were classified as "missing".

An identification code was assigned to each root and written to the database. The code number was derived from the order in which a root was traced within an image; the frame, minirhizotron and plot in which it was located; and the date on which it was imaged. The same code (except for the collection date) was used for each root during the analysis of subsequent images. We were able to identify the same roots at successive dates by using ROOTS to recall and overlay the tracings and identification numbers from an image at time t-1 when analyzing time t images. Complete records were kept for each root throughout its development, even after it died and/or disappeared. After the images from all sampling dates had been processed for each minirhizotron, the records for the entire year were combined. The final database for each minirhizotron was a time series of lengths and condition (live, dead or missing) for each root. Data presented here are from the upper 30-cm of the soil only.

To calculate root production, the total live root length present on the first imaging date (27/4/89, t = 0) was summed for each minirhizotron. Root length production was followed for the next 363 days (24/4/90). The production of new root length was calculated for the intervals t to t+1 by summing the lengths of new live or dead roots present at time t+1 that were not present at time t, and then adding the length growth of existing roots. Root "production" thus includes both the growth of existing roots and the production of new roots for a given time interval. Annual root length production was calculated by summing the production values for each observation period. The annual production rate, expressed as a percentage of initial root length, was calculated by dividing total annual length production by the initial (27/4/89) root lengths.

The data were analyzed under three different experimental arrangements: 1) a nested design with individual minirhizotrons as subsamples within replicate plots (s=4, r=3, n=12); 2) minirhizotrons as duplicates within replicated plots, with averages of the duplicates treated as the primary data (n=3); and 3) data from each minirhizotron pooled within replicate plots (n=3). To determine the extent to which root length production rates were related to the initial amount of root length present in each minirhizotron, a correlation of total annual length production with initial root length was made (n=12).

Results

A summary of the statistical analyses (Table 1) shows that the same data, analyzed under different experimental arrangements, can lead to different levels of variation around estimates of the mean. The mean initial root length densities ($mm \cdot cm^{-2}$) and root length production values ($mm \cdot cm^{-2} \cdot yr$) are the same regardless of the manner in which the data were arranged prior to analysis. However, the variation around the mean differs widely among the three analyses. When data from individual minirhizotrons are treated as samples within the replicated plots, coefficients of variation (CV's) for both initial root length density and annual root length production are around 50%. (The standard deviation in this arrangement was calculated from the experimental, i.e among plot, error mean square of the nested ANOVA; Steel and Torrie 1980.) Alternatively, when the data from each minirhizotron are averaged by plot and then analyzed, CV's for initial length and length production are 11 and 21%, respectively; a considerable reduction in variation. This improvement is not unexpected, as one source of variation (among minirhizotrons within plots) has been removed in this arrangement of the data. When minirhizotron data are pooled by plot prior to analysis, CV's for initial length and annual production are the same as those where the data is averaged over the tubes in each

Table 1. Analysis of initial root length, annual length production, and annual production rate (annual length production as a percentage of initial root length), under three experimental arrangements. Initial length and length production are expressed in mm of root length per cm^{-2} of minirhizotron viewing surface. Data shown are means, standard deviations and coefficients of variation.

	Mean	SD	CV%
Minirhizotron Data as Subsamples within Plots (s=4, n=3)			
Initial length (mm/cm^{-2})	3.57	2.02	56
Annual production (mm/cm^{-2})	3.83	1.83	48
Annual production rate ($\%/yr^{-1}$)	131	76	58
Minirhizotron Data Averaged within Plots (n=3)			
Initial length (mm/cm^{-2})	3.57	0.40	11
Annual production (mm/cm^{-2})	3.83	0.80	21
Annual production rate ($\%/yr^{-1}$)	131	38	29
Minirhizotron Data Pooled within Plots (n=3)			
Initial length (mm/cm^{-2})	3.57	0.40	11
Annual production (mm/cm^{-2})	3.83	0.80	21
Annual production rate ($\%/yr^{-1}$)	106	11	10

plot. Again, within-plot variation among minirhizotrons has been removed (combined into one sample) in this arrangement of the data. The means of percentage production rates differ among the three arrangements of the data (Table 1). The means for the nested and averaged data were the same. This was expected to be the case. The grand mean of n plot means, each derived from m minirhizotrons, will be the same as the overall mean of the nm minirhizotrons, provided that the number of minirhizotrons in each experimental plot is the same.

The production rate derived from the pooled data (106%) is considerably lower than the rate derived via the other two arrangements of the data (131%). There was no apparent relationship between the initial amount of root length present in a minirhizotron and the amount of root length produced along its surface (Figure 1). The Pearson product moment coefficient between initial root length and annual production was very low (0.008) and not significantly different from zero (alpha = 0.05).

The results of the nested ANOVA of total root length, with minirhizotrons as subsamples, are shown graphically (Figure 2). Variation in initial root length among minirhizotrons within a plot (sampling error) was greater than the variation among plots (experimental error). These data suggest that the spatial distribution of tree roots in the

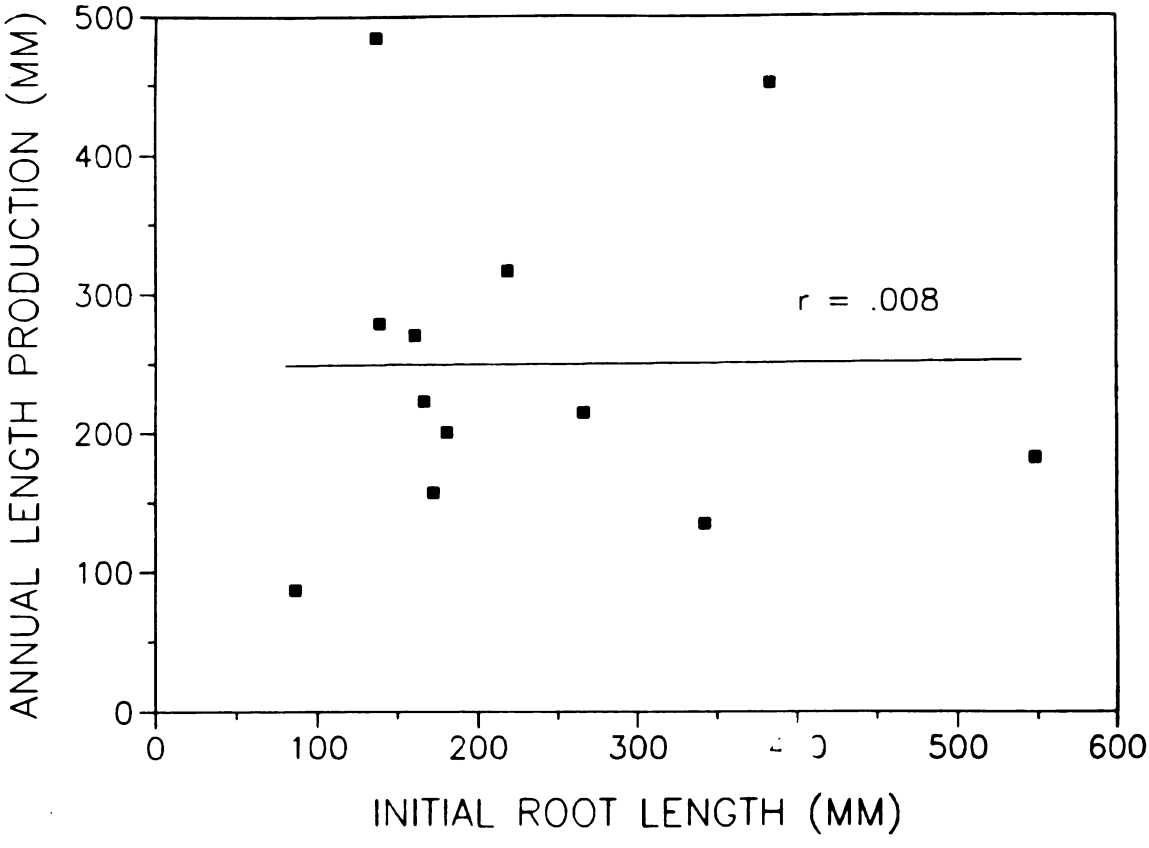

Figure 2.1 Relationship between initial root length (27/4/89) in the upper 30-cm of soil and total production during the following year, as viewed with the minirhizotrons. Data shown are from 12 minirhizotrons, four within each of three replicate plots.

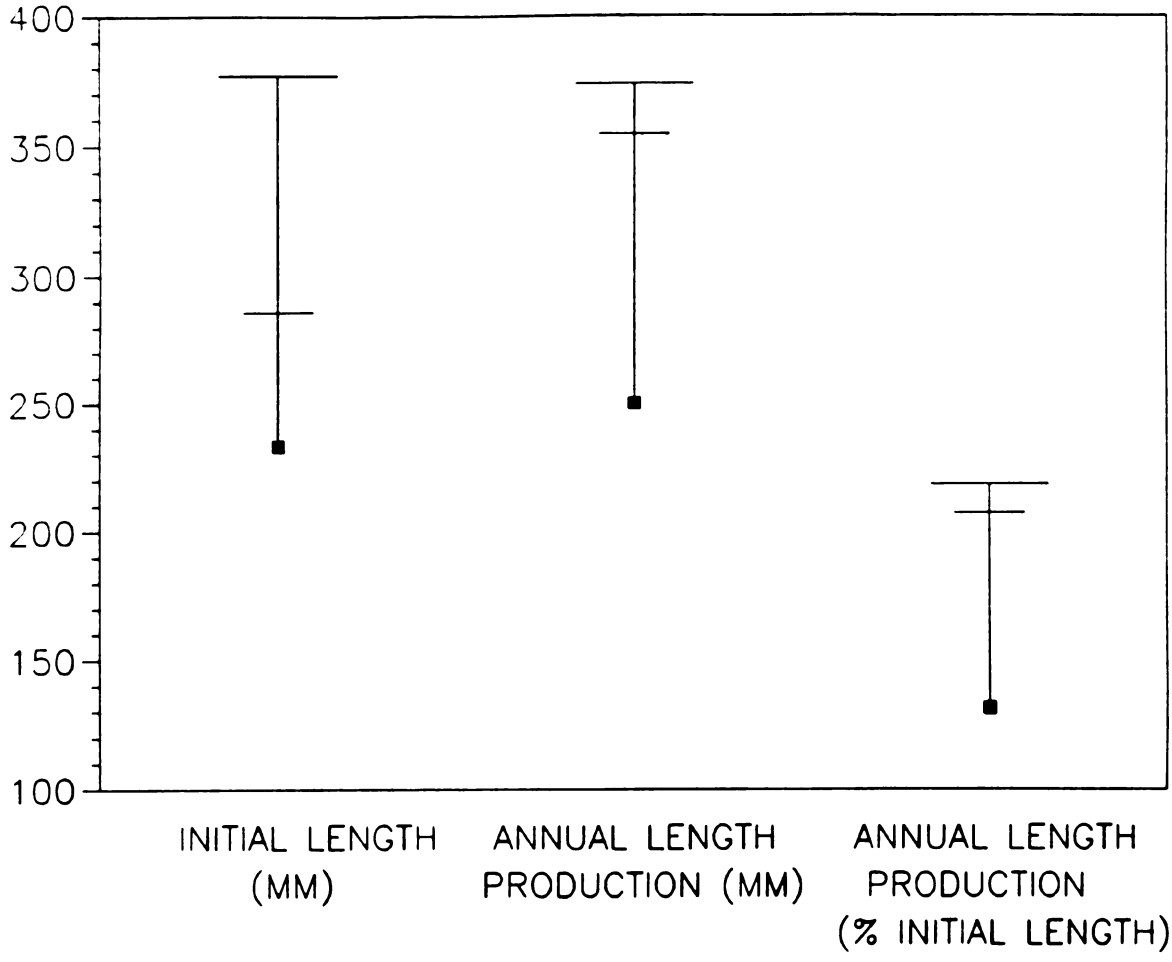

Fig. 2.2 Plot means, sampling (outer, wide bars) and experimental (inner, narrow bars) error for initial root length, annual length growth and and annual production as a percentage of initial length. Units for Y-axis are in parentheses below X-axis label for each estimate.

forest is highly variable over quite small areas; distances between minirhizotrons within plots vary from one to several meters, while plots are up to several 10's of meters apart. Length production and production rates show different spatial patterns. Large scale (among plot) variation in these variables is of approximately the same magnitude as small scale (within plot) variation.

Discussion

There is no one right way to analyze all types of minirhizotron data. Different experimental designs dictate different statistical analyses, as do the hypotheses and questions being addressed. However, general statistical principles should guide the process of analyzing data from an experiment in which the data are arranged in a nested or hierarchical fashion. For example, if more than one minirhizotron is sampled within each replicate experimental unit, or if more than one transect is sampled in each minirhizotron, the data should not be averaged prior to analysis. Averaging data from transects within minirhizotrons or minirhizotrons within plots is undesirable unless variability among the sampling units is effectively zero. However, our data (Figure 2) show that variability among the minirhizotrons within our plots is considerable, greater in fact than variation among plots. We suspect that this may be true in other studies and experimental scenarios

as well. The loss of information on among-sampling unit variability resulting from the analysis of averaged data leads to a more conservative estimate of experimental error and a greater risk of making a Type I error.

Instead of averaging, statistical analyses should be performed on either nested or pooled data; perhaps both. A nested ANOVA should always be performed first to ascertain the extent of variation at both the experimental and sampling unit levels. If sample unit variation is low relative to variation among experimental units, only a nested ANOVA should be performed; compositing or pooling the data will have little effect on estimates of means and variation. In these circumstances, the contribution of each minirhizotron should be weighted by the number of roots or amount of root length growing along its surface. If sampling error is large relative to experimental error, other options are available. It is possible to reduce intraplot variation by computational means (without increased replication) through an analysis of covariance (ANCOVA) in a nested design if root abundance and activity are related in a systematic fashion. However, abundance and growth are rather uncoupled in the root system we studied (Figure 1).

Increased replication or an adjustment in the number of sampling units can also be employed. When sampling error is

greater than experimental error, standard analyses of design efficiency are precluded and determining the proper number of experimental units and the allocation of sampling units among them can be difficult. It is apparent from our data that little gain in precision would be made by increasing the number of minirhizotrons within plots without a concomitant increase in the number of plots. The formulas presented by Sokal and Rolf (1981, pp 309-310) indicate that to achieve a mean standard error of 20% for length growth at our study site, a minimum of 5 replicate plots, each with 10 minirhizotrons, is required. This number is not excessively high from a logistical standpoint, but might be financially prohibitive if the cost of establishing replicate plots is high (as was our experience) or if a large number of experimental treatments are to be applied.

If deemed appropriate, data from multiple subsamples can be pooled prior to analysis to reduce variation among experimental units. Data should not be pooled as a matter of standard practice. Since small scale variability is incorporated into the estimate when compositing data, this approach is not appropriate if quantifying the extent of spatial variation in root distribution and activity is of interest. However, when the root systems of plant communities are the object of study, it is probably best to have as much of the root system as possible in each replicate sample.

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One of the primary advantages of analyzing pooled data is that the effects of heterogeneous distributions of roots among minirhizotrons are removed from estimates of production and other means. We feel that a serious problem with analyses of both averaged and non-weighted nested data is the failure to consider the relative contribution of each minirhizotron to the overall mean. Heterogeneous distributions of roots among minirhizotrons can result from many causes, including chance; various physical, biological or chemical soil factors; differences in species abundance and root morphology; inconsistencies in the minirhizotron-soil interface; and possibly others. In analyses of pooled or nested data, the result is that minirhizotrons with few roots or little root length present contribute proportionately more information to an estimate than do minirhizotrons with a greater number of roots or root length. This can be seen in our root production data (Table 1). The higher production rates associated with the nested and averaged data resulted from the presence of at least one minirhizotron per plot with a low initial root length exhibiting a large relative amount of root production during the year. The lower estimate of annual production derived from the pooled data is likely to be a more representative reflection of actual root system activity than the averaged or nested estimates, since each root is given full consideration in the pooled analysis.

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In summary, it is important that we keep in mind the object(s) of interest when planning minirhizotron experiments and subsequently analyzing the data. It is the acquisition of better information on the average root, not the average minirhizotron, that will help us answer our questions about roots and root systems.

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Chapter III

PATTERNS OF FINE ROOT MORTALITY IN TWO SUGAR MAPLE FORESTS

Abstract

The survival of contemporaneous root cohorts produced during succesive intervals of time was followed in two sugar maple (Acer saccharum Marsh.) forests for a period of two years. Analyses of the survival distributions of the cohorts showed that roots in the northern forest consistently lived longer than those in the southern forest. Differences were due principally to much greater rates of mortality early in the life of roots at the southern site; overwinter and second-year mortality rates were the same at both forests. An examination of site factors suggests that warmer soil temperatures seem to be associated with the more rapid rates of root death at the southern site. The results provide new insights into fine root dynamics in temperate deciduous forests, and have important implications for future studies of ecosystem productivity and carbon and nutrient cycling.

Introduction

A large proportion of the carbon assimilated by plants is allocated to fine root production (Gower et al. 1992, Grier et al. 1981, Keyes and Grier 1981, Harris et al. 1977, Fogel 1985), and the flux of carbon and nutrients to the soil from fine root mortality is as much or greater than that returned via leaf litter in many forests (Cox et al. 1978, Joslin and Henderson 1987, Raich and Nadelhoffer 1989, Vogt et al. 1986). However, our knowledge of the demographic processes underlying the dynamic nature of fine roots is incomplete, in large part because of limitations inherent in traditional methods of studying root systems. Given the importance of roots in ecosystem carbon and nutrient budgets, a better understanding of fine root mortality would improve our attempts to quantify broad-scale carbon budgets and model plant ecosystem processes (Raich and Nadelhoffer 1989, Vogt et al. 1986, Ewel and Gholz 1991, Landsberg et al. 1991). Here we present the results of an observational study utilizing recent advances in microvideo technology (Hendrick and Pregitzer 1992a, Upchurch and Ritchie 1983) in which we followed the mortality of fine root cohorts in two similar sugar maple (Acer saccharum Marsh.) forests during 1989 and 1990.

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Methods

In June 1988 we installed 12 clear, 5-cm diameter tubes (minirhizotrons) in each of two closely matched sugar maple forests (Table 1) located 80 km apart from north to south. There are no appreciable site differences in soil organic matter content, cation exchange capacity/saturation, total nitrogen (N), exchangeable Ca Mg, Al or K (MacDonald et al. 1991), N mineralization or growing season soil moisture content, and there were no significant differences in canopy leaf area, litterfall production or litterfall N in either 1989 or 1990 (Burton et al. 1991, Pregitzer and Burton 1991). We used a microvideo camera to record monthly images of fine root cohorts growing in the top 30 cm of the soil along a 1.8-cm-wide transect on the minirhizotron surface during the 1989 and 1990 growing seasons. Cohorts were comprised of all living fine roots 1.5 mm in diameter or less, pooled across the 12 minirhizotrons (Hendrick and Pregitzer 1992b), that were produced during the intervals between sampling dates (Table 2). We used a microcomputer software program (ROOTS, Atkinson 1992, Hendrick and Pregitzer 1992a) to identify and measure the length of individual roots within contemporaneous cohorts at each site, and subsequently follow their fate by repeatedly measuring the same roots at each sampling date.

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Table 3.1 Stand, soil and climatic characteristics of the study sites. Values are averages across plots, with standard errors of the mean in parentheses where shown.

General Stand Characteristics	Southern Forest	Northern Forest
Latitude	43°40′	44°23′
Longitude	86°09′	85°50′
Aboveground biomass ($Mg \cdot ha^{-1}$)	234	275
Overstory Age (yrs)	78 (5)	74 (11)
Basal Area ($m^2 \cdot ha^{-1}$)	30 (2.0)	30 (2.8)
Sugar Maple Basal Area (%)	75 (13)	83 (5)
Canopy Height (m)	24 (1)	28 (1)
Leaf Area Index (m^2/m^2)		
1989	7.9 (0.3)	7.1 (0.9)
1990	7.7 (0.4)	7.8 (0.5)
Mean Annual Air Temperature (°C)	7.6	5.8
Mean Annual Precipitation (mm)	850	810
Growing degree Days (>5.6 °C)	2083	1944
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(.46)	4.66(.27)
Bulk Density ($g \cdot cm^{-3}$)	1.27(.07)	1.27(.04)
Nitrogen ($kg \cdot ha^{-1}$)	1408(100)	1125(398)
N Mineralization ($mg \cdot kg^{-1} \cdot yr^{-1}$)	134.4	100.8
Phosphorus ($kg \cdot ha^{-1}$)	156(18)	191(58)
Organic Matter ($Mg \cdot ha^{-1}$)	41.7(3.3)	45.7(13.6)

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Table 3.2 Birth intervals and size (numbers and length in mm) of root cohorts observed during the study.

Southern Forest			Northern Forest		
Birth Interval	#'s	Length	Birth Interval	#'s	Length
1989:			1989:		
25/4 - 7/6	152	793	29/4 - 11/6	196	1074
7/6 - 21/6	87	342	11/6 - 22/6	78	398
21/6 - 18/7	105	357	22/6 - 18/7	85	390
18/7 - 16/8	70	274	18/7 - 16/8	108	493
16/8 - 16/9	97	376	16/8 - 16/9	64	262
16/9 - 14/10	56	223	16/9 - 14/10	26	103
1990:			1990:		
14/10 - 25/4	55	211	14/10 - 24/4	31	185
25/4 - 24/5	97	363	24/4 - 23/5	30	183
24/5 - 18/6	88	318	23/5 - 19/6	245	1135
18/6 - 21/7	102	421	19/6 - 22/7	58	225
21/7 - 18/8	95	307	22/7 - 19/8	61	285
18/8 - 18/9	57	170	19/8 - 19/9	56	305
18/9 - 16/10	56	217	19/9 - 26/10	61	298

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Results and Discussion

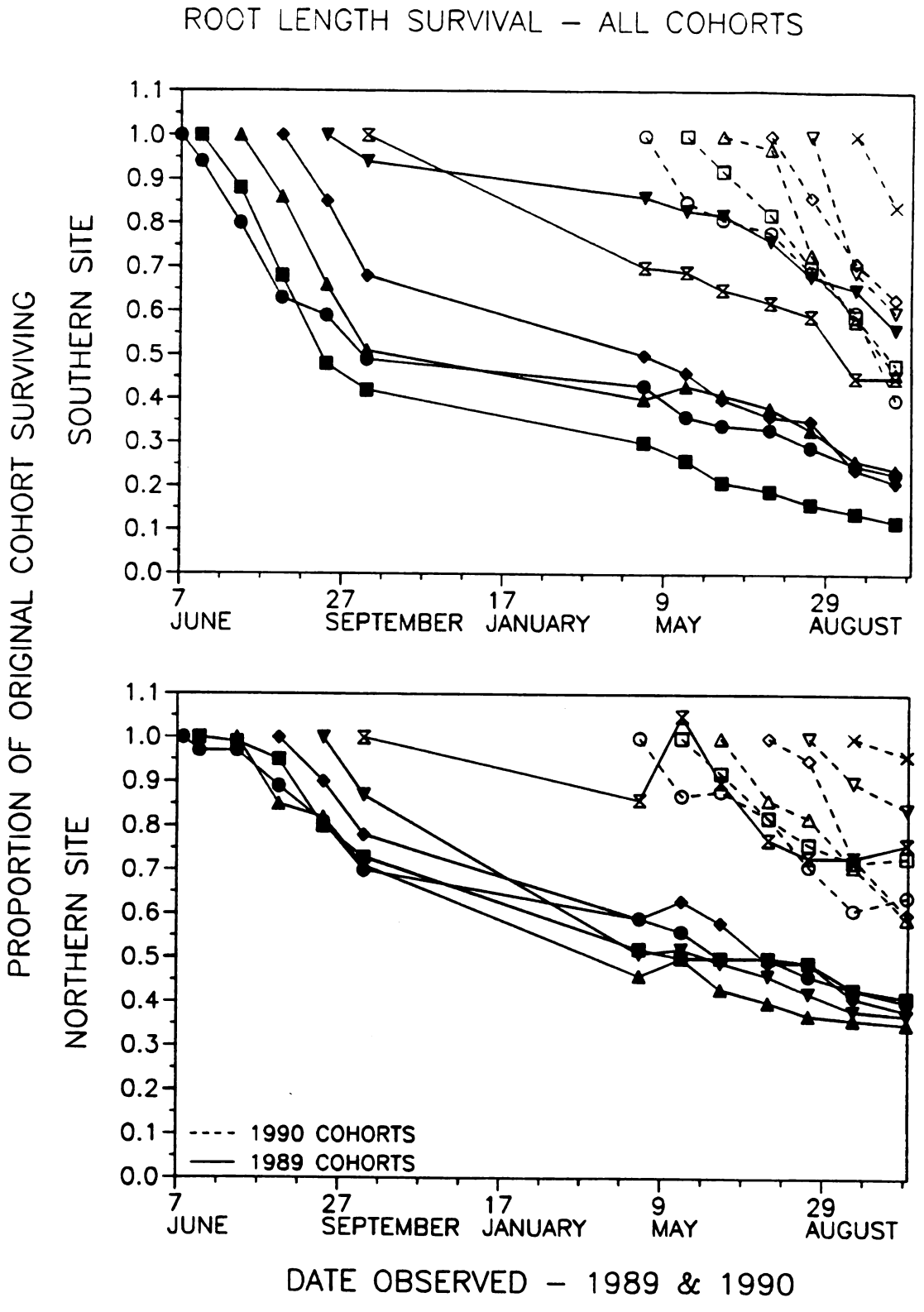
Our objectives were to quantify patterns of fine root mortality in these two closely matched ecosystems. We hypothesized that fine root length would be lost at a similar rate in both forests because of the similar site characteristics. However, we found large differences in root lifespans between the two forests (Figure 1). Gehan-Mantel (Pyke and Thompson 1986) tests of cumulative survival distributions of contemporaneous 1989 and 1990 cohorts revealed that roots at the northern site consistently lived longer on average than roots born during the same periods of time at the southern site (alpha = 0.05). The only exceptions were two 1989 cohorts; July (no site differences) and September (greater longevity at the southern site). The longer lifespan of roots in the northern forest was due to significantly lower first-season mortality rates (Figure 2). Regressions of root length survival against the number of days since a cohort was first observed showed that new roots were lost 64% faster at the southern forest (0.41 vs. 0.25 $\%\cdot day^{-1}$, $p < .01$.). Overwinter and second-year morality rates were not significantly different ($p > 0.5$; 0.14 vs. 0.12 $\%\cdot day^{-1}$).

The good fit of both sets of regressions was due to very similar patterns of mortality for all cohorts at each site (Figure 1). These results were unexpected because, although

Figure 3.1 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 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. 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 censored data [19] at an alpha of 0.05.

PROPORTION OF ORIGINAL COHORT SURVIVING

NORTHERN SITE SOUTHERN SITE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PROPORTION OF ORIGINAL COHORT SURVIVING
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9 MAY
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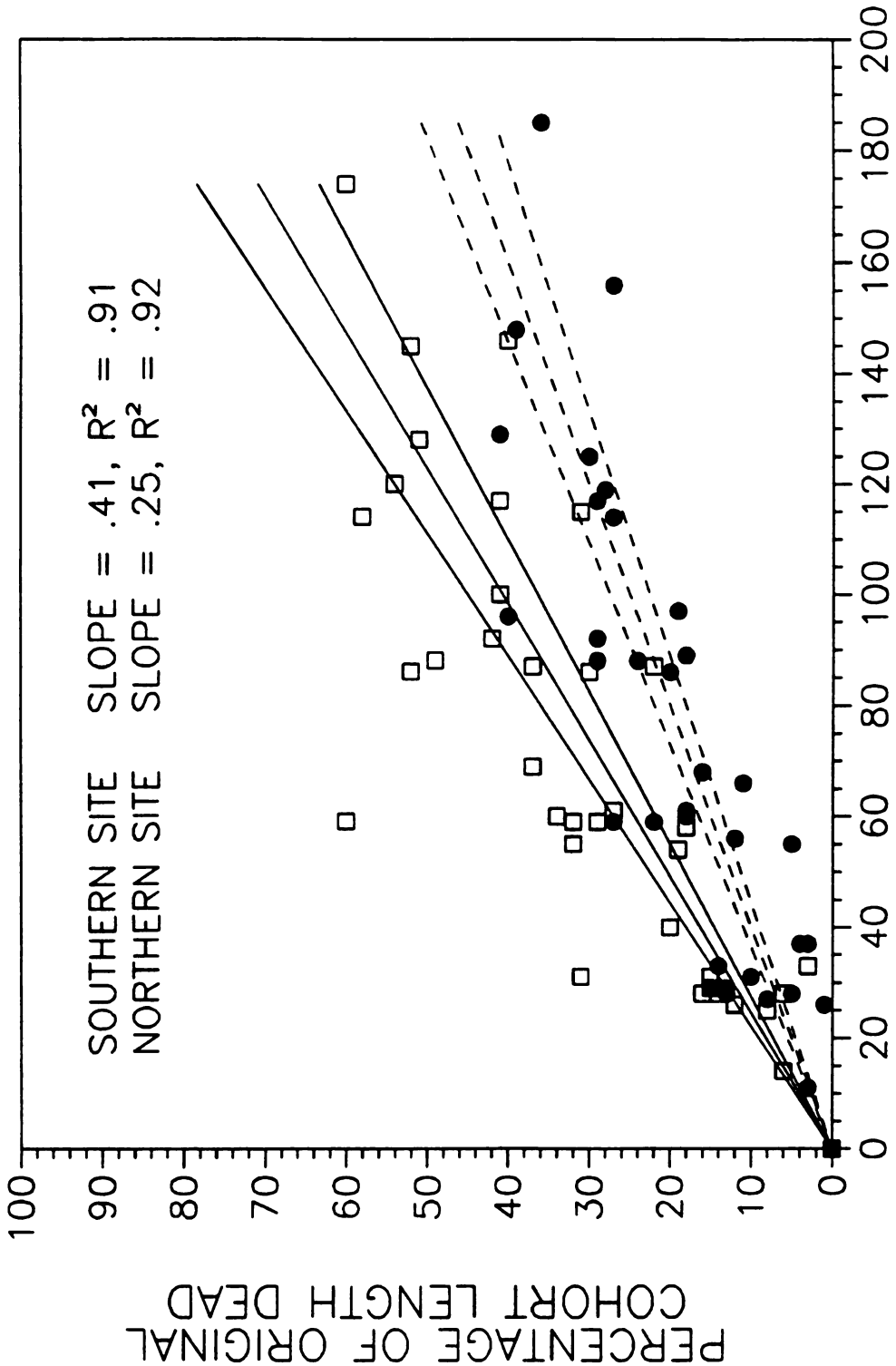
—— 1989 COHORTS
DATE OBSERVED – 1989 & 1990

Figure 3.2 Regressions of length mortality data against the number of days a cohort had been under observation during it's first growing season, with line forced through the origin. The slope (mortality rate) of the southern 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 alpha of 0.05.


SOUTHERN SITE SLOPE = .41, R² = .91
NORTHERN SITE SLOPE = .25, R² = .92
PERCENTAGE OF ORIGINAL COHORT LENGTH DEAD
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there have been no prior studies of differences in the mortality rates of roots produced at different times of the year, several studies have shown seasonal variation in fine root turnover as calculated from temporal changes in live and/or dead root biomass (Fogel 1983, Grier et al. 1981, Keyes and Grier 1981, McClaugherty et al. 1982, Persson 1979). This variation is often believed to partially reflect variable root mortality rates. However, assuming that the dynamics of root length and root biomass are similar, our results suggest that temporal differences in biomass "turnover" may be due to temporal variation in root production, not in root mortality, at least in northern hardwood ecosystems like the ones we studied.

Mortality rates of the 1989 cohorts were significantly less during the winter and second growing season than during the first growing season in both forests (Figures 1,2). Low overwinter mortality rates might be explained by lower root maintenance respiration rates under colder soil temperatures (Amthor 1984, Lawrence et al. 1983, Marshall and Waring 1985), but it is unclear why roots produced in the 1989 growing season should die at a slower rate during the 1990 growing season as well. Some of the longer surviving roots may undergo secondary growth and become a more permanent part of the root system, but of the 2216 roots that we followed in this study, only 1 developed any signs of secondary growth. Survival of these roots may have been

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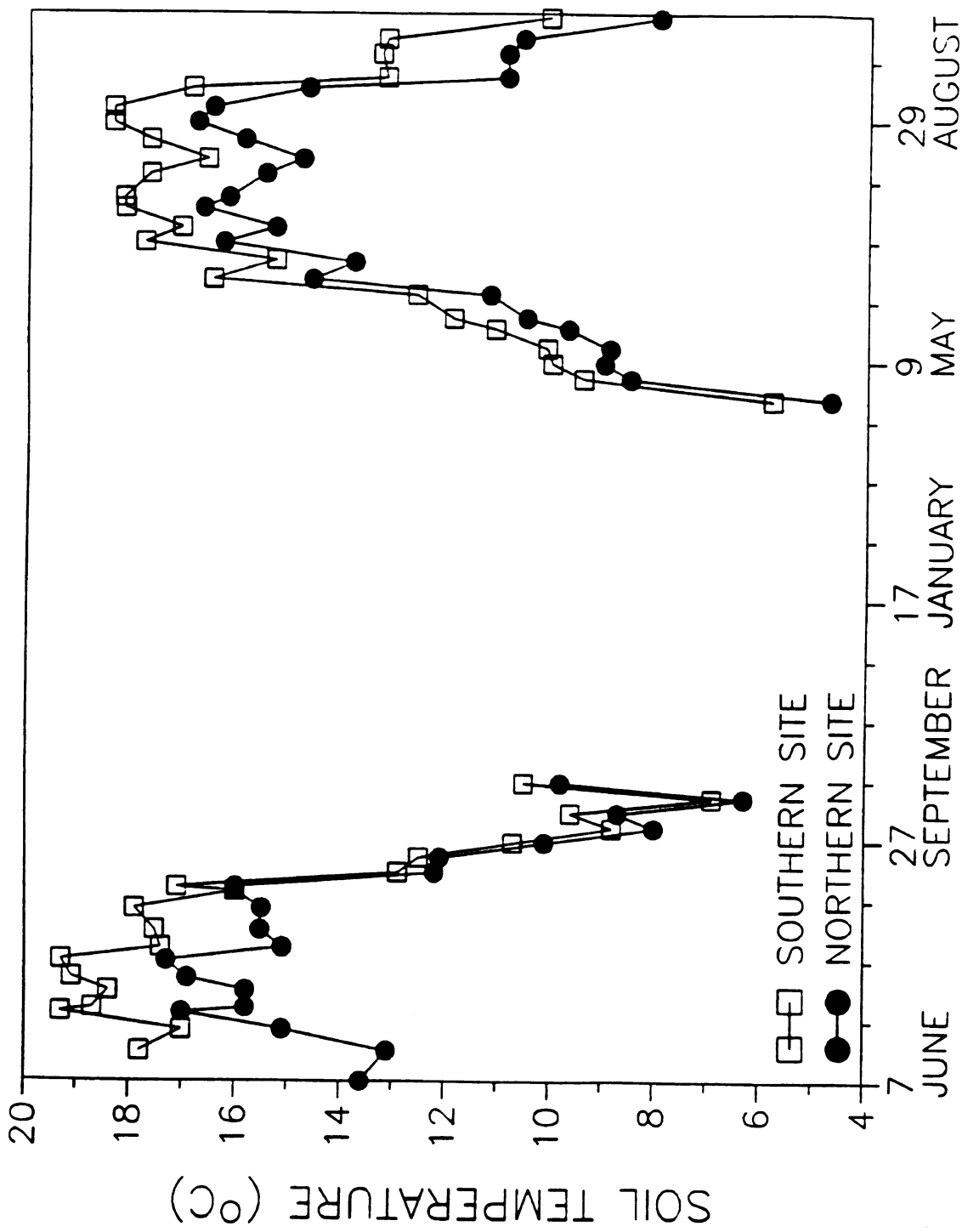
enhanced by greater lignification and/or suberization of cortical or epidermal cells, or perhaps they were located in resource-rich microsites. Our study was not designed to answer these questions, but they deserve further investigation.

The causal factors responsible for the large differences in fine root mortality rates between these two forests are not readily apparent. Both forests are of similar age, structure and composition (Table 1), and there are no substantial differences in leaf area, fertility, soil moisture holding capacity or other site factors (MacDonald et al. 1991, Burton et al. 1991, Pregitzer and Burton 1991) that can be invoked as obvious explanations for the differences in root mortality rates and survival distributions. It is possible that warmer soil temperatures contribute in part to greater fine root mortality rates in the southern forest (Table 1, Figure 3). Late-spring and summer soil temperatures at 15 cm depth were 2-4 ^{o}C warmer at the southern site in both 1989 and 1990. Soil temperatures were significantly warmer at the southern site from late April through mid-October during both years (paired t-test; $p < .001$) by an average of about 1.5 ^{o}C. Soil temperature was not controlled in our study, and so the evidence linking temperature and root mortality is circumstantial. However, previous studies have demonstrated increased root respiration rates and shorter root turnover

Figure 3.3 Weekly averages for soil temperature at 15 cm depth at both forests. Paired t-tests of site differences in average weekly temperatures (derived from the mean of three sensors at each site) showed that temperatures from 26/4/89 through 17/10/89 and 30/4/90 through 16/10/90 were significantly greater at the southern site ($p < .001$). Data were collected every 30 minutes with an Omnidata monitoring system (Omnidata International, Logan Utah, USA).



1989 & 1990 WEEKLY AVERAGES

times associated with higher soil temperatures (Amthor 1984, Lawrence et al. 1983, Marshall and Waring 1985), and we believe that higher soil temperatures act in part to accelerate mortality rates in the southern forest, probably through greater maintenance costs throughout the entire system of fine, absorbing roots.

Regardless of the factors responsible for the differential rates of root mortality that we observed, 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, in many models of forest ecosystem processes, the allocation and cycling of resources belowground are driven by site factors like nitrogen or water availability (Aber et al. 1991, Running and Gower 1991). In others, carbon and nutrient budgets are constructed to account for greater C costs due to increased root respiration under warmer soil temperatures (Bonan 1991, Ewel and Gholz 1991, Running and Gower 1991). But none that we are aware of make allowance for differences in root turnover rates within an ecosystem type, nor are root turnover rates intrinsically linked empirically or directly to soil temperature. A positive outcome from our study may result from our observation of highly predictable mortality rates for all roots produced within a given growing season. If similar patterns of mortality occur in other plant ecosystems, then it should be possible to quantify

belowground resource cycling in a changing environment solely from estimates of fine root production once an empirical relationship between soil environmental factors and root mortality rates has been established for a given ecosystem type.

The absence of functions and parameters describing the heterogeneity of root turnover rates within ecosystem types or under different soil temperature regimes should not be equated with flaws in current models of ecosystem processes. Instead, the incomplete nature of current models reflects how little is known of the demographic processes (like root mortality) that control belowground carbon and nutrient cycling, and our poor mechanistic understanding of the relationship between root demography and soil environmental factors (especially temperature). Given the present level of concern about the effects of postulated global climatic changes on the world's forest resources, and the fact that root systems account for substantial portion of ecosystem carbon budgets, the continuing need for more and better data on fine root dynamics in terrestrial ecosystems should be apparent. Even if temperature is 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 belowground processes that do not account for this phenomenon.

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CHAPTER IV

THE DYNAMICS OF FINE ROOT LENGTH, BIOMASS AND NITROGEN CONTENT IN TWO NORTHERN HARDWOOD ECOSYSTEMS

Abstract

The dynamics of fine (<2.0 mm) roots were measured in two sugar maple (Acer saccharum Marsh.)-dominated ecosystems (Northern and Southern sites) during 1989 and 1990 using both minirhizotrons and destructive harvests. More than 50% of annual length production occurred before mid-summer in both ecosystems, while the period of greatest mortality was from late summer through winter. About 1/3 of annual fine root production and mortality occur simultaneously, with little observable change in total root length pools. By using fine root length dynamics to derive biomass production and mortality, we calculated annual production values of approximately 8000 and 7300 $kg \cdot ha \cdot yr^{-1}$, respectively, at the Southern and Northern sites, representing about 60% of total NPP in both forests. Corresponding biomass mortality (i.e. turnover) values were 6700 and 4800 $kg \cdot ha \cdot yr^{-1}$, and total nitrogen returns to the soil from fine root mortality were 72 $kg \cdot ha \cdot yr^{-1}$ at the Southern site and 54 $kg \cdot ha \cdot yr^{-1}$ at the Northern site. Fine roots dominated total biomass and N litter inputs to the soil in both ecosystems, accounting for

over 55% of total biomass and nearly 50% of total N returns. In both ecosystems, roots <0.5 mm comprised the bulk of fine root biomass and N pools, and the contribution of these roots to northern hardwood ecosystem carbon and nitrogen budgets may have been underestimated in the past.

Introduction

Fine roots and mycorrhizae are important and dynamic components of temperate forests. More than 50% of annual net primary production is allocated belowground in many forests (e.g. Fogel and Hunt 1979, Grier et al. 1981, Harris et al. 1977, Keyes and Grier 1981), and nutrient inputs to the soil via fine root turnover can be as much or more than those returned in aboveground litter (Arthur and Fahey 1992, Cox et al. 1978, Joslin and Henderson 1987, Vogt et al. 1986a). However, the difficulties associated with studying fine roots have resulted in a paucity of belowground data for plant communities, and many aspects of fine root production and mortality are still poorly understood.

One of the most frustrating problems involves quantifying the magnitude and timing of concurrent root production and mortality (Fogel 1985, Kurz and Kimmins 1987, Santantonio and Grace 1987). Simulation models have shown that production and mortality can be significantly underestimated by failing to account for the simultaneity of both processes (Kurz and Kimmins 1987), and numerous computational approaches have been devised to overcome this problem (e.g. Joslin and Henderson 1982, McClaugherty et al. 1982). Periodic fine root production and mortality are typically estimated from sequential changes in live and/or dead root mass but, unfortunately, measuring root mass or nutrient

content at one time renders the sampling unit useless for further study. Not only does this add a spatial component to sampling variability, but necessitates that production and mortality between sampling dates be inferred by difference, as they cannot be measured directly (Santantonio and Grace 1987). It has been suggested that concurrent measurements of root decomposition rates could be combined with root biomass data to better predict production and mortality (Joslin and Henderson 1982, Santantonio and Grace 1987), and Joslin and Henderson (1987) used this approach to estimate fine production and turnover in a white oak (Quercus alba L.) forest. However, even when decomposition rates are used, production or mortality estimates (although perhaps more accurate) are still derived by difference, rather than by direct observation.

Questions about the reliability of different approaches to calculating root production and mortality have led to considerable debate about the relative merits of particular methods, as well as the accuracy of current estimates of root production and mortality (Fairley and Alexander 1985, Fogel 1985, Vogt et al. 1989, Singh et al. 1984, Vogt et al. 1986b). There is general agreement among scientists studying belowground processes that there is substantial room for improvement in root research methodology and technology (Fogel 1990, Laurenroth et al. 1986, Raich and Nadelhoffer 1989, Santantonio and Grace 1987, Vogt et al.

1989). The minirhizotron (a small observation tube inserted in the soil) is one tool that can be used to overcome some of the difficulties associated with techniques that rely on solely on the physical sampling of root systems (Fogel 1990, Hendrick and Pregitzer 1992a). Minirhizotrons provide us with the means to study the activity of root systems over extended periods of time in a non-destructive fashion, and with appropriate analytical techniques they can be used to directly measure root production and mortality independently of one another (Hendrick and Pregitzer 1992a). The small size and portability of the image recording systems used with minirhizotrons makes them ideal for field studies, and they have been used successfully to study root growth and mortality in both natural and agronomic ecosystems (e.g. Cheng et al. 1990, Hansson and Andren 1987, Keng 1988, Upchurch and Ritchie 1983, Eissenstat and Caldwell 1988, Hendrick and Pregitzer 1992a).

Although useful for studying root dynamics, minirhizotrons cannot be used to measure root biomass and nutrient content, despite continuing improvements being made in both minirhizotron technology and data analysis. Physical properties of root systems can be measured only by taking destructive samples of root tissue. We believe that a combination of direct observation and destructive sampling, capitalizing on the strengths of both approaches, can provide a more comprehensive understanding of the fine roots

(Hendrick and Pregitzer 1992a).

The goals of the research described in this paper were three-fold. First, we wanted to quantify the amount and seasonal patterns of concurrent fine (i.e. <2.0 mm diameter) root length production and mortality in two closely matched sugar maple forests using minirhizotrons. Our second objective was to use these estimates of fine root length production and mortality to predict the dynamics of fine root biomass and nitrogen content, and to test the accuracy of our predictions. Our overall objective was to determine the importance of fine roots in the carbon and nitrogen budgets of these two forests.

Methods

Site Description

The study sites are second-growth northern hardwood forests located in the northern lower peninsula of Michigan (Table 1), and are separated from each other by a north-south distance of 80 km. The two forests will be referred to as the Southern site and Northern site throughout the paper. Sugar maple (Acer saccharum Marsh.) is the dominant species in all structural layers of both of these well-stocked forests (Table 1). Other overstory species include red maple (Acer rubrum L.), northern red oak (Quercus rubra L.),

Table 4.1 Stand, soil and climatic characteristics of the study sites. Values are averages across plots, with standard errors of the mean in parentheses where shown.

General Stand Characteristics	Southern Forest	Northern Forest
Latitude	43°40′	44°23′
Longitude	86°09′	85°50′
Overstory Age (yrs)	78 (5)	74 (11)
Basal Area ($m^2 \cdot ha^{-1}$)	30 (2.0)	30 (2.8)
Sugar Maple Basal Area (%)	75 (13)	83 (5)
Canopy Height (m)	24 (1)	28 (1)
Leaf Area Index (m^2/m^2)		
1989	7.9 (0.3)	7.1 (0.9)
1990	7.7 (0.4)	7.8 (0.5)
Mean Annual Air Temperature (°C)	7.6	5.8
Mean Annual Precipitation (mm)	850	810
Growing degree Days (>5.6 °C)	2083	1944
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(.46)	4.66(.27)
Bulk Density ($g \cdot cm^{-3}$)	1.27(.07)	1.27(.04)
Nitrogen ($kg \cdot ha^{-1}$)	1408(100)	1125(398)
N Mineralization ($kg \cdot ha^{-1} \cdot yr^{-1}$)	171	128
Phosphorus ($kg \cdot ha^{-1}$)	156(18)	191(58)
Organic Matter ($Mg \cdot ha^{-1}$)	41.7(3.3)	45.7(13.6)

American beech (Fagus grandifolia Ehrh.), and black cherry (Prunus serotina Ehrh.). The herbaceous community is depauperate in both forests, with an average cover value of less than 3%, and there are virtually no shrubs. The soils at the Northern site are Alfic and Typic Haplorthods, while those at the Southern site are Entic Haplorthods. Further site and soil descriptions can be found in Hendrick and Pregitzer (1992a), MacDonald et al. (1991), Burton et al. (1991b) and Pregitzer and Burton (1991).

Three 30 m by 30 m plots were established at each site in 1987, selected so that a maximum degree of homogeneity existed among them with respect to physiography, soils and vegetation (Burton et al. 1991a). In June of 1988, four minirhizotrons (2 m long x 5.08 cm inside diameter) were permanently installed in each plot at a 45^{o} angle to the soil surface to a depth of 165 cm along their length (= 110 cm in vertical depth) at both sites. The portion of the minirhizotrons extending above the soil surface was painted and capped with a rubber stopper to prevent rainfall and light from entering. Numbered image frames were scribed every 1.2 cm onto the exterior surface of each minirhizotron prior to installation so that we could return to the same location within the minirhizotrons at all sampling dates. The scribed image frames were oriented vertically during minirhizotron installation. Only data from the upper 35 frames (= 30 cm vertical depth) are presented here. All

minirhizotron images were collected on VHS videotape with a Circon Microvideo 9011 Color Agricultural Camera (Circon Co., Santa Barbara CA). Each minirhizotron was imaged at approximately 1 month intervals throughout the 1989 and 1990 growing seasons. The data presented in this paper were collected at the Northern site on 4/27, 6/11, 6/22, 7/18, 8/18, 9/16 and 10/14 in 1989, and on 4/24, 5/23, 6/19, 7/22, 8/19, 9/19 and 10/26 in 1990. The corresponding sampling dates at the Southern site were 4/25, 6/7, 6/21, 7/18, 8/16, 9/16 and 10/14 in 1989 and 4/25, 5/24, 6/18, 7/21, 8/18, 9/18, and 10/16 in 1990.

Fine Root Length Dynamics

An interactive PC-based software program (ROOTS) that we have developed was used to analyze the minirhizotron video images (Hendrick and Pregitzer 1992a, Atkinson 1992). Beginning with images from the first sampling date at each site, the length and diameter of all roots present in each frame were traced using a mouse, and the measurements (in mm) were calculated and written to a database file (dBASE III+, Ashton-Tate, Torrance, CA) by ROOTS. The tracings of each root were permanently saved by ROOTS on a separate disk file. An identification code was assigned to each root and written to the database. The code was derived from the order in which a root was traced within an image; the frame, minirhizotron and plot in which it was located; and the date

on which it was imaged. The same code (except for the collection date) was used for each root during the analysis of subsequent images. We were able to identify the same roots at later dates by using ROOTS to recall and overlay the tracings and identification code from an image at time t-1 when analyzing time t images. Complete records were kept for each root throughout its development, even after it died and/or disappeared.

Each root was assigned a development stage code after it had been traced and measured. Roots were classified as "new" if they first appeared in an image as white in color, and "white" at subsequent dates if they remained white or cream in color. Roots that turned, or first appeared as, tan to brown in color were classified as "brown". Those that turned very dark grey or black were classified as "dead". As roots decayed and disappeared, or disappeared without first moving into a "dead" state, they were classified as "missing". When all the images from a given date had been analyzed, the database records from the four minirhizotrons on each plot were composited into one database per plot (Hendrick and Pregitzer 1992b). After the images from all dates had been processed, the records for the entire year were combined. The final database for each replicate plot at each site was a time series of lengths, diameters and development stages for each root.

To calculate monthly and annual root length production and mortality for 1989, the white, brown and total (white + brown) root lengths present on the April, 1989 (time t = 0) sampling dates were summed separately for each plot. Root length production and loss was followed until April 24, 1990. The production of new root length was calculated for the intervals t to t+1 by summing the lengths of roots present at time t+1 that were not present at time t, and adding the length growth of existing roots. Mortality was calculated by summing the length of roots that moved into the dead or missing class during the same period, plus the length of any roots that were dead when they first appeared at time t+1. Percent production and mortality estimates for the intervals between sampling dates (relative to initial root lengths) were calculated by dividing the production and loss of white, brown and total root length during the interval by the initial (April 27, 1989) length standing crop. Production and mortality rates for 1990 were calculated likewise using the April 1990 length standing crops at each site. The length data were standardized in a length density format ($mm \cdot cm^{-2}$).

Stand Biomass and Productivity

Aboveground: Tree bole and branch biomass were calculated indirectly from measurements of diameter at breast height (DBH) and tree height and published allometric equations for

each species (Monteith and Jacobs 1979, Crow and Erdmann 1983). Measurements of each tree >5 cm DBH on all plots were made at each site in the fall of 1988 and 1989 after at least 50% leaf fall. Net biomass increment was calculated for the 1989 growing season as the difference between the fall 1989 and fall 1988 living biomass.

Aboveground litterfall was measured from eight 0.5 m^2 litter traps randomly located on each plot. Material was collected on a monthly basis from spring through late summer, and weekly during leaf fall in the autumn. Litter samples were air dried at 70 ^{o}C for 48 hours and weighed after they had been sorted into foliage, reproductive (seeds, flowers, etc.), woody and insect frass components. Litter was composited across sampling dates on a plot basis and analyzed for Kjeldahl N following sulfuric acid digestion (Technicon Industrial Systems 1977). Nitrogen content was calculated by multiplying the N concentration of each litter component by its biomass.

Canopy leaf area index (LAI) was calculated at each site by multiplying leaf biomass by specific leaf area (SLA). On each litter sampling date, the area and mass of all the leaves from one-half of each trap was determined before drying and weighing. Species-specific LAI's were calculated by multiplying a species litter weight by its SLA, and canopy leaf area was then calculated by summing LAI's across

all species. LAI's were corroborated by allometric equations derived from destructive harvests at each site, as well as canopy light transmittance; further details can be found in Burton et al. (1991).

Belowground: Root biomass and nutrient content was determined from soil cores collected on the April and October 1989 image sampling dates at each site. Eight cylindrical 5.08 x 30 cm biomass cores were randomly collected from a 10 m wide border strip surrounding each plot, and one additional core was collected within 0.5 m of each of two randomly selected biomass core samples on each plot for determination of root nitrogen concentrations. Soil cores were transported on ice to the Michigan State University campus. Roots were recovered from the soil using an automated root washer (hydropneumatic root elutriator, Smucker et al. 1982). The elutriator uses air bubbles to transport organic material through a water/soil/root-filled tube onto a 0.42 mm screen. Recovery of roots from a washed soil sample is >99% (Smucker et al. 1987). After washing, roots were stored at 2-3 ^{o}C in a 20% methanol solution until they could be sorted into 3 size classes: 0.0-0.5 and 0.5-2.0 mm (collectively termed "fine roots") and 2.0-10.0 mm. Roots in the two largest size classes were dried at 70 ^{o}C for 48 hrs, and weighed.

The biomass of roots <0.5 mm was determined indirectly. First, total root length per sample was calculated using Newman's line intercept method (Newman 1966) after all roots >0.5 mm had been removed. The grid array used for length determination was calibrated with segments of monofilament fishing line cut into segments ranging from 0.2-5.0 cm in length, and in amounts proportional to those in actual root samples. Estimated monofilament length was compared with actual length in increments of 5.0 m, from 5.0 to 25.0 m. The presence of many short roots/segments a few millimeters in length resulted in a systematic underestimation of true length, and it was necessary to multiply our initial root length estimates by a factor of 1.59. Next, random segments of roots 0.5 mm in diameter, totaling 50 cm in length, were collected from each core sample after length determination. These samples were dried as above, weighed to the nearest 0.0001 g, and average root length density ($g \cdot cm^{-1}$) ratios for roots 0.5 mm were calculated.

The <0.5 mm root length of each sample was converted to biomass by multiplying the length of each sample by the mean specific root length of all 8 samples from each plot for a given date and site. Sample biomass of both size classes was converted to units of $kg \cdot ha^{-1}$. Root N content at each date and site was determined by multiplying the N concentration of each size class (determined as for aboveground litter) by its biomass. Biomass and N content

means at each site were determined from plot values derived from the average of the 8 cores sampled on each plot.

Predicting Root Biomass Production and Mortality

Annual total fine (<2.0 mm) root production (April 1989 to April 1990) at each site was calculated by multiplying the initial (April 1989) biomass by the ratio of annual length production to initial length density along the minirhizotrons. Total biomass mortality (turnover) was calculated similarly by multiplying initial root biomass by the ratio of annual length mortality to initial root length density. The amount of N allocated to new root production, and the N lost to the soil through root death, were calculated by multiplying initial root N content by the length production and mortality ratios, respectively. (These two ratios express annual production and mortality in terms of initial conditions, and represent the proportion of original length, biomass or N that was gained and lost during the year.)

To check the accuracy of our estimates of root biomass and N production and turnover, we compared the October 1989 fine root biomass and N content data measured at each site with predicted standing crops derived from the minirhizotron data. Predictions of October biomass (and N content) at each site were made by determining the amount of biomass and

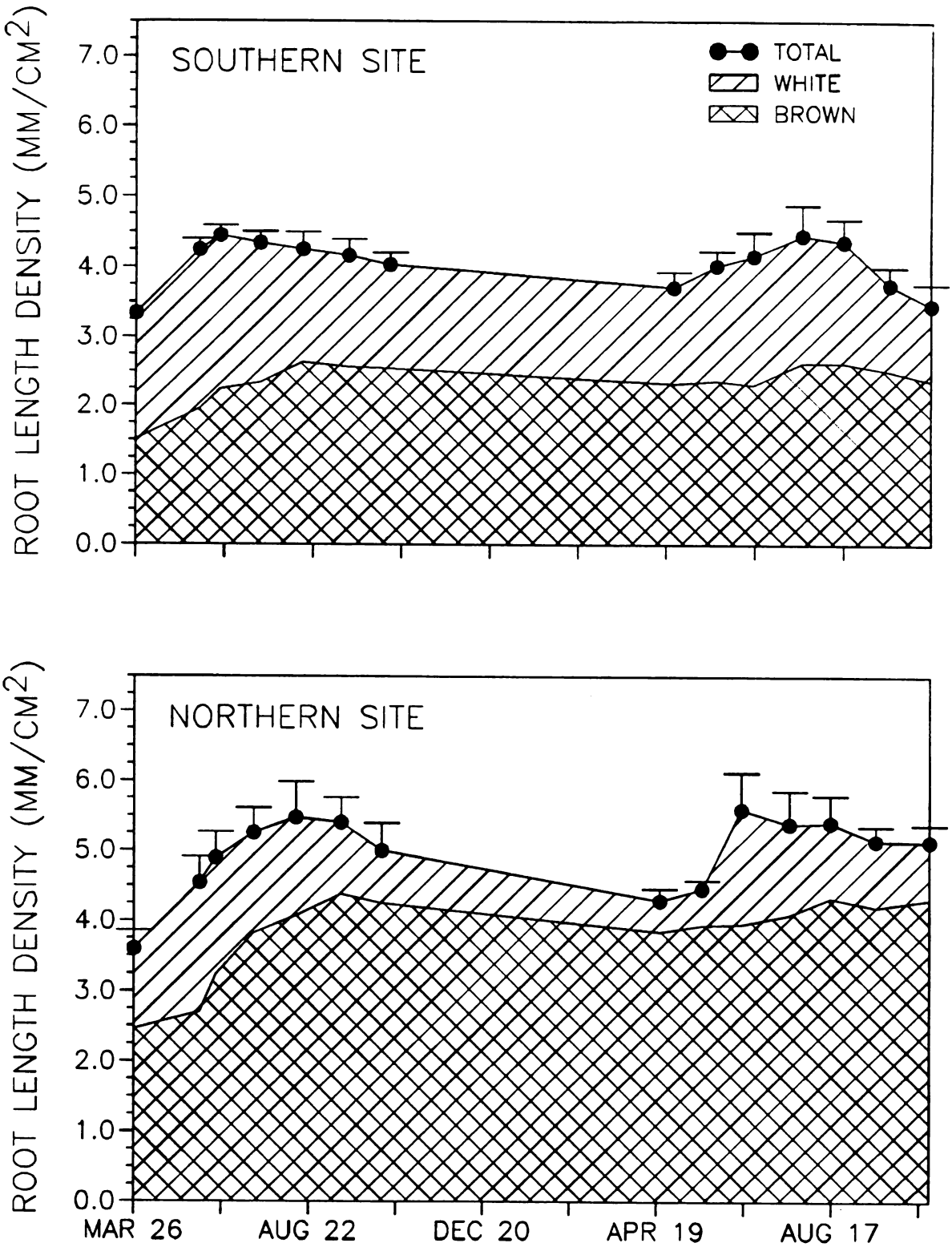
N allocated to new roots from April to October based upon the production of root length, and subtracting from this value the biomass and N lost due to turnover (determined from root length mortality) during the same period of time. Root biomass (and N) production and mortality from April through October were calculated in the same manner as annual production and mortality, except April-October root length density production and mortality values were used when computing ratios of length production and mortality to initial length density values. Final N content data were adjusted to reflect the actual October N concentrations of each size class.

Results

Fine Root Length Dynamics Along the Minirhizotrons

Fine root length density along the minirhizotrons exhibited a unimodal pattern of increase and subsequent decline at both sites during the 1989 and 1990 growing seasons (Figure 1), although there were some differences among sites and years in the timing of maximum root length densities. At the Southern site, root length density peaked in late June in 1989, but not until mid-July in 1990. The April-June 1989 increase was rather abrupt, and length loss was minimal during the fall and over winter. In 1990, the increase and decrease were both gradual. Root length densities in the

Figure 4.1 Total, white and brown fine root length densities (mm root per cm^2 minirhizotron surface) at the Southern and Northern sites from April 1989 through October 1990. Data are plot means with standard error bars.


SOUTHERN SITE
TOTAL
WHITE
BROWN
ROOT LENGTH DENSITY (MM/CM2)
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
NORTHERN SITE
ROOT LENGTH DENSITY (MM/CM2)
MAR 26
AUG 22
DEC 20
APR 19
AUG 17
DATE OBSERVED – 1989 & 1990

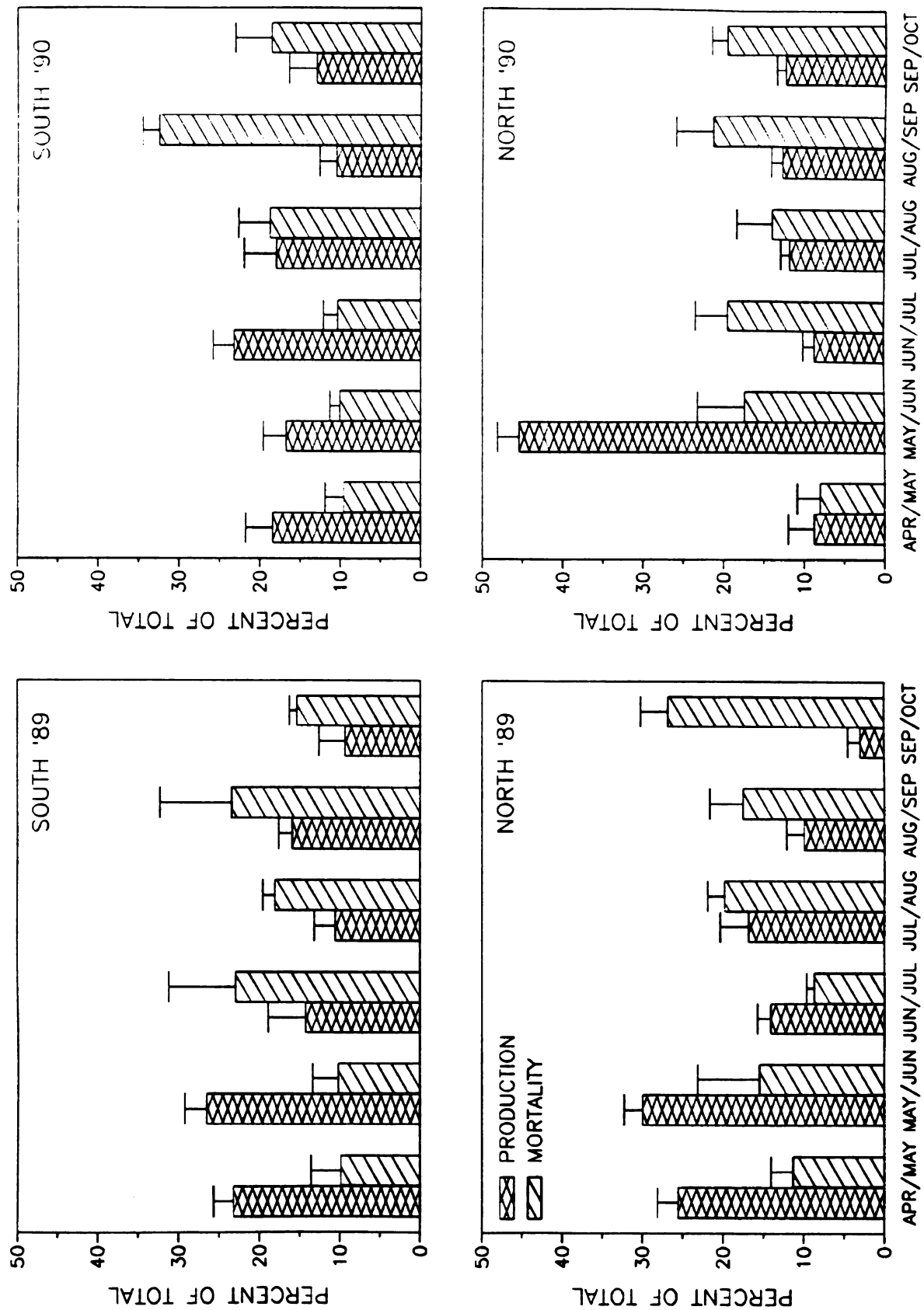
Northern forest followed a different pattern of development;maximum root length density occurred in August 1989 and mid-June in 1990. The increase and decrease in length densities were gradual in 1989, but there was an abrupt increase in 1990, with minimal loss through October. Root production was greater than mortality for the one year period from April 1989 to April 1990 at both sites (Table 2), resulting in net increases inApril 1990 length (Figure 1). At the Southern site, relatively greater mortality during 1990 resulted in October 1990 length densities that were not significantly different from April 1990 values (t-test, alpha = .05)). However, length density at the Northern site continued to increase during 1990 as well.

The composition of root length, with respect to white and brown roots, was greatly different among the sites (Figure 1). In the Southern forest, white roots comprised 32 to 55% of total root length throughout the study period, but only 10 to 41% of total root length at the Northern site. The difference in length composition is due to site differences in mortality rates of the newer white and older brown roots. Equal amounts of white and brown root length contributed to total mortality at the Southern site (Table 2), while nearly 3/4 of root length mortality in the Northern forest was due to the death of brown roots. White roots were most abundant in the late spring and early summer at both sites during 1989 and 1990 (Figure 1).

Table 4.2 Site means (and standard errors) of initial root length density, annual length production and annual mortality (April 1989 to April 1990).

	Southern Site	Northern Site
Initial Length Density ($mm \cdot cm^{-2}$)	3.34 (.08)	3.60 (.26)
Total Annual Length Production ($mm \cdot cm^{-2} \cdot yr^{-1}$)	3.38 (.61)	3.83 (.50)
Total Annual Length Mortality ($mm \cdot cm^{-2} \cdot yr^{-1}$)	2.82 (.38)	2.56 (.57)
White Length Mortality (% Total)	50.5 (13)	25.4 (3)
Brown Length Mortality (% Total)	49.5 (13)	74.6 (3)

Figure 4.2 Percentage distribution of total growing season (April-October) fine root production and mortality occurring between minirhizotron sampling dates. April/May and May/June data in 1989 were calculated from April-early June and early June-late June data by interpolation, assuming that production and mortality were evenly distributed during the 6 week interval from late April to Early June at both sites.


SOUTH '89
SOUTH '90
NORTH '89
NORTH '90
PRODUCTION
MORTALITY
PERCENT OF TOTAL
0
10
20
30
40
50
APR/MAY MAY/JUN JUN/JUL JUL/AUG AUG/SEP SEP/OCT

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produ
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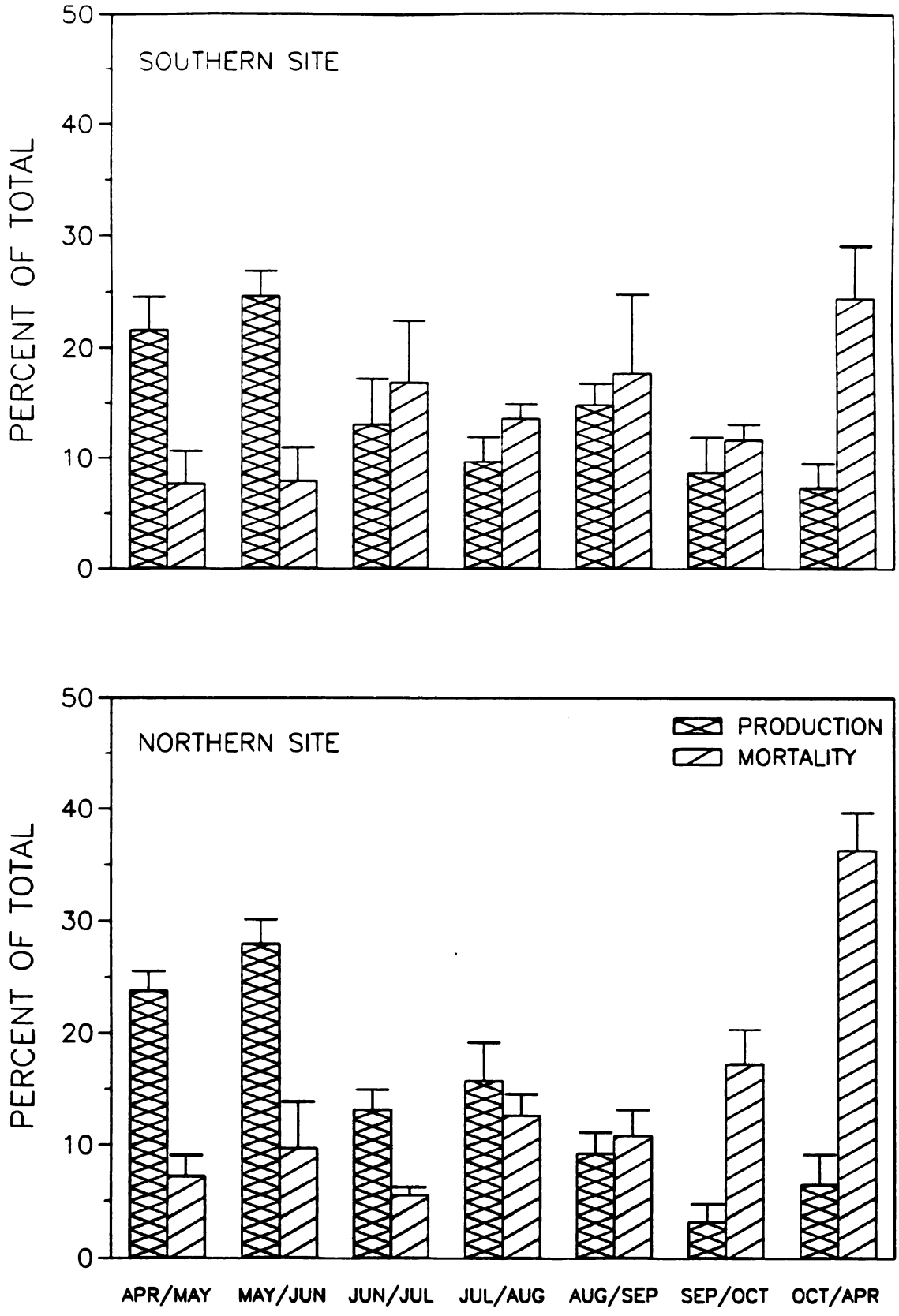
There were distinct seasonal patterns of root length production and mortality during the 1989 and 1990 growing seasons (April - October) at both sites (Figure 2). Although a significant amount of both production and mortality occurred simultaneously, more than 50% of total growing-season production took place between late April and mid-to-late July. Patterns of length production were similar both years at the Southern site, at the Northern site but there was a distinct peak in production during the 1990 May/June interval (Figure 2). The effect of this sudden burst of production is evident as an abrupt increase in root length density at this site during the same period of time (Figure 1).

The greatest amount of root mortality occurred after mid-summer, although relative amounts of root mortality varied somewhat within and between years. There was a large die-off of root length during the August/September 1990 interval at the Southern site, the effects of which are manifested in total root length density (Figure 1). Expressed on an annual basis (April 1989 to April 1990) it is apparent that over winter losses of root length contribute a much greater amount to total root mortality at the Northern site (Figure 3). Only 25% of total annual root mortality occurred during the six month interval from October 1989 to April 1990 at the Southern site, but nearly 40% of total annual root length mortality took place during the same period of time

Figure 4.3 Percentage distribution of annual (April 1989 - April 1990) fine root production and mortality occurring between minirhizotron sampling dates.


SOUTHERN SITE
NORTHERN SITE
PRODUCTION
MORTALITY
PERCENT OF TOTAL
0
10
20
30
40
50
APR/MAY
MAY/JUN
JUN/JUL
JUL/AUG
AUG/SEP
SEP/OCT
OCT/APR

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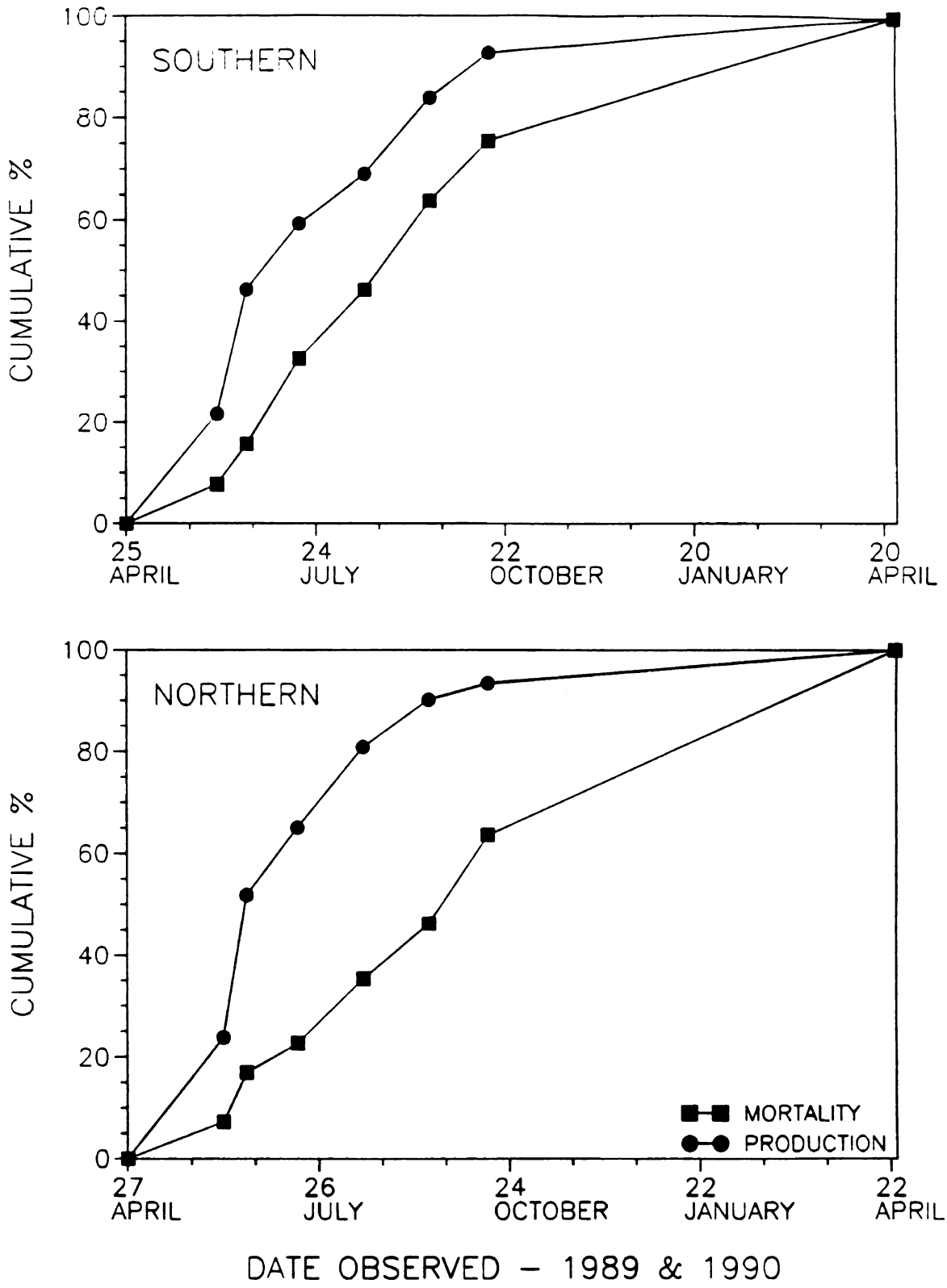
Fall and over winter root production contributed little to total annual production at either site (Figure 3). From 85 to 90% of all root length was produced prior to mid-September at both sites (Figure 4), and over winter production contributed only 7% to the total. The greatest amount of production occurred from late April to June, also the period in which budburst occurs (early-to-mid May) and canopy leaf expansion reaches 100% (late May to early June) in both forests (unpublished data).

The asynchrony of maximum relative root birth and death rates results in a distinct lag between cumulative length production and mortality (Figure 4). The two-week period between the mid and late-June 1989 observations was that in which the most rapid divergence of production and mortality occurred at both sites. The lag between production and mortality was greatest at the Northern site, due to relatively less root length mortality during the growing season. The greater lag between the production and mortality curves, and the lower annual root length mortality at the Northern site (Table 2) suggest that fine roots are living longer in this forest. Indeed, survival analyses of root cohorts born during the intervals between observations show that fine roots in the Southern forest consistently die at rate 64% greater than roots in the Northern forest

Figure 4.4 Cumulative (%) fine root production and mortality at the Southern and Northern study sites. The horizontal distance between the two curves at each site is a relative index of turnover time.


SOUTHERN
CUMULATIVE %
100
80
60
40
20
0
25 APRIL
24 JULY
22 OCTOBER
20 JANUARY
20 APRIL
NORTHERN
CUMULATIVE %
100
80
60
40
20
0
27 APRIL
26 JULY
24 OCTOBER
22 JANUARY
22 APRIL
MORTALITY
PRODUCTION
DATE OBSERVED – 1989 & 1990

(unpublished data).

Fine Root Biomass and Nitrogen Content

Patterns of biomass distribution among the three size classes of roots were similar at both sites and on both sampling dates (Table 3). There was a considerable amount of mass in the smallest class of roots (<0.5 mm): about 6,000 $kg \cdot ha^{-1}$ at the Southern site and 5,500 $kg \cdot ha^{-1}$ at the Northern site. In fact, the April <0.5 mm fine root biomass was nearly equal in magnitude to the combined mass of the two other size classes. However, there was a considerable (though not statistically significant) biomass increase in the largest size class (2.0-10.0 mm) by October, so that the masses of the smallest and largest classes were nearly equal (Table 3). The least amount of biomass was in the intermediate (0.5-2.0 mm) class of roots at both sites and on both sampling dates; about 1/3 that of the smallest roots in the spring and about 1/2 the mass of the smallest roots in the fall. The intermediate class increased significantly (t-test, alpha = 0.5) in biomass from April to October, but there were virtually no seasonal differences in the mass of the smallest roots.

The biomass of the smallest roots (<0.5 mm) was greatest at the Southern site on both dates, but differences among sites were statistically significant only in April (t-test, alpha

Table 4.3 Biomass and nitrogen content ($kg \cdot ha^{-1}$) of roots <0.5, 0.5 to 2.0 and 2.0 to 10.0 mm in diameter, as determined from soil cores. Plot means with standard errors in parentheses.

	Southern Site		
	<0.5	0.5 - 2.0	2.0 - 10.0
April 1989 Biomass	6110 (97)	1791 (84)	5389 (599)
April 1989 N Content	70 (2)	15 (1)	28 (5)
October 1989 Biomass	6249 (352)	3281 (153)	6550 (662)
October 1989 N Content	73 (7)	26 (1)	27 (5)
	Northern Site		
	<0.5	0.5 - 2.0	2.0 - 10.0
April 1989 Biomass	5413 (46)	1474 (79)	3377 (103)
April 1989 N Content	72 (1)	13 (1)	17 (1)
October 1989 Biomass	5553 (422)	2414 (78)	5392 (1442)
October 1989 N Content	52 (4)	16 (1)	29 (8)

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= 0.05). The mass of the other size classes was consistently greater at the Southern site as well, but the only statistically significant difference in addition to that described above was for the 0.5-2.0 size class in October. The combined April and October biomass of the two smallest classes of roots was, respectively, 7901 and 9530 $kg \cdot ha^{-1}$ at the Southern site and 6913 and 7967 $kg \cdot ha^{-1}$ at the Northern site.

Patterns of root N content were similar to those for biomass. At each site, the greatest amount of N was found in roots <0.5 mm in diameter on both sampling dates. Differences in N content between the two largest size classes tended to be less pronounced than biomass differences because of higher N concentrations in the 0.5-2.0 mm roots (Table 4). There was no difference between the April and October N content of smallest roots at the Southern site. However, there was a substantial drop in the N content of these roots at the Northern site, due to a 25% decrease in N concentration (Table 4). Among the two largest size classes, only the N content of 0.5-2.0 mm roots at the Southern site changed significantly (t-test, alpha = 0.05) from April to October. In contrast to the smallest roots at the Northern site, the temporal difference in the N content of this class was due to a change in biomass, not concentration (Table 4). There was a substantial, though not statistically significant (alpha = .05), increase in the

Table 4.4 Nitrogen concentration (%) of roots <0.5, 0.5 to 2.0 and 2.0 to 10.0 mm in diameter. Plot means with standard errors in parentheses.

	Southern Site		
	<0.5	0.5-2.0	2.0-10.0
April 1989	1.15	0.84	0.51
October 1989	1.16	0.79	0.41
	Northern Site		
	<0.5	0.5-2.0	2.0-10.0
April 1989	1.33	0.88	0.51
October 1989	0.93	0.66	0.54

October N content of the largest roots at the Northern site, again due to a change in biomass and not N concentration. There were no consistent site differences in N contents of the two largest classes of roots, but they tended to be higher at the Southern site. At the April sampling date, only the N content of the largest roots was significantly different (t-test, alpha = 0.05) among the sites, while in October both the smallest (alpha = .10) and intermediate (alpha = 0.05) size classes at the Southern site had more N.

Root Production, Mortality and Standing Crop Predictions

At both sites, predicted fine (<2.0 mm) root production for the period April 1989 to April 1990 was greater than predicted mortality (Table 5). Predicted production and mortality at the Southern site were approximately 8,000 and 6,700 $kg \cdot ha^{-1} \cdot yr^{-1}$, respectively. The corresponding values at the Northern site were 7,300 and 4,800 $kg \cdot ha^{-1} \cdot yr^{-1}$. Total N allocated to new roots (i.e. production) was nearly the same at both sites (85 and 86 $kg \cdot ha^{-1} \cdot yr^{-1}$) despite the nearly 800 $kg \cdot ha^{-1} \cdot yr^{-1}$ difference in biomass production. This was due largely to the higher N concentration of roots in April at the Northern site (Table 4). Total N returns to the soil via root mortality were estimated 72 and 54 $kg \cdot ha^{-1} \cdot yr^{-1}$ at the Southern and Northern sites, respectively.

Table 4.5 Comparison of measured and predicted 1989 total fine (0.0-2.0 mm) root biomass and nitrogen content standing crops, and predicted annual (April 1989 - April 1990) production and mortality. Values are in $kg \cdot ha^{-1}$, with standard errors in parentheses.

	Southern Site		Northern Site	
	Measured	Predict	Measured	Predict
April Biomass	7901 (76)		6887 (192)	
Annual Biomass Production		8081 (1619)		7302 (663)
Annual Biomass Mortality		6682 (892)		4843 (929)
October Biomass	9530 (555)	10299 (757)	7968 (866)	10708 (514)
April N Content	86 (1)		85 (2)	
Annual N Production		87 (17)		88 (8)
Annual N Mortality		72 (9)		54 (9)
October N Content	99 (7)	106 (7)	68 (8)	91 (4)

Our predictions of October fine root biomass and N standing crops (i.e. measured April standing crops + estimated April to October production less estimated April to October mortality) varied among the two sites in their accuracy. Our estimate of an October biomass standing crop of 10,299 $kg \cdot ha^{-1}$ at the Southern site was 8.1% greater than the measured standing crop of 9530 $kg \cdot ha^{-1}$ (Table 5), but the two values were not significantly different (alpha = 0.05). Similarly, the estimate of an October N content of 106 $kg \cdot ha^{-1}$ was 7.1 % greater than the measured value of 99 $kg \cdot ha^{-1}$, and again not statistically different (alpha = 0.05). However the predicted and measured biomass and N standing crops were substantially different at the Northern site. The predicted October biomass standing crop was 34.4% greater than the measured value (10,708 vs. 7,968 $kg \cdot ha^{-1}$), and the predicted N content of the roots was 33.8 % greater than the measured value (91 vs. 68 $kg \cdot ha^{-1}$). Both differences were statistically significant (t-test, alpha = 0.05)

Above- and Belowground Standing Crops, Production and Litterfall

Aboveground woody biomass was greatest at the Northern site (Table 6); 277,300 $kg \cdot ha^{-1}$ vs. 236,200 $kg \cdot ha^{-1}$ at the Southern site. Foliage biomass was just over 4,000 $kg \cdot ha^{-1}$ at both sites, and not significantly different among the

Table 4.6 Above- and belowground (less coarse roots >10 mm) April 1989 biomass, in $kg \cdot ha^{-1}$. Plot means with standard errors in parentheses.

	Southern Site	Northern Site
Aboveground Woody	236,200 (17,300)	277,300 (17,600)
Foliage	4,225 (412)	4,068 (357)
Roots (in mm)		
2.0-10.0	5,389 (599)	3,377 (103)
0.5-2.0	1,791 (84)	1,474 (79)
0.0-0.5	6,110 (97)	5,413 (46)
Total	253,715	291,632

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sites (Burton 1991b). Total biomass of roots <10.0 mm was 13,290 $kg \cdot ha^{-1}$ at the Southern site and 10,264 $kg \cdot ha^{-1}$ at the Northern site. Expressed as a percentage of total standing crop, biomass distribution was nearly the same at both sites. Aboveground woody biomass accounted for 93.1%, foliage 1.7% and roots 5.2% of total standing crop at the Southern site. The corresponding values at the Northern site were 95.1, 1.4 and 3.5%. Of course these values do not reflect the actual total distribution of biomass in these forests, as the mass of roots >10.0 mm (often roughly 20% of true total standing crop) was not determined.

Total above and belowground NPP (less the coarse root increment) was nearly equal at both sites (Table 7), with about 7% more production at the Southern site. The distribution of NPP among the three components we measured was also the same at both sites. Only about 10% of NPP was allocated to the production of bolewood and branches (1,222 and 1,233 $kg \cdot ha \cdot yr^{-1}$ at the Southern and Northern sites, respectively). Foliage production accounted for 30% of NPP, while about 60% was allocated belowground to roots <2.0 mm.

Leaf litterfall and fine (<2.0 mm) root turnover dominated carbon and N inputs to the forest floor and soil (Table 8). Leaf litter accounted for 35% of total above- and belowground litter biomass at the Southern site, and just over 40% at the Northern site. Most of the remaining litter

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Table 4.7 Above- and belowground net primary production (NPP), in $kg \cdot ha^{-1} \cdot yr^{-1}$, for the period April 1989 through April 1990. Data are plot means, with percentage of total NPP in parentheses.

	Southern Site	Northern Site
Aboveground		
Woody	1,222 (9)	1,233 (10)
Foliage	4,225 (31)	4,068 (32)
Roots <2.0	8,081 (60)	7,302 (58)
Total	13,528	12,603

Table 4.8 Above- and belowground litter biomass and N returns to the soil from April 1989 to April 1990. Data are expressed in units of $kg \cdot ha^{-1}$, and as a percentage of total litterfall. Plot means with standard errors in parentheses.

	Southern Site			
	Biomass	% Total	Nitrogen	% Total
Foliage	4225 (412)	35.1	36.7 (5.7)	29.5
Reproductive	622 (115)	5.1	12.6 (3.7)	10.1
Woody	514 (101)	4.3	2.9 (0.5)	2.3
Root <2.0mm	6682 (892)	55.5	72.3 (9.3)	58.1
Total	12,043		124.5	
	Northern Site			
	Biomass	% Total	Nitrogen	% Total
Foliage	4068 (357)	40.8	38.7 (1.8)	35.2
Reproductive	715 (181)	7.2	15.9 (4.1)	14.5
Woody	348 (126)	3.5	2.3 (0.7)	2.1
Root <2.0mm	4843 (929)	48.6	53.1 (8.6)	48.3
Total	9,974		110.0	

input at both sites was due to fine root turnover (around 50%). The total contribution of reproductive and small branch litter was about 10% at both sites. Patterns of N return were similar, although reproductive litter accounted for over 10% of total N returns by itself (12.6 and 15.9 $kg \cdot ha \cdot yr^{-1}$ at the Southern and Northern sites, respectively). The amount of N in leaf litter was 36.7 $kg \cdot ha \cdot yr^{-1}$ at the Southern site and 38.7 $kg \cdot ha \cdot yr^{-1}$ at the Northern site. The corresponding values for root N inputs were 72.3 and 53.1 $kg \cdot ha \cdot yr^{-1}$.

Discussion

We observed a unimodal seasonal pattern of fine root length densities during 1989 at both sites, and there appears to be a large degree of both temporal and spatial consistency in the cycles of fine root length gains and losses in these northern hardwood ecosystems. This pattern of root length increase and decline may be linked to phenological and physiological events in the canopy. There is a substantial increase in root length as the canopy flushes in late spring, and maximum amounts of root length occur in mid-summer when evaporative demand is high and soil water is typically at relatively low levels in these forests. Fine root length subsequently declines around the onset of canopy senescence and leafall. The summer maximum in root length that we observed is in general agreement with the trends

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biomass data from some other deciduous (Joslin and Henderson 1987, McClaugherty et al. 1982) and coniferous (Gholz et al. 1986, Nadelhoffer et al. 1985) forests in eastern North America.

Seasonal patterns of fine root length densities reveal little about the dynamics of fine root production and mortality, as changes in root length reflect only the net effect of these two processes. There has been much discussion in the literature regarding the need to identify peaks and troughs in seasonal fine root biomass so that production and turnover can be accurately measured (e.g. Kurz and Kimmins 1987, McClaugherty et al. 1982, Vogt et al. 1989, and there has been even more discussion as to the definition of "real" temporal increments and decrements in biomass (Fairley and Alexander 1985, Laurenroth et al. 1986, Persson 1978, Singh et al. 1984, Vogt et al. 1986). Nevertheless, neither the identification of fine root biomass minima and maxima, nor significant temporal differences in standing crops, is sufficient to accurately calculate fine root production and mortality. Kurz and Kimmins (1987) demonstrated that calculating fine root production from changes in root biomass can result in large underestimates of actual belowground productivity and turnover if root production and mortality are co-occurring in time. And, the greater the degree of temporal synchrony between production and mortality, the greater the

underestimation of either process.

The fine root minirhizotron data obtained from our study sites consistently show a large amount of concurrent production and mortality; much more than could be calculated solely from changes in live or dead root mass. Although the majority of fine root production occurs in the spring, and the bulk of mortality in the fall and winter (Figures 2 and 3), both processes are nearly equal in magnitude during the summer. Total fine root length changes relatively little during this time (Figure 1), but over 1/3 of annual production occurs between June and September at both sites, and approximately 40% and 30% of annual mortality occurs during the same period of time at the Southern and Northern sites, respectively. Clearly, any physical sampling scheme or accounting procedure that relies solely on changes in root biomass (live or dead) to calculate production and turnover will result in considerable underestimates of true values in these forests. The measurement of fine root decay rates should increase the accuracy of root production and turnover estimates if live and dead roots can be separated consistently. However, we have shown that fine roots in these forests generally disappear much more rapidly than buried-bag decomposition data would suggest (Hendrick and Pregitzer 1992a). Fine roots are no longer visible in the minirhizotrons within a month or so after death, similar to the disappearance rates observed by Rogers (1939) for apple

roots. The absence of an accumulating pool of dead roots or root-derived detritus in these and other forests suggests that current estimates of fine root decomposition rates are too low (Fahey 1992), and in need of further study.

A notable difference between the two forests we studied is in the balance of white and brown root length observed throughout the year, and the contribution of these two classes of roots to total root turnover (Table 2). Although all roots are white when first produced, there is always a higher proportion of brown root length visible in the minirhizotrons at the Northern site. We have previously shown that white roots in this forest are consistently more likely to turn brown rather than die throughout the year (Hendrick and Pregitzer, 1992a). Conversely, white roots at the Southern site are equally (or more) likely to die than to turn brown from one sampling date to the next (unpublished data). As the mortality data from this study show (Table 2), a much higher proportion of total root length mortality is comprised of white roots at the Southern site, with white and brown roots contributing equally to total length turnover. A lower proportion of standing white root length at the Northern forest may have important implications for nutrient uptake capacity, as the brown roots probably lose much of their ability to actively take up nutrients via symplastic pathways once the living tissue of their cortex is shed.

The autumnal decline in the N concentrations of roots <2.0 mm at the Northern site is partially a result of spring vs. fall differences in the relative abundance of white and brown roots (Figure 3). While roughly 1/3 of all root length was white in color in April 1989, only a little over 10% was white in October of the same year. We have previously shown that the white roots of sugar maple in this forest lose about 40% of their N as they turn brown (Goldfarb et al. 1990), and we attribute the October drop in average N concentration from 1.33 to 0.93% to the greater abundance of brown roots in the fall. The fact that the proportions of white and brown roots remained fairly stable at the Southern site is probably responsible for the constant N concentration in fine roots at this site.

Our estimates of total fine (<2.0 mm) root biomass are generally greater than those reported from other North American deciduous forests (Table 9). Our values are reasonably close to Powell and Day's (1991) estimate of 7430 $kg \cdot ha^{-1}$ for roots <2.0 mm in a mixed hardwood forest in the Great Dismal Swamp, and to Cox et al.'s (1978) report of 8500 $kg \cdot ha^{-1}$ for roots <5.0 mm in a Liriodendron tulipifera stand. There are fewer N content data for comparison but again, with the exception of Cox et al. (1978) our estimates are considerably higher than other published values. Fine roots <0.5 mm accounted for the bulk of the <2.0 mm root

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Table 4.9 Comparison of fine root biomass and nitrogen standing crops and annual production in some North American deciduous forests. Biomass and N standing crop and production values are in units of $kg \cdot ha^{-1}$ and $kg \cdot ha^{-1} \cdot yr^{-1}$, respectively.

	Standing Crop		Production		
Forest Type	**Biomass**	**N**	**Biomass**	**N**	**Reference**
Sugar maple	4280	50	4020	47	Nadelhoffer et al. 1985
Red oak/maple	5100	57	4900 9900	73 184	McClaugherty et al. 1982
Sugar maple	3230		6500 1060		Aber et al. 1985
White oak	4120	48	850	10	Joslin and Henderson 1987
Tulip poplar	8500	96	6750	76	Cox et al. 1978
Oak, gum, maple	7430		9890 3450		Powell and Day 1991
Sugar maple	7901 6887	85 85	8081 7302	87 88	This study

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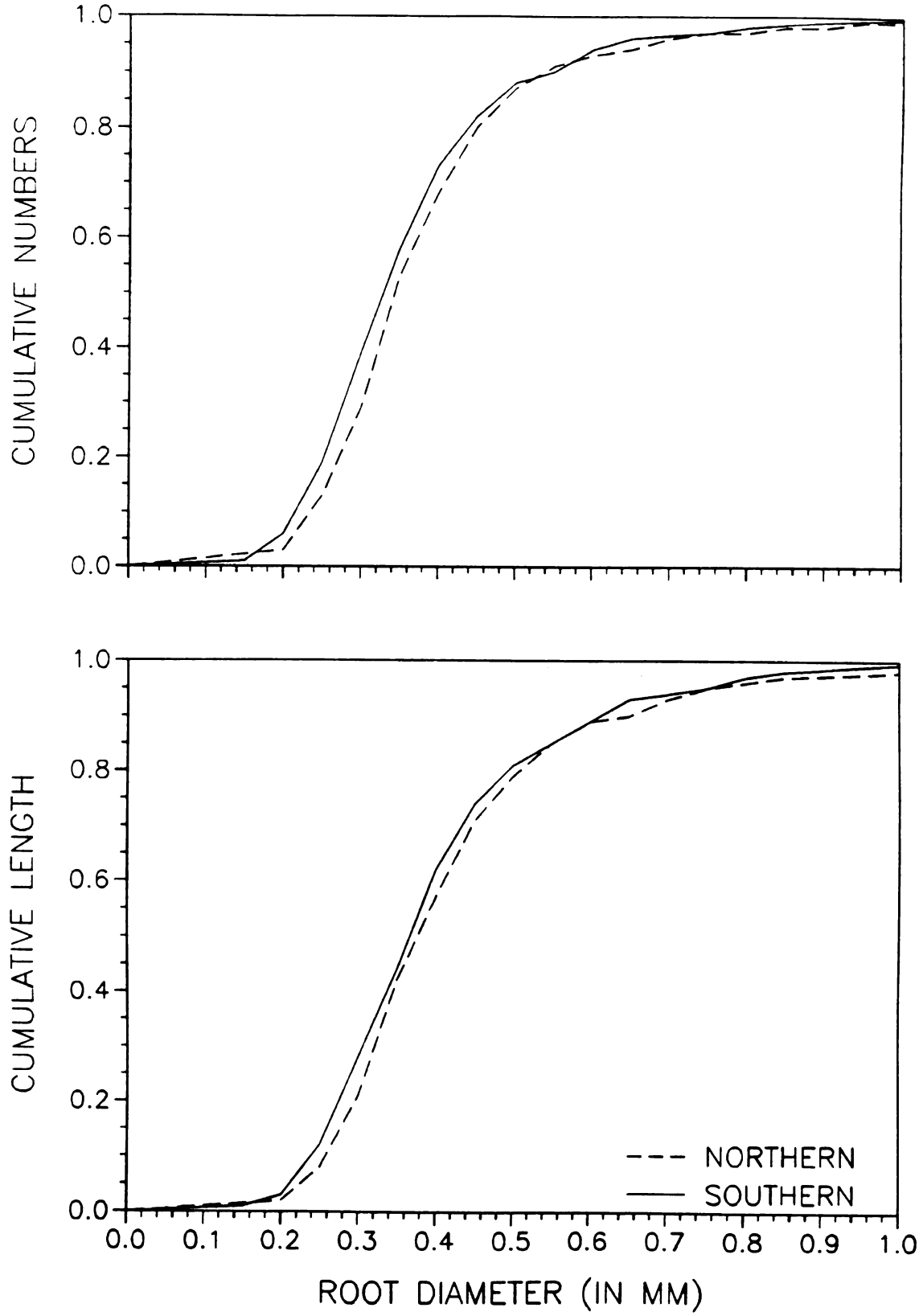
mass and nutrient content in the forests we studied (greater than 70% of root mass and total N is in these roots), and are largely responsible for the disparity between our data and other reports. In fact, the biomass and N values of the <0.5 mm roots in our forests (Table 3) are equal or greater than most other investigator's estimates of the mass for all roots <2.0 or 3.0 mm. We estimated the mass of roots <0.5 mm indirectly (by converting length to mass), and there is always a degree of uncertainty when using an indirect method to estimate an ecosystem component. It is possible that we overestimated total root length before converting to biomass, but we believe not. We incrementally calibrated our procedure against known lengths of monofilament line that bracketed the lengths estimated from our core samples.

We believe that a better recovery of the very fine roots, largely due to the mechanical root washing system we used, is responsible for most of the differences between our results and those of other investigators. The hydropneumatic elutriation system (Smucker et al. 1982) uses air bubbles and water to separate roots from soil, and to subsequently gently deposit the roots on a 0.4 mm mesh screen. In other studies (e.g. Joslin and Henderson 1987, Nadelhoffer et al. 1985, Powell and Day 1991), fine roots have been recovered by washing soil samples through fine screens with mesh openings equal to or greater than 0.5 mm (as much as 2.0 mm) in size, or by a combination of hand

Figure 4.5 Cumulative diameter distribution of fine root length and numbers at both study sites on the July 1989 sampling date. Data represent values summed across all plots: 587 roots and 3262 mm of root at the Southern site, with corresponding values of 662 and 4059 at the Northern site.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sorting and sieving (McClaugherty et al. 1982). Our minirhizotron data indicate that at least 80% of all roots at our study sites are <0.5 mm in diameter (Hendrick and Pregitzer 1992a, Figure 5), and it is likely that we would have missed many of these roots if we had washed our samples by hand through a larger screen. Although some of these very small roots may remain attached to larger roots during hand washing, in our elutriated samples almost all roots of this size are detached. The number of these small, delicate roots in a soil core sample is staggering, and they would be virtually impossible to recover by hand. The fact that the percentages of total root length (80%) and numbers (ca. 85%) comprised of roots <0.5 mm (as observed in the minirhizotrons, Figure 5)) are similar to the percentage of total root biomass (>70%) accounted for by roots <0.5 mm in diameter gives us further confidence that our biomass estimates are reasonably accurate. Visual inspection of the graphical data of McClaugherty et al. (1982), who hand sorted their roots into size classes, shows that the mass of roots <0.5 represented about 1/2 to 2/3 of the total mass of all roots <3.0 mm in the organic layer of the soil. These proportions are not greatly different from ours, given the wider diameter class they used, although their data for mineral soil horizons indicates a more equal distribution of biomass among the size classes. It is our belief that the contribution of the very finest roots (ca. <0.5 mm) to total root system biomass and nutrient content has probably been

underestimated to some extent in some past studies. This might be especially true in forests dominated by deciduous trees, where fine non-woody roots generally have small average diameters (Fahey et al. 1988, Goldfarb et al. 1990, Pregitzer et al 1990) and where many species (like sugar maple) form vesicular-arbuscular mycorrhizal (VAM) roots that are more easily broken during handling than ectomycorrhizal roots.

We observed a substantial (although not statistically significant) April-to-October increase in the biomass of roots >2.0. mm at both sites (Table 3) that may be have been due to an autumnal loading of storage carbohydrates, rather than an increase in structural biomass. Starch levels in sugar maple roots reach minimal levels in late spring after budbreak (Wargo 1979), begin increasing in July, and reach a maximum in late fall (Wargo 1971). Carbon is allocated preferentially to storage carbohydrates, rather than to radial growth in the coarse roots of sugar maple, and little growth occurs until after leaf fall (Wargo 1979). Similar patterns of carbohydrate deposition in roots have been shown for other deciduous species including red (Q. rubra) and white (Q. alba) oak (Wargo 1976), hybrid poplar (Nguyen et al. 1990), and turkey (Q. laevis Walt.) and bluejack (Q. incana Bartr.) oak (Woods et al. 1959).

As was true for standing crops, our estimates of fine root biomass and N production and turnover (Tables 5 and 9) are greater than many published values. However, relative to initial or average standing crops, our estimates are in general agreement with many others. Annual (April-April) biomass and N allocation to fine root production was just slightly greater than the April standing crops, and Cox et al. (1978), McClaugherty et al. (1982), Nadelhoffer et al. (1985) and Powell and Day (1991) also report annual production estimates that are very similar to standing crop values. The annual production data of Aber et al. (1985) from a sugar maple stand in Wisconsin range from about 33 to 200% of standing crop, depending on the method of calculation used, while Joslin and Henderson (1987) estimated that annual production of roots <2.0 mm is only about 20% of standing crop (Table 9). The similarity between our production data (expressed as a percentage of initial standing crop) and those of other investigators leads us to believe that the absolute differences in production, like standing crop, are again due to a greater amount of very fine (ca. <0.5 mm) roots measured in our forests than in other ecosystems.

With respect to total (above- and belwoground) stand biomass, fine roots (<2.0 mm) represented a relatively small proportion in both of the forests we studied; 3.1% of total biomass (less coarse roots >10.0 mm) at the Southern site

and 2.4% at the Northern site (Table 6). Similar values have been found by numerous other researchers in a wide array of forests types (Arthur and Fahey 1991, Fogel and Hunt 1979, Gower et al. 1992, Grier et al. 1981, Keyes and Grier 1981). However, as has also been observed in a number of forest types, a substantial proportion of annual net primary production, about 60%, is allocated to fine roots in the ecosystems we examined. Fine root production is roughly twice foliage production, and six times bole and branch production, in both forests. Fine root (<2.0 mm) turnover also dominated carbon and nutrient inputs to the soil, accounting for approximately 56 and 49% of total C, and 58 and 48% of N cycled annually at the Southern and Northern sites, respectively.

Our estimates of the contribution of fine roots to stand NPP (Table 8) are considerably higher than those of Nadelhoffer et al. (30%, 1985) and Aber et al. (41%, 1985) for sugar maple forests in Wisconsin. It should be noted, however, that our estimates of aboveground standing crop and leaf area are also greater than these Wisconsin forests. Nadelhoffer and Raich (1992) have recently suggested that fine root production may be positively correlated with aboveground productivity. Greater total stand biomass and productivity in the forests we studied may also reflect a longer growing season or more moderate climate on the leeward side of Lake Michigan. Our fine root data are

comparable to those of Cox et al. (1978), who estimated that fine root death and decay accounted for 67% of biomass litter production and about 60% of N cycled via detritus in a tulip poplar stand. And, although higher than the estimates of Keyes and Grier (1981), Gower et al. (1992) and Arthur and Fahey (1992), our production and turnover values are similar to some of the data from western coniferous forests. Grier et al. (1981) estimated that 55% of total ecosystem NPP was allocated to fine roots in a 23 year old Pacific silver fir stand in Washington, while the corresponding value from a 180 year old site was nearly 69%. Fogel and Hunt (1983) estimated that about 73% of NPP is allocated to fine roots and mycorrhizae, and that fine root and mycorrhizal turnover was responsible for about 85% of all detrital N inputs, in an Oregon Douglas-fir forest.

One of the reasons that the 1989 fine root allocation and litter return percentages in our forests were so high was because stem and branch production was quite low relative to other years. Annual bole and branch biomass production was just over 1,200 $kg \cdot ha^{-1} \cdot yr^{-1}$ in both forests during 1989, while 1990 production was 6,000 and 5,500 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 1990 at the Southern and Northern sites, respectively. We suspect that the low amount of aboveground production in 1989 may have been a residual effect from the 1988 drought. Also, fine root growth is inhibited and turnover rates are accelerated at low levels of soil moisture availability

(e.g. Bartsch 1987, Kuhns et al. 1985, Rogers 1939, Santantonio 1982), and it is likely that a large amount of root production occurred in 1989 as absorbing area was re-established in these forests. The effects of substantial root production on total ecosystem productivity would be likely to show up as reduced stemwood production, since fine roots are a higher C allocation priority (Waring and Pitman 1985). Pregitzer and Burton (1991) demonstrated a direct tradeoff between the production of foliage and reproductive litter in the forests, and similar tradeoffs in whole-tree carbon allocation may be occurring with respect to fine root and bolewood production.

In the forests we studied, more C and N was cycled via fine root turnover than aboveground litterfall. The same phenomenon has been observed in a number of forests worldwide (Vogt et al. 1986a), and comparative data from other studies suggests that fine root production surpasses foliage production in most deciduous forests of the eastern U.S. (Table 10). The ratio of root production to total foliage biomass at both of our study sites is close to the value of 1.92 derived by Raich and Nadelhoffer (1989) for the ratio of aboveground litterfall carbon to total root carbon allocation, although they included root respiration in addition to biomass production. Our data fall somewhere in the middle of the range of values we derived from other ecosystem studies, including the sugar maple stands studied

Table 4.10 Annual fine root production per unit leaf weight and leaf area in some temperate North American deciduous forests. Leaf biomass data were derived from published estimates of leaf litter production.

Forest Type	kg Root/ kg Leaf	kg Root/ m^2 Leaf	Reference
Sugar Maple	1.40[a]	----	Nadelhoffer et al. 1985
Sugar Maple	3.10[a]	----	Pastor et al. 1984, Aber et al. 1985
Oak-Red Maple	1.23[b]	----	McClaugherty et al. 1982
White Oak	0.26[c]	----	Joslin & Henderson 1987
Tulip Poplar	2.04[d]	0.095	Cannell 1982, Cox et al. 1978
Sugar Maple (Southern)	1.91	0.10	This Study
Sugar Maple (Northern)	1.79	0.10	This Study

[a] production calculated by difference using nitrogen budgeting technique

[b] production calculated as difference of minimum and maximum annual root mass

[c] production calculated by balancing production, mortality and decomposition

[d] production calculated as root death/decay data

by Nadelhoffer et al. (1985) and Aber et al. (1985). Our data are quite similar to the value of 2.04 for the tulip poplar stand of Cox et al. (1978). Perhaps of even more functional significance is the relationship between leaf area and fine root production. Even though there were some site differences in both leaf area (Table 1) and root production (Table 5), the ratio of root mass production to leaf area was the same in both forests. Unfortunately, there are very few other published data from deciduous forests for comparison, but our estimates are again nearly the same as to that derived from the data of Cox et al. (1978) and Cannell (1982).

The validity of our estimates of the role of fine roots in ecosystem processes in these forests is dependant upon the accuracy of our estimates of root production and mortality. We calculated April 1989 to April 1990, and April-October 1989, production as being greater than concurrent mortality during the corresponding periods of time in both forests. Consequently, we predicted that the October 1989 standing crops should be greater than the April values. Encouragingly, the October 1989 increase in biomass standing crops (Table 5) indicates that the increases in root length that we observed with the minirhizotrons during the growing season were real and reflected corresponding changes in biomass. However, the accuracy with which we were able to predict fine root production and mortality, and changes in

standing crops, from the biomass and minirhizotron data are somewhat mixed. Based upon the close agreement (not significantly different at alpha = .05) between actual and predicted October biomass and N standing crops, we appear to have predicted biomass and N production and mortality fairly closely at the Southern site, and we have a high degree of confidence in our estimates for this site. However, we overestimated October biomass and N content at the Northern site by about 34%, indicating that either our production estimates for this site are too high, our estimates of April or October fine root biomass are incorect, or our mortality estimates are too low. It is our opinion that the discrepancy between the actual and predicted October 1989 biomass values at the Northern site is due primarily to an underestimate of root mortality, and to a lesser degree an overestimate of root production.

The reasoning for this statement lies in our belief that root length and age distributions had probably not equilibrated along the minirhizotron surface when we began imaging in 1989. These forests experienced a 50 yr drought in 1988. Because root growth is inhibited (Deans 1979, Kaufmann 1977, Kuhns et al. 1985, Taylor and Davies 1990, Teskey and Hinckley 1981) and root aging (i.e. "suberization") and turnover rates are accelerated (Bartsch 1987, Kuhns et al. 1985, Rogers 1939, Santantonio 1982) at low soil moisture potentials, new root growth was probably

comparatively low during most of the 1988 growing season and root mortality rates may have been rather high. As a result, the initial root length densities along the minirhizotron surface may have been somewhat lower than they would have been had we had normal amounts of precipitation in 1988, and age distributions would have been skewed towards younger roots. Because production and mortality rates were derived as a proportion of initial root length densities, actual production would have been overestimated, and root mortality underestimated. A bias towards younger roots would result in a systematic underestimate of root mortality, since roots (especially young ones) are always more likely to live rather than die. Because of the tendency for roots to live longer at the Northern site, with lower overall production, attainment of "equilibirium" length densities and age distributions would take longer than at the Southern site. This may be why there seemed to be little or no "recolonization" effect at the Southern site, and why our predictions were so accurate. If we computationally adjust April-October 1989 production and mortality at the Northern site to reflect the ratio of 1990 mortality and 1990 production to the April 1990 standing crop (and assuming that equilibrium root length densities had been attained by April 1990), we obtain a predicted October 1989 biomass value of 8440 $kg \cdot ha^{-1}$; a value only 6% greater than the measured value of 7968.

Conclusions

1. Although the major pulses of fine root birth and death are separated in time in these forests, there is a large amount of concurrent production and mortality throughout the growing season. Failure to account for the simultaneity of these two processes leads to substantial underestimates of total annual belowground biomass and nutrient production and turnover.

2. Our data offer further empirical support to the generally accepted view that the processes of fine root production and turnover play an important, sometimes dominant, role in the carbon and N economies of forests. Roughly 60% of ecosystem NPP is allocated to fine (<2.0 mm root production) in the two sugar maple forests that we studied, and fine root turnover is responsible for approximately 1/2 of carbon and N returned to the soil via plant litter inputs.

3. Surprisingly, roots <0.5 mm account for a large proportion of the carbon and nutrients in fine root standing crops, as well as fine root production and mortality. These roots play a major role in the carbon and nutrient cycles of northern hardwood forests, and care should be taken to fully recover very fine roots in future studies.

4. There may to be a consistent relationship between leaf area and fine root biomass in these forests, probably reflecting the functional interdependence of the absorbing and transpiring surface areas of plants. Further investigations in other forest types and under varying environmental conditions may reveal differences in patterns of carbon allocation that are attributable to differential absorbing/transpiring efficiencies among species, or to changes in resource allocation elicited in response to varying environmental factors within a forest type.

5. Given low aboveground productivity during 1989 relative to other years, and large relative amounts of fine root production during the same period of time, our observations support the premise that fine roots and foliage receive high-priority during resource allocation. Our minirhizotron and biomass data suggest that fine root dieback probably occurred during the record 1988 drought, and that fine root absorbing area was re-established in 1989 at the expense of bolewood production.

6. Based upon our original predictions for the Southern site, and our adjusted predictions for the Northern site, it would appear that root length dynamics measured with minirhizotrons (once root length densities have stabilized) closely parallel changes in root biomass, and provide an index of belowground carbon and nutrient production and

turnover. Production and mortality can be directly and independently measured using minirhizotrons, and changes in length used to predict the amount of carbon and nutrients allocated and cycled belowground.

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