THE EFFECTS OF FERTILIZATION AND COMPETITION CONTROL ON LOBLOLLY PINE FINE ROOT DYNAMICS

by

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(Under the direction of Ronald Hendrick)

ABSTRACT

We studied the effects of annual fertilization (F) and complete competition control via herbicides (H) on fine root dynamics in 13yr. old *Pinus taeda* stands. We measured fine root length, mass, and production. Relative to the control, both F and H decreased fine root length and mass. The single-factor effects were greatest for H, which reduced both root mass and length by half. In combination (HF) fine root mass was reduced by 66%. With respect to above vs. below ground mass, both F and H increased the amount of leaf area supported per unit root mass and length. Their combined effects (HF) were nearly additive. Relative to control, all treatments decreased root production and show apparent increases in root longevity. The results suggest that both fertilization and herbicides alter patterns of allocation, and that in combination they produce nearly additive effects with respect to increasing wood production per unit of root length or mass.

INDEX WORDS: Fine Root, Carbon, Pine, Fertilization, Competition control, Allocation

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CHAPTER 1

INTRODUCTION

Fine roots and mycorrhizae are important contributors to the carbon and nutrient cycles of forest ecosystems. However, knowledge of fine root dynamics has been greatly delayed compared to other components of forest ecosystems and most data include only the above ground biomass and productivity components (Kimmins 1987). Annual net primary production below ground and fine roots in particular can return as much if not more nutrients to the soil as above ground litter (Gower et al. 1992, Hendrick and Pregitzer 1993). Grier et al. (1981) demonstrated the substantial role of fine roots and mycorrhizae when it was observed that together these relatively small biomass components of the forest ecosystem accounted for 55 and 69% of total net production in 23 and 180-year-old *Abies amabilis* stands, respectively. Therefore, quantifying the root component is critical to understanding carbon dynamics in both natural and manipulated forest ecosystems.

The overall wood yield of a managed forest plantation is greatly influenced by the level of nutrients and water in the soil, as well as the intensity of competition by non-woody species. With changes in nutrient and water availability plants may be prompted to modify the size and morphology of the above and below ground components. Plasticity in the root system can be manifested in allocation changes between root and shoot structures, allocation changes between different root sectors (different root diameters), or alteration of fine root architecture (Grime et al. 1991).

Silvicultural amendments, such as fertilizer application and complete competition control, have proven effective in increasing overall tree growth via manipulation of crown structure, leaf area, and patterns of carbon allocation (Keyes and Grier 1981, Vose and Allen 1988, Clason 1993, Teskey et al. 1994, Haynes and Gower 1995). Even though these growth improvements are well documented, the effects of fertilizers and herbicides on fine root production have rarely been observed. Understanding these root responses when attempting to predict or manipulate root system development and resource acquisition in forest plantations is critical.

Many theories have been developed concerning fine root responses to nutrient application (Grime 1977, Nadelhoffer 1985, Vogt 1986, Aerts 1992, Gower 1992), but the response of fine roots to complete competition control is still ambiguous. Competition control does influence site productivity, however, little is known about the possible mechanisms responsible for carbon allocation and lifespan changes in fine root systems when subjected to competition control (via herbicides) or fertilization in conjunction with competition control.

Measuring fine root dynamics- the minirhizotron technique

Measurements of the below ground component of a forest ecosystem are problematic and have limited our knowledge of the system as a whole. A majority of the data from previous studies has focused on above ground components. Fine roots, on the other hand, are difficult to study under natural conditions since the soil environment they are imbedded in poses many technical limitations for root measurement. As a result, the data related to processes beneath the soil surface are lacking.

Many methods have been developed to measure and estimate fine root biomass and lifespan dynamics (ie. soil cores, ingrowth cores, mesh bags, minirhizotrons). Minirhizotrons provide a unique method by which individual root segments can be directly and repeatedly measured over multiple time intervals. In addition, because minirhizotrons are less destructive in nature, they enable researchers to minimize soil disturbance as well as the confounding of spatial and temporal variation associated with other root research methods such as core collection (Bohm 1979) or mesh ingrowth bags (Persson 1980, Steen 1991, Ludovici and Morris 1996). In this study, I chose to use minirhizotrons to observe the simultaneous production and mortality of loblolly pine (*Pinus taeda*) fine roots in response to fertilization and herbicide treatments.

Although minirhizotrons have proven to be one of the most effective tools for quantifying below ground dynamics its frequency of use can sometimes be limited by the labor and time intensity of the manual image analysis procedure (Hendrick and Pregitzer 1996). In addition to the field study of loblolly pine, I also addressed this limitation and attempted to reduce image analysis time. I explored the possibility of using root numbers as a substitute parameter to accurately estimate root length production and mortality. The ideal substitute parameter would have to be easier to extract from video images and demonstrate a high correlation to individual root segment lengths. By doing a regression analysis of various pre-existing minirhizotrons data sets, we found that root numbers were good predictors of root length production and mortality. The new method was implemented in this study to reduce image analysis time.

Objectives

This project' s overall goal is to understand the mechanisms by which fertilization and herbicides affect loblolly pine (*Pinus taeda*) growth. The goals of this portion of the project are to assess changes in fine root biomass accumulation, carbon allocation, and production under the three management treatments: fertilizer (F), herbicide (H), and herbicide plus fertilizer (HF). My specific questions are:

a) Is there a significant difference in biomass accumulation, carbon allocation, and production under the three management treatments.

b) Compare individual treatment effects (F and H) to their combined effect (HF). Are they additive?

c) Are there changes in the relationship between the above and below ground components for each treatment? How do they vary?

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CHAPTER 2

LITERATURE REVIEW

A. Fine root carbon allocation and lifespan dynamics

Generally, plants can respond to poor environmental conditions by reducing growth rates, changing morphology (i.e. specific root length [SRL], specific leaf area [SLA] and leaf area index [LAI]), or by altering allocation patterns in an attempt to minimize growth limitations by any one factor. For example, if light is the limiting factor then allocation to the leaves is favored (Brouwer 1983, Aerts 1992). Conversely, if nutrients or water are limiting then biomass tends to shift towards root structures in order to maximize the uptake of the limiting factor at its source (Brouwer 1983). By fine-tuning the allocation patterns of carbon with respect to the limiting environmental factor(s) plants may minimize losses so that all resources are equally limiting (Bloom et al. 1985). Therefore, regardless of environmental conditions, a plant is capable of approaching a functional balance between above and below ground components so that resource acquisition is approximately balanced (Garnier 1991).

When fertilization (F) is applied to forest plantations there is typically an increase in absolute biomass accumulation coinciding with a decrease in root:shoot ratios (Ahlstrom 1988). Ludovici and Morris (1996) reported increases in root biomass in response to nitrogen fertilization in both sweetgum (*Liquidambar styraciflua*) and loblolly pine (*Pinus taeda*) seedlings. In most cases, however, a surplus of nutrients decreases the relative energy expenditure for acquisition of below ground resources and root biomass in favor of light absorption, a response that Axelsson and Axelsson (1986) state is primarily responsible for increases in above ground biomass production. Below ground biomass reductions were also reported by Keyes and Grier (1981) when they observed that root biomass decreased below ground in high fertility sites from 8100 kg ha^{-1} to 4100 kg ha^{-1}, but increased absolute above ground mass. Some (Grime 1977, Orians and Solbrig 1977, Chapin 1980) suggest that absolute fine root biomass decreases in response to elevated nitrogen via decreases in annual fine root production. Accordingly, Haynes and Gower (1995) found significant decreases in fine root production in unfertilized (2510 kg ha^{-1}) versus fertilized (940 kg ha^{-1}) red pine (*Pinus resinosa*) stands for first year observations but only slight differences in year two (1800 vs. 1940 kg ha^{-1}, respectively). Others hypothesis that fine root longevity may be less on nutrient rich sites, offsetting the lower below ground biomass values commonly reported for nutrient rich systems (Nadelhoffer et al. 1985).

Two hypotheses have been proposed by Hendricks et al. (1993) to explain changes in allocation patterns with respect to root carbon and lifespan: 1) Fine root biomass decreases as nitrogen availability increases but fine root longevity is not affected, or 2) the proportion of carbon content in fine roots (i.e. biomass) remains relatively constant and may even increase across nitrogen availability increases but fine root longevity decreases, thereby making fine root standing biomass appear low.

Various studies examining fertilization effects support both hypothesis 1 (Vogt et al 1986, Gower et al 1992) and hypothesis 2 (Safford 1974, Ericsson et al 1980, Cuevas et al 1988). These hypotheses, however, do not address all possibilities and ignore potential increases in root longevity and possible differences in the magnitudes of below ground responses. Within different systems some studies show a decrease in carbon allocation to fine roots while others report increases. This may be partially explained by variations in species, fertilizer type, or geographic region but for the most part is governed by root lifespans. For example, fertilizer application may significantly increase both above and below ground biomass but there could either be relatively greater shifts in allocation to above ground structures or significant decreases in fine root longevity that may cause apparent decreases in root biomass (Aerts 1992).

Control of herbaceous vegetation via herbicide application typically increases above ground biomass production in young stands (Will et al. 2002), but it is not known if it induces a reallocation effect similar to that of fertilizer. As crowding and competition increase, the mean size per pine tree is reduced (competition-density effect). Crowded pine stands may also exhibit self-thinning, and the degree of growth inequality among pines may increase with time. These effects can be modeled by assuming that individual plants compete by preempting other plants access to resources (Tilman 1990). Clason (1993) stated that unwanted vegetation, such as under-story hardwoods, exerted growth stresses that hindered pine growth. Furthermore, herbaceous weeds and hardwood brush reduced merchantable wood volume from 182 m^3 ha^{-1} in competition control treatments to 141 m^3 ha^{-1} in non-suppressed treatments, thus, decreasing harvest values. Ludovici and Morris (1996) reported that herbaceous and woody competitors negatively effected above ground loblolly pine biomass accumulation and that there was a positive correlation between shoot height and root volume for loblolly pine seedlings. Competition control has been shown by Shan et al. (2001) to elicit a greater shift of biomass accumulation away from root biomass relative to fertilizer treatments, reducing fine root mass by one third in fertilized stands and by one half in competition control stands.

In combination, fertilization and competition control have the potential to dramatically increase above ground growth, but it is unclear how this treatment may affect root dynamics. Some studies have shown significant effects of competition and nutrient supply on growth. Aerts et al (1991) observed that competitive effects appeared to be more severe at higher levels of resource availability; however, Ludovici (1996) observed that the presence of competitors reduced pine root growth regardless of the level of nitrogen or soil water content. Ludovici (1996) also observed that, when stressed by low water availability, loblolly pine roots only responded to increased nitrogen in the absence of competitors.

B. Above and below ground morphology

Plants can alter their morphology (i.e. changes in LAI, SLA, or SRL) in response to environmental conditions, which may alter our interpretation of apparent changes in biomass allocation and accumulation. Gholz (1982) showed that leaf area index (LAI: m^2 m^{-2}) is closely related to productivity and increases in the presence of favorable conditions.

Comparisons of above ground components such as LAI with their respective root length and root mass should provide useful insight into the mechanisms of treatment responses. Two different treatment regimes may result in similar below ground biomass accumulations but may exhibit differences in their above ground morphology (i.e. LAI or SLA). For example, sivilcultural treatments that result in a high leaf area per unit of root length or root mass improve growth potential by both increasing photosynthetic capacity and allocating less carbon to root structures. It is also important to note that a high specific root length (SRL: mass per unit root length) may account for apparent reductions in below ground biomass (Aerts et al. 1991).

C. Hypotheses

Absolute fine root biomass and lifespan–

Some research (Nadelhoffer et al. 1985) suggests that fine root turnover (i.e. shorter fine root lifespans) may be greater on nutrient rich sites than they are on poorer sites, causing below ground biomass to appear diminished. In contrast, Shan et al. (2001) reported no significant changes in turnover rates with fertilization, however, there was a greater reallocation of biomass away from the fine root component. Shan et al. (2001) also reported that below ground biomass in fertilizer and herbicide treatments was reduced by one-third and one-half, respectively.

Hypothesis A: All treatments will exhibit similar effects by significantly increasing absolute biomass of pine relative to the control. The size and mechanisms of these effects for each treatment will vary and the balance between below ground biomass and foliage mass among treatments will be non-equal.

Corollary 1. Fertilizer (F) will increase overall nutrient availability and reduce the importance of fine root biomass for seeking out nutrients, causing a relatively small reallocation of biomass from below ground to above ground structures. The presence of competition will still generate the need for a relatively large root system compared to herbicide treatments. Overall, however, trees will increase biomass accumulation to both above and below ground components.

Corollary 2. Eliminating competition (H) will free up available resources increasing above ground growth and decreasing fine root mass. The absence of competition will cause this treatment to have a relatively lower fine root mass than F alone.

We expect allocation patterns to vary in a similar manner to the changes reported by Shan et al. (2001) for slash pine (*Pinus elliottii*) subjected to similar treatments. Shan's (2001) competition control plots showed a significantly greater shift in carbon allocation to above ground structures than those reported for fertilized plots. Therefore herbicide plots should reallocate biomass significantly to above ground structures (i.e. lower standing fine root biomass.

Corollary 3. The combination of F and H (HF) will elicit responses characteristic of both individual treatment responses; however, the magnitude of change will be greater since both competition control and fertilization enhance nutrient availability. The combination of effects will potentially enable this treatment to produce the most above ground biomass per unit of root length and mass. The response of this combination is not expected to be additive, but exhibit benefits of both individual effects.

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CHAPTER 3

SUBSTITUTING ROOT NUMBERS FOR LENGTH: IMPROVING THE USE OF MINIRHIZOTRONS TO STUDY FINE ROOT DYNAMICS[1]

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Abstract

Minirhizotrons provide a unique way to repeatedly measure the growth and fate of individual root segments, while minimizing soil disturbance and the confounding of spatial-temporal variation. However, the time associated with processing videotaped minirhizotron images limits the amount of data that can be realistically extracted. We have found that this limitation can be minimized using a substitute parameter, root numbers, to estimate root length dynamics. Linear regression models were fit between root length and root number for production and mortality of seven sample data sets of varying species and treatments. The resulting r^2 values ranged from 0.79 to 0.99, suggesting that root numbers can be reliably used to predict root lengths. Slope values, representing the average length of a root segment, ranged from 2.34 to 8.38 mm root segment^{-1} for both production and mortality. Most treatments did not significantly alter mean root segment length (MRSL), the exceptions being CO_2 treatments and a girdling treatment that altered plant community composition and, consequently, root morphology. The presence of high r^2 values for all data demonstrated a robust relationship irrespective of the nature of species or treatments. Once the quantitative relationship between root length and number has been established for a particular species-treatment combination, quantifying changes in root number through time should substantially decrease the time required to quantify root dynamics.

Keywords

Fine roots, minirhizotrons, mortality, production

Abbreviations

MRSL:Mean root segment length (mm root segment^{-1})

b_p: Live root length vs. live root number slope value (mean root segment length of live roots in mm root segment^{-1})

b_m: Dead root length vs. dead root number slope value (mean root segment length of dead roots in mm root segment^{-1})

Introduction

Minirhizotrons can be effective tools to observe and quantify root system dynamics. They provide a unique method by which individual root segments can be repeatedly measured over multiple time intervals. Moreover, because they are less destructive during installation and sampling, minirhizotrons enable researchers to minimize soil disturbance as well as the confounding of spatial and temporal variation associated with other root research methods such as core collection (Bohm 1979) or mesh ingrowth bags (Persson 1980, Steen 1991, Ludovici and Morris 1996). Most importantly, minirhizotrons allow the production and mortality (rate of disappearance) of fine roots to be measured as separate processes and, thus, provide direct observations of these two parameters (Hendrick and Pregitzer 1996a). Alternative methods that do not account for simultaneous production and mortality have been shown to underestimate the rates of these processes (Kurz and Kimmins 1987).

While the benefits of minirhizotrons are now more widely recognized, they are still not as frequently utilized as some other methods. Hendrick and Pregitzer (1996a) review the main limitations and possible reasons for this infrequent use, including the time and difficulty associated with the extraction of root data from videotaped images within a reasonable period of time. Manual image analysis is a time-intensive process that typically requires every root segment in each minirhizotron to be digitized for length and diameter (or width). This can represent a substantial time investment and research cost, in that analysis times per minirhizotron tube often range from 30 minutes to 8 hours per sampling period (personal observation).

Various alternative techniques have been devised for extracting data from minirhizotron images, but most fail to follow the fate of individual roots, negating the primary advantage of minirhizotrons over other methods. For example, variations of the grid intersection method originally proposed by Newman (1966) have been utilized to convert root-line intersections to root lengths or root length densities, but these yield only net changes in total root length. Counts of roots in contact with the minirhizotron surface can be used for conversions to root length densities (Upchurch, 1987), but the approach has not been used on an individual-root basis. Automated image analysis shows potential for expediting data extraction but, again, currently available software does not facilitate the tracking of individual roots.

Other approaches involve direct and repeated manual tracing of individual roots using PC-based digitizer software. Hendrick and Pregitzer (1996a) cite some of the current image analysis programs that do facilitate the tracking of individual roots. These include an interactive PC-based program, ROOTS (Michigan State University, E. Lansing, MI, USA), a Macintosh and PC-based RooTracker program (Duke University Phytotron, Durham, NC, USA), and a Macintosh based NIH-image program (Smit and Zuin 1996).

It is likely that considerable time savings would result if we could identify a variable other than root length that still accounted for individual roots, was easy to extract from minirhizotron images, and demonstrated a high correlation to individual root segment length.

Pregitzer et al. (2001) studied nine different trees from across North America and report that the majority of fine root length is accounted for by short lateral branches only a few millimeters in length, and that lateral root branches appear to be deciduous. The length of individual roots of a given order did not vary significantly within a given species (Pregitzer et al. 2001). These findings led us to hypothesize that there should be a strong relationship between root length and number in the temperate and boreal tree species we have previously studied. Likewise, Persson (1978) reported a close relationship between fine root length and changes in the number of fine root tips (roots < 1mm in diameter) of another species, *Pinus sylvestris*, using soil cores and the Newman grid intersection method. The objective of the present study was to determine if we could use root number to predict fine root length. We utilized data sets from several different biomes across North America to study variability in the relationships among fine root length and number.

Materials and Methods

Data Sets

Seven existing minirhizotron data sets were selected to represent a wide variety of tree species (*Acer saccharum, Liquidambar styraciflua, Pinus elliottii, Picea glauca,* *Salix* spp*.*, *Populus tremuloides*) and a variety of study treatments (Table 1). Each study is described briefly below.

Data from two *Pinus elliottii* experiments were utilized for our analysis. The first study, located in the Upper Coastal Plain of Georgia (USA), examined the response of fine root production and mortality to artificial gap formation similar to that created by the southern pine beetle (Schroeer et al. 1999). Treatments consisted of controls and artificial gaps (37.5 m radius). The second *Pinus elliottii* study, located in northern Florida (USA), examined the effects of fertilization and complete competition control on carbon storage and root dynamics. Treatments consisted of control, fertilizer (280 kg ha^{-1} di-ammonium phosphate, 280 kg ha^{-1} urea, and 228 kg ha^{-1} KCl), herbicide (3% solution of Roundup prior to site preparation), and fertilizer plus herbicide treatments (Shan et al. 2001).

An *Acer saccharum* study, located in the north of the lower peninsula of Michigan (USA), was originally established to understand the spatial and temporal dynamics of roots in two forests separated by a north-south distance of 80 km. There were no experimental manipulations applied in this study (Hendrick & Pregitzer 1993a; 1993b; and 1996b).

Minirhizotrons were also used to quantify fine root production, mortality (rate of disappearance) and standing root crop dynamics in an intensively managed *Liquidambar styraciflua* coppice stand located in the Middle Coastal Plain of Georgia (USA). Treatments consisted of two levels of fertilizer (19:9:19 NPK): a low (560 kg ha^{-1} yr^{-1}) and a high level (1120 kg ha^{-1} yr^{-1}) application (Price & Hendrick 1998).

Two of the datasets are from the boreal forest of interior Alaska (USA) where the fine root demography of *Picea glauca* fine roots was measured in three mature forests located on the Tanana River floodplain in interior Alaska (USA). Again, no experimental manipulations were applied to the selected sites in this study.

In early successional *Salix* spp. communities, minirhizotrons were used to characterize the effects of aboveground mammalian browsing on rates of fine root production, mortality, and decomposition. Three large exclosures (30 X 50 X 5 m) were paired with unexclosed plots of the same size to create both browsed and non-browsed treatments (Ruess et al. 1998).

The final data are from a study conducted in Michigan (USA) that was designed to examine the effects of atmospheric CO_2 and nitrogen fertilization on root production and mortality in *Populus tremuloides*. Two levels of CO_2 and two levels of nitrogen were examined in a factorial design (Pregitzer et al. 2000).

Although production measurements refer to the occurrence of new roots as well as the growth of existing roots in the minirhizotron tubes, mortality measurements primarily track the rate of disappearance of the fine roots, as it is difficult to determine when roots actually die. All studies implemented here report a rapid disappearance rate, so it is possible that some mortality is missed. In all studies, 80-85% of all roots measured were <0.5mm in diameter.

Modification of dBase program

In the past, we have used a dBase program (Ruess at http://mercury.bio.uaf.edu/~rruess.faculty /Programs.htm) to calculate production and mortality based upon complete root segment length measurements. In order to calculate both root numbers and root lengths from the existing minirhizotron datasets, a count function was added to the original program. The new program calculated production of both root length and root numbers as well as mortality of both root lengths and root numbers between sample dates. The new program was then executed for each minirhizotron file of the seven sample data sets. Output files, within each dataset, were then collated into their respective treatments. The resulting output provided values of root numbers and the corresponding root lengths for both production and mortality data.

Linear regression models

For these analyses we fit linear regression models of the form $y = bx$, where y = root segment length and the independent variable (x) was the number of roots. Models were constructed for each species-treatment combination, and included length-number relationships for both production (b_p) and mortality (b_m). The models were restricted to force the intercept through zero. The resulting slope value (b) represents the mean root segment length (MRSL) for each species and treatment. Once the regression analysis of each species- and treatment-specific dataset was completed, we compared the slopes (i.e. MRSL) of the regressions to determine if any of the within-dataset treatments had altered the slope. Differences in regression slopes were determined using paired t-tests (α =0.05).

To determine if there were any significant temporal changes in MRSLs (among image dates), the *Pinus elliottii* intensive management study was selected for further examination. We chose these data because of the large number of treatments and because its b and r^2 values fell in the mid range of all data points. A repeated measures analysis of minirhizotron image dates (α= 0.05) was implemented with and without treatments for both production and mortality.

Results

Generally, the predictive value of root numbers for root lengths was strong, even though there was considerable variation among slopes. With respect to root number vs. length productivity estimates, slope values (b_p) ranged from 2.34 – 8.29 mm root segment $^{-1}$, with r^2 ranging from 0.81 to 0.98. Slope values for mortality regressions (b_m) ranged from 3.03 – 8.38 mm root segment^{-1}, with r^2 ranging from 0.79 to 0.99 (Table 2).

The *Pinus elliottii* gap study had its lowest *b* value in gap treatments, 2.34 mm root segment^{-1} ($b_{p,}$ or MRSL of live roots). The highest *b* values were found in control plots, 4.28 mm root segment^{-1} ($b_{m,}$ or MRSL of dead roots). The r^2 values for this study were generally high, ranging from 0.87 to 0.92 (Table 2). In the intensively managed *Pinus elliottii* stands, the lowest b_p value (or MRSL) was in the control plots (4.46 mm root segment^{-1}), and the highest was in the fertilized plots (4.76 mm root segment^{-1}). With respect to mortality (rate of disappearance), the lowest b_m value was in the herbicide plots (4.39 mm root segment^{-1}). The highest was again in the fertilized plots, at 4.84 mm root segment^{-1}. The r^2 values of productivity regressions for this study ranged from 0.90 to 0.94. Mortality r^2's were somewhat lower, ranging from 0.83 to 0.93 (Table 2).

In the *Acer saccharum* dataset, the shortest root lengths were at the south site for both b_p (3.69 mm root segment^{-1}) and b_m (3.62 mm root segment^{-1}). Greater lengths were found in the north site at 4.57 (b_p) and 3.94 mm root segment^{-1} (b_m). This study yielded the lowest r^2, ranging from 0.79 to 0.88 (Table 2). MRSLs of the *Liquidambar styraciflua* study ranged from 3.37 (b_p) to 4.22 mm root segment^{-1} (b_m) and yielded the highest r^2 of all data sets at 0.95 to 0.99 (Table 2). There were no differences among the fertilizer treatments.

In the *Picea glauca* study, Site A had the shallowest slopes (i.e. shortest MRSLs) at 3.01 (b_p), and 4.36 (b_m). Conversely, Site C had the steepest slopes (and therefore longest MRSLs) at 3.73 (b_p) and 4.36 (b_m). The r^2 values were generally high, varying from 0.88 to 0.94. All sites were significantly different from each other, with site C > B > A for both b_p and b_m (Table 2). The shortest MRSLs (i.e. shallowest slopes) in the *Salix* spp. browsing study were in the browsed plots (4.72 b_p and 5.27 b_m), while the control plots were significantly greater (4.99 b_p and 5.48 b_m). The relationship between root numbers and root lengths was very strong in this study with r^2 values at 0.94 to 0.97 (Table 2). The *Populus tremuloides* MRSLs (i.e. slopes) were the greatest of all the data sets. The shortest roots in the productivity data (i.e. shallowest b_p's) were in the ambient CO_2 plus high nitrogen treatment (7.04 mm root segment^{-1}) and the longest were in the ambient CO_2 plus low nitrogen treatment (8.29 mm root segment^{-1}). For mortality (b_m), the shortest lengths were present in the elevated CO_2 plus high nitrogen treatment, 5.31 mm root segment^{-1}, whereas the longest roots were in the elevated CO_2 plus low nitrogen treatment, 8.38 mm root segment^{-1}. The r^2 values of productivity regressions for this study ranged from 0.95 to 0.98 and mortality r^2 were somewhat lower, ranging from 0.86 to 0.94 (Table 2). All data sets except the *Acer saccharum* and *Populus tremuloides* studies had greater MRSLs for mortality data than for production (i.e. $b_m > b_p$).

Temporal analysis of the *Pinus elliottii* intensive management study indicated that there was no significant time effect on MRSL production or mortality over all treatments (Figure 1).

Discussion

An Overview of minirhizotron data extraction

The ease with which minirhizotron data are now collected belies the difficulties associated with data extraction. Since the advent of minirhizotrons, researchers have devised various techniques to extract meaningful data for such parameters as rooting depths, root length densities, root morphology, and root dynamics. Root length has often been estimated using some variation of the Newman grid intersection method (Newman, 1966; Tennant, 1975). Manually counting the intersections of roots with etched lines on the minirhizotron surface, either random or fixed transects (McMichael & Taylor, 1987), allows the user to convert root counts to root lengths with Newman's method but requires a fine grid system with many interceptions to obtain realistic data (Smucker et al., 1987). Aside from intersection methods, a count of roots in contact with the tube surface within a specified area has also been utilized, by then converting counts to length densities via regression against washed root lengths.

Now that videotape recording is most commonly used, video images are often manually processed by tracing and recording the lengths and diameters of root segments in contact with the minirhizotron using PC-based computer software. This approach is an effective way to extract data about the development and fate of individual roots.

However, manual image processing is time consuming and laborious, hindering the utilization and desirability of the minirhizotron system.

The linear regressions derived from the datasets used in this study generally had high coefficients of determinations (r^2). Most of the calculated r^2 values fell in the range of 0.79 to 0.99 for both production and mortality (rate of disappearance), suggesting that root counts can be used to estimate root lengths routinely. The *Acer saccharum* study was the only data set where r^2 values were consistently below 0.90, while the best fit was found in the *Liquidambar styraciflua* study (r^2= 0.95 - 0.99).

Not only is the relationship between the root counts and root segment lengths apparently quite strong within each dataset, manipulative treatments and site differences appeared to have little absolute effect on the magnitude of the relationship despite statistically significant treatment differences in all but one of the studies (*Liquidambar styraciflua*). In the data from the studies we utilized, only two treatments substantially altered MRSL: elevated CO_2 and gap treatments. The MRSLs of the *Populus* elevated CO_2 treatments were unusually high (5.31 - 8.38 mm root segment^{-1}) whereas MRSLs of the *Pinus elliottii* gap treatments (where invading herbaceous roots predominated, Schroeer et al. 1999) were unusually low (2.34 - 3.03 mm root segment^{-1}). All other treatments had MRSLs anywhere from 3.01 to 5.48 mm root segment^{-1}. This suggests that the effect of many common experimental treatments or manipulations may not significantly alter MRSLs. In our data, the effects seem to be limited to treatments that substantially altered carbon allocation and total root growth (e.g. elevated CO_2) or plant community composition (e.g. gap formation), both of which appear to alter root morphology. Changes in soil structure (e.g. compaction) may alter MRSLs, however, our manipulations did not explicitly test these effects.

Using Root Numbers to Predict Length

To implement this simplified approach to quantifying root length production and mortality using minirhizotrons, one would first need to completely digitize the length of root segments in the minirhizotron images from the first (or an early) sample date. On the following sampling date, only new and newly dead roots would be digitized for length (or substitute the last known live length for roots that have already disappeared). These data would then be used to establish the relationship between root length production and mortality and the corresponding birth or loss of root numbers.

Assuming that both regressions yielded acceptable coefficients of determination, images on most subsequent dates could be digitized for root counts only. In practice, this means that the appearance of new roots and the mortality of existing roots can be quantified by procedures easily and quickly implemented. However, it is possible that the relationship between root length and root numbers (i.e. the magnitude of b_p or b_m) could change over time if roots of substantially different lengths were being produced or dying at different times (e.g. phenological differences between species with different root morphologies). Therefore, error checks should be made on one or more subsequent dates to confirm that b_p or b_m does not differ significantly among dates. In our intensively managed *Pinus elliottii* (Shan et al. 2001), we confirmed that there were no significant temporal differences in either b_p or b_m, but this might not necessarily be true for other species, treatments, or geographic locations. We suggest that periods of known or suspected episodes of high root production and mortality (e.g. spring and winter, respectively) might prove most useful for error checking.

We found that the MRSL of dead roots for a given treatment group ranged from 2-20% greater than their corresponding production MRSL (i.e. $b_m > b_p$). The most likely explanation for this difference is the extension of root length just prior to root disappearance. The magnitude of extension growth was not consistent in or among our datasets, and may be related to species, treatment or temporal effects. However, assuming that extension growth is a constant proportion of total root production in any given species-treatment combination, its magnitude can be quantified as the difference between b_p and b_m. This difference in slope, if any, can then be added to b_p to calculate total, rather than just new, root length production for any time period.

Summary

We hypothesized that a manual count of roots could be used to accurately estimate root lengths after an initial quantitative relationship between the two parameters was established. Our results indicate that root number was indeed a good predictor of root length in all of the studies we examined. This method could be applied to minirhizotrons to substantially reduce current analysis time of videotaped minirhizotron images.

Knowledge of root dynamics has been delayed compared to other components of the plant system, and, despite certain limitations, the minirhizotron is clearly one of the most effective systems for quantifying below ground dynamics (Hendrick and Pregitzer, 1996a). Despite its obvious advantages, however, the minirhizotron is not as frequently used as some other methods. The projected analysis time reported, 30 minutes to 8 hours per sampling period for each tube, discourages its use in many studies that would otherwise benefit from an improved understanding of fine root dynamics. Reducing image analysis time will help ameliorate the main limitation of this method.

How much time can potentially be saved by substituting root numbers for length? Much of it depends upon root segment densities within individual images, their average length, and the ability of investigators to digitize. Some preliminary estimates in our own work suggest that this time savings may be in the range of 33 to >75%, meaning that image processing could potentially be increased as much as four-fold.

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Table 3.1. Stand, soil, and climatic characteristics of seven minirhizotron study sites.

Study	Location	Soil type	Mean annual precipitation (mm)	Mean annual temperature (^{o}C)	Overstory age (yrs)	Understory and other vegetation	Study duration (months)	Experimental treatments
Populus tremuloides	Pellston, MI	n/a [b]	n/a	n/a	n/a	n/a		2 levels of CO_2 & 2 levels of nitrogen in a factorial design
Pinus elliottii [a]	Upper coastal plain, GA	Arenic Plinthic Kandiudults	1225	14	20–25, 40– 49	*Prunus serotina* *Quercus phellos* *Quercus nigra*	18	Controls & artificial gaps (37.5m radius).
Pinus elliottii	Bryceville, Callahan, & Yulee, FL	Typic Haplanods			20	*Ilex glabra* *Aristida stricta* *Serenoa repens*	11	Control, fertilized, herbicide, fertilized + herbicide plots.
Acer saccharum	Northern lower peninsula, MI	Alfic/Entic & Typic Haplorthods	810– 850	5.8– 7.6	74 – 78	*Acer rubrum* *Quercus rubra* *F. grandifolia*	18	2 sites separated by a north-south distance of 80km.
Liquidambar styraciflua	Middle coastal plain, GA	Plinthic Paleudults & Kandiudults	1150	19.1	20		12	2 levels of fertilizer (19:9:19 NPK): 560 & 1120 kg ha^{-1} yr^{-1}
Pinus glauca	Tanana river floodplain, AK	Typic Cryofluvents	269	-4.3	150 - 250	*Alnus spp.* *P. balsamifera* *Betula papyrifera*		3 mature forests. No manipulative treatments.
Salix spp.	Tanana river floodplain, AK	Histic Pergelic Cryaquepts	269	-3.3	10	*Alnus tenuifolia* *P. balsamifera* *Picea glauca*	24	3 browsed & 3 non-browsed plots. (30x50x5m)

[a] *Pinus elliottii* gap study (Schroeer 1999)

[b] Not applicable, growth chamber study

Table 3.2. Root lengths vs. root number. Regression data for treatments of seven minirhizotron data sets. Values indicate coefficients of determination (r^2) and significance (alpha=0.05) of slopes (b) within each data set. Slope values represent the mean root segment length (MRSL) in mm root segment^{-1}.

Study	Treatment	df	Production		Mortality	
			r^2	b_p	r^2	b_m
Populus tremuloides	Amb CO_2+ low N	65	0.98	8.29 c	0.86	6.59 b
	Amb CO_2+ high N	89	0.95	7.04 a	0.92	5.41 a
	Elev CO_2+ low N	83	0.97	7.59 b	0.94	8.38 c
	Elev CO_2+ high N	95	0.96	7.13 a	0.87	5.31 a
Pinus elliottii	Control	287	0.91	4.10 b	0.91	4.28 b
	Gap	287	0.87	2.34 a	0.92	3.03 a
Pinus elliottii	Control (C)	179	0.91	4.46 a	0.89	4.79 a
	Fertilizer (F)	178	0.90	4.76 b	0.93	4.84 b
	Herbicide (H)	155	0.94	4.54 ab	0.83	4.39 a
	F + H	179	0.92	4.54 ab	0.89	4.63 a
Acer saccharum	South site	428	0.81	3.69 a	0.79	3.62 a
	North site	467	0.88	4.57 b	0.82	3.94 b
Liquidambar styraciflua	Low N	83	0.96	3.45 a	0.99	4.20 a
	High N	82	0.95	3.37 a	0.99	4.22 a
Pinus glauca	Site A	119	0.88	3.01 a	0.90	3.42 a
	Site B	119	0.89	3.39 b	0.89	3.66 b
	Site C	119	0.91	3.73 c	0.94	4.36 c
Salix spp.	Control	80	0.95	4.99 b	0.97	5.48 a
	Browsed	80	0.94	4.72 a	0.95	5.27 a

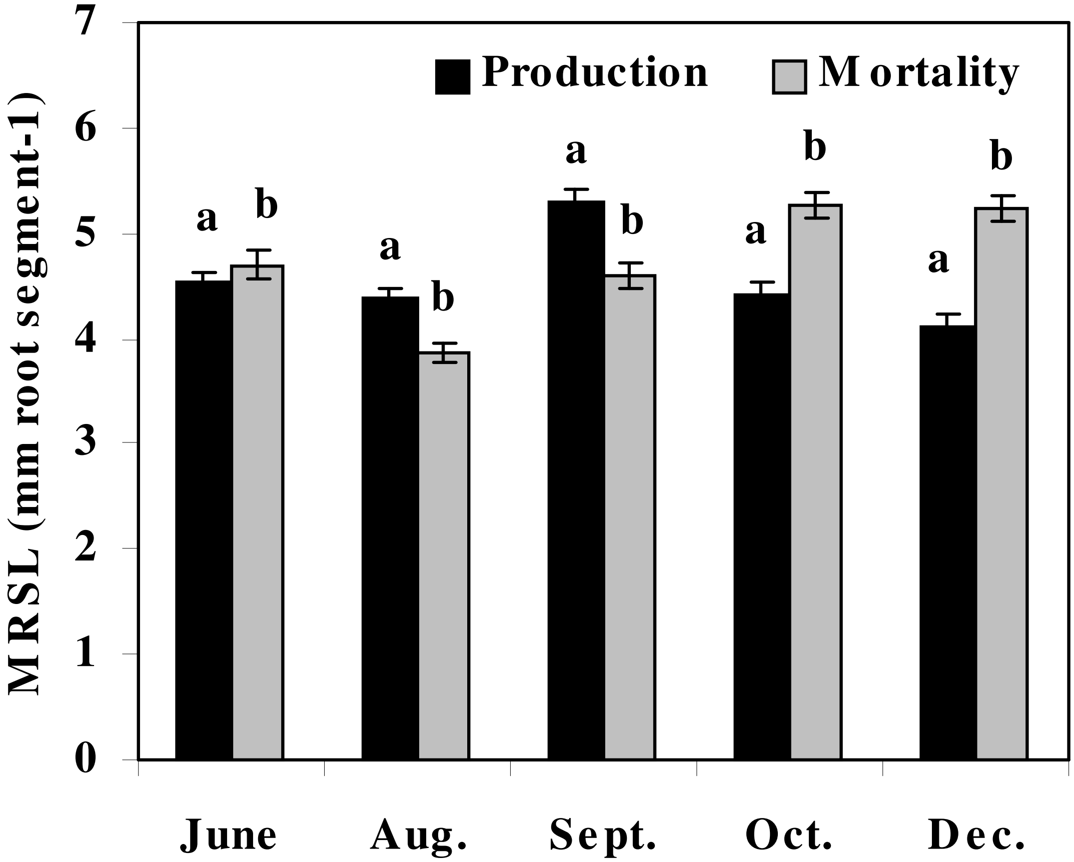

Figure 3.1. Temporal analysis of mean root segment lengths (MRSL, in mm root segment^{-1}) ± 1 SD, for the *Pinus elliottii* intensive management study in northern Florida collected in 1997 - 1999. Comparisons are between bars of similar color (i.e. productivity vs. productivity). No significant temporal differences were found (alpha=0.05).

CHAPTER 4

THE EFFECTS OF FERTILIZATION AND COMPETITION CONTROL ON LOBLOLLY PINE FINE ROOT DYNAMICS[1]

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[1] Crocker, T.L., Hendrick, R.L. To be submitted to *Journal of Applied Ecology*.

Abstract

We studied the effects of annual fertilization (F) and eliminating inter-specific competition via herbicides (H) on fine root dynamics in 13yr. old loblolly pine (*Pinus taeda*) stands in Waycross, GA. We measured fine root length and mass with soil cores, and used minirhizotrons to study root production. Generally, both F and H decreased fine root length and mass relative to the control (C). The single-factor effects were greatest for H, which reduced both root mass (55.59 vs. 27.95 g m^{-2}) and length (1713 vs. 798 m m^{-2}) by half. The combined effects of both treatments (HF) further reduced fine root mass and length by 66 and 57% relative to C, respectively. With respect to above vs. below ground production or mass, both F and H increased the amount of leaf area supported per unit root mass (C = 0.026, H = 0.059, F = 0.058 m^2 g^{-1}) and root length (C = 0.0008, H = 0.0021, F = 0.0018 m^2 m^{-1}). Their combined effects (HF) were nearly additive. The relationship between fine roots and wood volume were similar in magnitude and direction. Treatment effects on root mass and apparent allocation are explained, at least partially, by their effects on root length production and mortality. For example, minirhizotron data indicated that, relative to C, all treatments decreased both root length production (C = 0.129, H = 0.085, F = 0.085, HF = 0.045 mm mm^{-2} yr^{-1}) and mortality (C = 0.134, H = 0.082, F = 0.079, HF = 0.043 mm mm^{-2} yr^{-1}). Root mortality was generally lower than root production in response to H and F, indicating longer lived roots relative to C. The results suggest that both fertilizers and herbicides alter patterns of allocation and overall productivity, and that in combination they produce nearly additive effects with respect to both increasing wood production and LAI per unit of root length or mass.

Keywords: fine root, carbon, pine, fertilization, competition control, allocation

Introduction

Wood yield in a forest plantation is greatly influenced by the level of nutrients and water in the soil, as well as the intensity of competition by non-woody species. Silvicultural amendments, such as fertilizer application and complete competition control (via herbicides), have proven effective in increasing above ground tree growth by manipulation of the crown structure, leaf area, and therefore carbon allocation (Clason 1993; Haynes and Gower 1995; Teskey et al. 1994; Vose and Allen 1988; Keyes and Grier 1981). There is, however, relatively little information on how nutrient enhancements from these types of amendments affect fine root dynamics and biomass allocation.

According to Grime et al. (1991) the root system can respond to changes in resource availability via allocation changes between root and shoot structures, allocation changes between different root sectors, or alteration of fine root architecture. Similarly, theories proposed by Bloom et al. (1985) suggest that plants may also adjust by allocating new biomass to structures involved in the acquisition of those resources most limiting growth. For example, if light is the limiting factor then allocation to the leaves is favored (decreasing root:shoot ratios) (Brouwer 1983, Aerts 1992). Conversely, if nutrients or water are limiting then biomass tends to shift towards root structures (increasing root:shoot ratios) in order to maximize the uptake of the limiting factor at its source (Brouwer 1983). Therefore, regardless of environmental conditions, a plant is capable of approaching a functional balance between above and below ground components so that resource acquisition is approximately balanced (Garnier 1991). Bloom et al. (1985) also describe that by increasing nutrient availability via fertilization, root:shoot ratios will decrease in order to reduce the carbon stress (reduction in carbohydrates associated with fertilization) to approach a more favorable carbon and nutrient balance for growth.

Empirical data show that increasing nutrient availability will generally increase absolute biomass accumulation and decrease root:shoot ratios (Ahlstrom 1988). In most cases, the addition of nutrients through fertilization decreases the relative energy expenditure for acquisition of below ground resources and production of root biomass in favor of light absorption, a response that is primarily responsible for increases in above ground biomass production (Axelsson and Axelsson 1986). Root biomass in a high fertility Douglas fir stand (4100 kg ha^{-}1) was less relative to low fertility stands (8100 kg ha^{-1}), even though above ground biomass was greater (Keyes and Grier 1981). Some, however, suggest that fine root biomass decreases in response to elevated nitrogen via decreases in annual fine root production (Grime 1977, Orians and Solbrig 1977, Chapin 1980). For example, significant decreases in fine root production were found in fertilized (940 kg ha^{-1}) versus unfertilized (2510 kg ha^{-1}) stands for first year observations but only slight differences in year two (Haynes and Gower 1995).

The control of inter-specific vegetation via herbicide application (i.e. freeing up available resources as opposed to adding nutrients via fertilization) typically increases above ground biomass production in young stands (Will et al. 2001), but there is some evidence to suggest that the biomass allocation between roots and shoots may be different than those observed with fertilization. For example, Shan et al. (2001) demonstrated that the removal of inter-specific competition decreased fine root biomass and elicited a larger reallocation of biomass from below to above ground structures than fertilized stands, reducing fine root mass by one third with fertilization and by one half with complete competition control. In managed pine plantations high competitive stress (i.e. from unwanted vegetation such as understory hardwoods or non-woody species) exerted growth stresses that hindered pine growth and reduced merchantable wood volume from 182 m^3 ha^{-1} in competition control treatments to 141 m^3 ha^{-1} in control treatments (Clason 1993). In a study by Ludovici and Morris (1996) herbaceous and woody competitors negatively affected above ground loblolly pine growth and reduced pine root growth regardless of the level of nitrogen or soil water content.

Although fine root responses to fertilization in pine have been studied at length (Nadelhoffer et al. 1985, Haynes and Gower 1995, Albaugh et al. 1998, Shan et al. 2001), little is known about the effects of inter-specific competition control except for its positive influences on site productivity (Clason 1993). The objective of the current study was to quantify the effects of fertilization and competition control singularly and in combination, on root production and carbon allocation in managed loblolly pine forests.

Materials and Methods

Study Sites

This study was conducted on long-term field study sites established in 1987 for the primary purpose of monitoring loblolly pine (*Pinus taeda*) growth in response to intensive silvicultural amendments. The specific sites selected for this study were two 13-year-old *Pinus taeda* stands located near Waycross, GA (lower coastal plain). All plots measured 30x30 m and were replicated four times per treatment (C, H, F, HF):

Control (C) - preparation of planting site using a shear-rake treatment followed by bedding.

Herbicide (H) - use of non-soil active herbicides to maintain total control of competing woody and herbaceous vegetation throughout the duration of the study.

Fertilization (F) - a yearly fertilization regime. First two growing seasons: 280 kg ha^{-1} di-ammonium phosphate (DAP) plus 112 kg ha^{-1} potassium chloride (KCL) in the spring followed by 56 kg ha^{-1} of ammonium nitrate mid-summer. Subsequent years: 168 kg ha^{-1} ammonium nitrate was broadcast in early spring. At age 10 336 kg ha^{-1} ammonium nitrate plus 140 kg ha^{-1} triple super phosphate. At age 11 616 kg ha^{-1} Super Rainbow with micronutrients plus 168 kg ha^{-1} ammonium nitrate early spring. At age 12 forward 336 kg ha^{-1} ammonium nitrate early spring.

Herbicide + Fertilizer (HF) – both the H and F treatments.

Root length and biomass from soil cores

To determine standing fine root biomass, eight randomly located soil cores were collected from each plot on 9/23/99 (5 cm diameter x 10 cm depth). Loose debris (i.e. pine straw) was removed from the core surface prior to coring. Cores were stored at 4°C until washed with a hydropneumatic elutriation system (Smucker 1982). Samples were then placed in a 20% ethanol solution and analyzed within 1-10 days of washing.

Washed root samples were poured into a grid tray and distributed evenly throughout the tray area. To determine larger root biomass, roots > 0.5 mm were removed, sorted into three diameter size classes (0.5-1 mm, 1-3 mm, and > 3 mm) and dried at 70°C for 48 h.

The biomass of roots < 0.5 mm was determined indirectly using procedures similar to Newman (1966) and Tennent's (1975) line intersect method. Once all roots > 0.5 mm were removed, root intersections were counted (1 count = any root crossing a grid line) in four randomly selected 10 cm^2 grids, consisting of 1 cm^2 squares. Counts were tallied over two criteria: total root (all size classes) and fine root (roots < 0.5 mm in diameter). To determine specific root length (SRL in m g^{-1}), 50 cm of fine root length was extracted from each sample and dried at 70°C for 48 h. Only pine roots were utlilized in this study.

A simple calibration procedure was utilized to estimate fine root length from fine root intersections. The conversion factor was developed by cutting monofilament fishing line into lengths representative of those in actual root samples (ranging from 0.5–8 cm) and counting filament intersections in one meter increments to a total of 15 m. Intersections were counted, recorded, and averaged across all 8 grids. A regression analysis of length vs. counts yielded a conversion factor of 0.06645 m (0.06645* (intersects) m, $r^2 = 0.99$). Following the protocol of Hendrick and Pregitzer (1993) root length (meters) was divided by SRL (m g^{-1}) to determine fine root mass per sample (g $sample^{-1}$), the new value was then multiplied by the area conversion obtained from the core volume (509.2946) to determine g m^{-2} of fine root. Biomass data were analyzed in a randomized block design using ANOVA and differences in means were tested using Tukey's studentized range test (alpha = 0.05).

Root length and mass production from minirhizotrons

In June 1999, four minirhizotron tubes were installed in each plot at a 45° angle to the soil surface. Each tube pair was installed so that one tube descended into a bed while the second tube descended into a row. To exclude light and moisture from the tubes, the bottoms of the tubes were sealed with rubber stoppers, the above ground portions were wrapped with a foil adhesive and capped with insulation tubing covered by painted soft drink cans. Video images were taken monthly on 9/23/99, 10/28/99, 2/25/00, 3/31/00, 5/12/00, 6/16/00, 7/20/00, 8/26/00, 9/20/00, 11/4/00, 2/27/01, excluding over-winter periods. Images were then captured and analyzed using a TARGA (Truevision, Inc., Indianapolis IN) frame grabber and the software program ROOTS (Hendrick and Pregitzer, 1992). Specific cohorts of roots were followed to determine simultaneous root production and mortality (mm root mm^{-2}). Individual roots were digitized and classified as new, live, dead, or missing. Data were analyzed using a split- split plot in a randomized block design (alpha = 0.05) where depth (0-30 cm) was split on treatment and time was split on depth.

To calculate root production on a mass basis we used minirhizotron data in conjunction with core data. Standing root length (0-10 cm depth) was calculated for the 9/23/99 date (same date biomass cores were taken) then linked to the corresponding biomass core data (0-10 cm) to calculate annual root mass production (g m^{-2} yr^{-1}) (Hendrick and Pregitzer, 1993). Annual root mass production values only represent production in the 0-10 cm depth. Annual root length production in the 0-10 cm depth is also presented because it is more comparable to the soil core data (0-10 cm).

Modifications to the usual digitizing procedure were made to expedite the previously time intensive data extraction process (Crocker et al., in submission). We used a substitute parameter, root numbers, to estimate root length dynamics. To establish the quantitative relationship between root length and number for each treatment, linear regression models were fit between root length vs. root number for production and mortality. The resulting r^2 values ranged from 0.85 to 0.94, suggesting that root numbers were accurate enough to predict root lengths. In application, this meant that complete length digitizing was implemented for only 3 of 11 dates (9/23/99, 10/28/99 and 6/16/00), while all other dates only counted root numbers. Repeated measures analysis on previous minirhizotron data sets showed that time did not significantly affect regression output (i.e. coefficient of determination) (Crocker et al., in submission).

Results

Both fertilization and competition control greatly affected stand productivity and allocation patterns. Generally, both F and H decreased fine root length and mass relative to the control (Table 2). The single-factor effects were greatest for competition control, which reduced both root mass (55.59 vs. 27.95 g m^{-2}) and length (1713 vs. 798 m m^{-2}) by half relative to the control. Fertilization, although not statistically significant, reduced fine root mass by 34 % (55.59 vs. 42.52 g m^{-2}) and root length by 20 % (1713 vs. 1352 m m^{-2}) of the control. (Table 2). The combined effects of both treatments (HF) further reduced fine root mass and length by 66 and 57% relative to the control, respectively. SRL (m g^{-1}) were not significantly different among the treatments ($P = 0.0632$); however the combined treatment (HF) generally had the greatest increase in length per unit mass relative to both single factor treatments (H = 28.6, F = 31.8, and HF = 38.1 m g^{-1}) (Table 2).

Annual fine root mass production (g m^{-2} yr^{-1}) at 0-10 cm depth was reduced by 61 and 64% for F and H, respectively (Table 2). The combined effects of both treatments

(HF) further decreased annual fine root mass production by 79%. Annual fine root length production (mm mm^{-2} yr^{-1}) at the same depth (0-10 cm) declined in a similar manner as annual fine root mass production, although the magnitude of decline was not as great (F = -43, H = -32 and HF = -57% relative to C) (Table 2).

The relationship between the above and below ground components allows us to observe the relative proportions of above and below ground biomass allocation within each treatment. With respect to above vs. below ground production or mass, both F and H increased the amount of leaf area supported per unit root mass (C = 0.026, H = 0.059, F = 0.058 m^2 g^{-1}) and root length (C = 0.0008, H = 0.0021, F = 0.0018 m^2 m^{-1}) (Table 3). For each calculated above:below ground ratio F and H exhibited very similar values and their combined effects were nearly additive (HF = 0.147 m^2 g^{-1} and HF = 0.0039 m^2 m^{-1}). The relationship between fine roots and wood volume or biomass were similar in magnitude and direction where HF>H=F>C (Table 3). The percent decrease in fine root mass relative to C was –24, -50 and –66%, whereas the percent increase in wood volume was 128, 45 and 153% for F, H and HF, respectively. In terms of above and below ground tradeoffs, F stands were most effective at increasing above ground wood volume per decrease in fine root mass (5.3), relative to C, than either H (0.9) or HF (2.3) (Table 4).

The proportion of fine roots (< 0.5 mm diameter) to coarser roots (> 0.5 mm diameter) was similar between C and F treatments (0.22 for both), but was reduced by half for H and HF treatments (0.11 and 0.10, respectively). The proportion of roots 0-1 mm diameter to all other size classes (1- >3 mm diameter) varied such that C (1.45) > F(0.89) > H(0.64) > HF(0.58) (Table 5).

Fine root length production and mortality were measured to a 30 cm depth using minirhizotrons. Relative to C, all treatments decreased both root production (C = 0.129 (0.045), H = 0.085 (0.029), F = 0.085 (0.040), HF = 0.045 (0.018) mm mm^{-2} yr^{-1}; standard deviations in parentheses) and mortality (C = 0.134 (0.041), H = 0.082 (0.028), F = 0.079 (0.038), HF = 0.043 (0.020) mm mm^{-2} yr^{-1}; standard deviations in parentheses) (Table 6). HF stands had the greatest reduction in both production and mortality, -65 and –68% respectively. Reductions in annual root length mortality were greater than annual length production for all treatments indicating increases in root longevity relative to C (Table 6).

Temporal patterns of root length production were variable among treatments. Fine root length production in the 0-30 cm depth increased over summer months and decreased in early winter for both F and H treatments (Figure 1). The greatest mortality occurred through summer and early winter. The combination of single factors (HF) shows almost no temporal variability in fine root length production or mortality; however, slight seasonal peaks similar to other treatments were evident for root length mortality (Figure 1). In the Control, both root length production and mortality were greatest from February through June.

Minirhizotron data (0-30 cm) show that fluctuations in root length production and mortality values between observation dates decreases in the order C>H>F>HF (Figure 1), where HF has the least absolute fluctuation. After converting root production and mortality to a mass basis (calculated by combining core data with minirhizotron length data), at a shallower depth class (0-10 cm), similar patterns were observed (Figure 2). At this depth (0-10 cm), the H treatment reduced both the temporal variation and the magnitude of root mass production in a manner similar to HF, such that C>F>H>HF.

Generally, depth distribution of fine root length production and mortality (0-30 cm) did not seem to vary (Table 7), although significant differences were found between the upper (0-10 cm) and lower (40-50 cm) depths. All sites experienced drought conditions during the course of the study, which may have induced deeper root production, accounting for the low variation in root depth distribution. The percentage of fine root length production in the top 0-10 cm compared to the total depth (0-50 cm) was fairly consistent across all treatments (21.4 – 25.3 % of total), indicating that length production is proportionally distributed with soil depth (Table 7). Fine root length mortality was more variable (15.4 – 31.3 % of total).

For the minirhizotron length production data the treatment main effect (P = 0.0004), date main effect (P = <0.0001) and treatment x date interaction (P = 0.0098) were significant for fine root length production, indicating that treatment effects were not consistent over time. For example, during summer months, length production in F and C treatments were greater than either herbicide-inclusive treatments. For fine root length mortality, there were significant treatment main effects (P = <0.0001) and date main effects (P = 0.0089), however, there was no significant interaction. Instead there was a significant treatment x depth interaction (P = 0.0264), indicating that the depth related mortality effects were not consistent across treatments. There were no significant treatment x depth x date interactions for either production or mortality.

Discussion

Carbon allocation

Herbicides (H) had a strong negative effect on fine roots, reducing both root length and mass by half relative to the control. The nearly 50% decline in root length and mass in H stands implies a strong reallocation of biomass away from below ground structures (mainly fine roots) while increasing above ground mass by 45%. Although fertilization (F) had a less absolute reduction in fine root mass (-24%) and length (-21%) (a small absolute reallocation effect), the primary effect of this single factor was to grow a bigger tree with greater root and shoot mass (+ 128%) relative to H (Table 4). The F treatment was most effective at increasing above ground growth, likely due to the enhanced canopy development (i.e. increased LAI and mass) associated with the continuous addition of nutrients as shown by Will et al. (2001). Similarly, Shan et al. (2001) found that the reallocation of carbon away from fine root structures in slash pine (*Pinus elliottii*) plantations subjected to herbicides was greater in magnitude than changes observed in fertilized only stands. Our results also compare favorably to Haynes and Gower (1995) where below ground carbon allocation in red pine plantations declined from 332 – 395 g C m^{-2} yr^{-1} in unfertilized stands to 188 – 317 g C m^{-2} yr^{-1} in fertilized stands. In general, this indicates that below ground carbon allocation, at least in many pines, is negatively related to nutrient availability. Therefore, freeing up resources through reduction of inter-specific plant competition and adding resources through fertilization both appear to have generally similar effects (i.e. increasing above ground mass while decreasing below ground mass), but differ in magnitude.

Silvicultural amendments that result in a high leaf area per unit of root length or root mass are, in a sense, increasing the growth potential of a forest plantation. With respect to above vs. below ground production or mass, both F and H increased the amount of leaf area supported per unit root mass and root length. Interestingly, for each calculated ratio, F and H exhibited very similar values (Table 3). This indicates that both single factor treatments supported relatively similar proportions of above ground mass per unit of fine root mass, however, F stands were characterized by both greater mass both above and below ground relative to H. Their combined effects were nearly additive signifying the contribution of both F (high above ground growth) and H (low root mass) effects.

When H and F are used in combination (HF) trees retain the low fine root length and mass associated with the competition control with further enhancement of above ground growth, characteristic of the fertilization effect. The effects seem to be complimentary and somewhat additive with HF plots supporting twice or more the leaf area, stem wood mass, and wood volume per unit root mass and length of the single factor treatments (Table 3). Similar changes in stem wood and fine root relationships were observed by Albaugh et al. (1998), in which the combination of fertilizers and irrigation in 1993 substantially decreased the partitioning of total biomass to fine roots from 27% (control plots) to 7%, while single factor treatments reduced partitioning to fine roots by 19% (irrigation) and 12% (fertilization). Stem wood production was inversely related to root biomass, increasing the partitioning of total biomass to stem wood from 25% (control plots) to 31% (combination of fertilizers and irrigation) (Albaugh et al. 1998). Linder and Axelsson (1982) studied the effects of fertilization on

Pinus sylvestris in which increases in above ground production with fertilizer additions were hypothesized to be at the expense of root biomass (reductions in below ground biomass). The substantial decline in fine root production and mortality in our HF treatment were almost additive as well.

Productivity

The allocation effects of both F and H are due largely to reductions in root production and mortality, and apparent increases in root longevity. At 0-30 cm H, F, and HF reduced root length production with an even greater reduction in annual root length mortality. This contradicts the hypothesis that low below ground biomass values commonly reported for nutrient rich systems are accounted for by shorter root lifespans (Nadelhoffer et al., 1985). Although we have not specifically quantified fine root lifespan, the larger reduction in annual mortality likely indicates increases in root longevity (i.e. production > mortality) relative to C, and that reductions in root production may be the main contributing factor to reductions in absolute below ground biomass in these loblolly pine stands.

The response of fine root production to fertilization and competition control in our loblolly stands contradicts the hypothesis that higher nutrient availability induces greater fine root production (Grime, 1977; Orians and Solbrig, 1977; Chapin, 1980; Nadelhoffer et al. 1985). However, our results, indicating large decreases in fine root production in response to higher nutrient availability, are similar to results reported for some other studies (Keyes and Grier, 1981; Vogt et al. 1987; Gower et al., 1992; Haynes and Gower, 1995). For example, it was observed that fine root production in 40-year-old Douglas fir stands declined from 5689 to 1422 kg ha^{-1} with increasing fertility (Keyes and Grier

1981). Haynes and Gower (1995) reported a reduction in red pine fine root production from 2510 (unfertilized) to 940 (fertilized) kg ha^{-1} yr^{-1} for their first growing season; however, there were no significant changes in the second growing season.

For loblolly pine in this study, annual fine root mass production (0-10 cm) decreased from 298 g m^{-2} yr^{-1} in the control to 113, 104 and 61 g m^{-2} yr^{-1}, for F, H and HF respectively (Table 2). Fine root biomass declined comparably (C = 55.6, F = 42.5, H = 27.9, and HF = 19.1 g m^{-2}) (Table 2). The values we report for loblolly pine fine root production and biomass are on the low end reported for other conifers. For example, Vogt's (1991) survey of *Pinus* species in temperate forests indicated a range of 500-1100 g m^{-2} yr^{-1} for below ground biomass production. Gower et al.(1992) reported a pre-treatment fine root biomass of 399 g m^{-2} in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) stands and annual fine root production at 364 and 146g m^{-2} yr^{-1} for control and fertilized treatments, respectively. Our values are more similar in magnitude to those reported by Albaugh et al. (1998) for loblolly pine under nutrient and irrigation amendments (70 – 240 g m^{-2} yr^{-1} for fine roots < 2 mm). It should be noted, however, that we are reporting only fine roots < 0.5 mm, if we added in the 0.5 - 1 mm data our biomass and production data would be more comparable to other studies.

Seasonal patterns in root growth in response to environmental cues (i.e. soil temperature and moisture) are widely known and demonstrated in a number of forest ecosystems. For example, Hendrick and Pregitzer (1996) reported that root growth was greatest in spring and early summer, and declining significantly over winter months in northern hardwood forests. Similar trends were observed by Keyes and Grier (1981, *Pseudotsuga menziesii*), Nadlehoffer et al. (1985), Shan et al. (2001, *Pinus elliottii*), and

Gholz et al. (1986, *Pinus elliottii*). We found some evidence of seasonality, primarily in the control, in which large periods of root growth where evident from mid-spring through summer, tapering off in late summer with further declines over winter (Note that the November to February time period represents three months in which no data was collected) (Figure 1). Root mortality maintained similar increases over summer but contrary to root production, was high over winter months as well (Figure 1). More unexpectedly, however, we found that increasing nutrient availability (H and F, alone and especially in combination) attenuated the natural periodicity of root growth. The effect was greatest in the HF treatment where there was virtually no variation in root growth between sample dates. From these observations there appears to be some relationship between nutrient availability and the periodicity of root growth. We are not aware of any other reports of this phenomenon.

Forest industry has expressed interest in optimizing the timing of nutrient additions via fertilizers to correspond with annual root activity. However, if adding resources attenuates root growth than this presents some complications. In other words, there may be no advantage to timing nutrient additions.

Large fluctuations in production and mortality in the control may indicate that root growth was most dependent upon climatic factors such as rainfall events and temperature from which natural pulses of nutrients may be unpredictable. For H, F, and HF stands the attenuation effect is probably due to less pronounced shortages of resources (i.e. nutrients or water) during the growing season, alleviating the need for root growth to respond as strongly to temporal patterns of nutrient availability. In more seasonal environments or during significant rain events this effect may be less pronounced. Our sites, for example, experienced extended drought conditions beginning in 1998.

The fluctuation in fine root length production and mortality (30 cm depth) was greatest in the control and decreased with increasing management intensity such that HF had the greatest attenuation effect (Figure 1). Fine root mass (Figure 2) and length production at the shallower depth class (0-10 cm) showed similar trends except that both herbicide-inclusive treatments exhibited the greatest reductions in root mass production, both in magnitude and periodicity (between observation dates). It may be assumed that in the herbicide-inclusive plots root production is more dynamic at greater depths whereas fertilizer alone is most dynamic (i.e. significant summer production peaks and early winter mortality peaks) in the shallower depths.

In summary, increasing nutrient availability, either through additions (F) or loss of inter-specific competition (H), effects fine root production and carbon allocation in loblolly pine plantations. These allocation effects are due largely to reductions in fine root production and mortality as well as apparent increases in root longevity. Fertilizer and herbicide application to loblolly pine plantations had similar effects on above (increasing wood mass and volume) and below ground growth (decreasing root length and mass), however, it is apparent that they vary greatly in magnitude. Fertilizers are most effective at increasing above ground growth while retaining a relatively large root mass and, although competition control does increase above ground growth it is most effective at decreasing root mass (50% reduction). Treatment effects appear to be complimentary and somewhat additive such that, in combination, trees retain the low root mass and length associated with herbicides with the greatest enhancement in above ground growth associated with fertilization. In general, effects of fertilization and competition control on loblolly pine fine root dynamics and patterns of growth allocation appear to be similar to those reported for slash pine (Shan et al. 2001). This suggests that response mechanisms, if not magnitudes, are similar across these species.

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Table 4.1. Site description and above ground parameters for 13 yr old loblolly pine stands in Waycross, GA (1999-2000) (Will et al. 2002).

	C	F	H	HF
Average July temperature, °C	33.2	---	---	---
Average January temperature, °C	4.1	---	---	---
Average annual precipitation, cm	130	---	---	---
Density (trees ha^{-1})	1660	---	---	---
LAI (m^2 m^2)	1.30	2.46	1.65	2.82
Woody biomass (tons ha^{-1})	166	381	240	423
Wood volume (m^3 ha^{-1})	27.12	61.84	39.20	68.57
Height (m)	14.9	20.1	16.5	20.3

Table 4.2. Below ground biomass for 13 yr old loblolly pine stands in Waycross, GA (1999). FR represent roots <0.5 mm in diameter at 0-10 cm depth. Annual root length data is presented as it is more comparable to core data. Annual root mass is a combination of both core and minirhizotron data. Standard deviations in parentheses, letters respresent significance between means (alpha =0.05). C = control, H = herbicide only, F = fertilizer only, HF = herbicide plus fertilizer.

Site	FR length ($m\ m^{-2}$)	FR mass ($g\ m^{-2}$)	SRL ($m\ g^{-1}$)	0.5–1 mm diameter ($g\ m^{-2}$)	Annual root length production ($mm\ mm^{-2}\ yr^{-1}$)	Annual root mass production ($g\ m^{-2}\ yr^{-1}$)
C	1713 (780) b	55.69 (29) b	30.8 a	129.4 (93) b	0.0417	289
F	1352 (597) b	42.52 (39) bc	31.8 a	68.4 (39) a	0.0240	113
H	798 (404) a	27.95 (15) ac	28.6 a	80.9 (68) a	0.0286	104
HF	730 (410) a	19.17 (15) a	38.1 a	56.9 (40) a	0.0180	61

Table 4.3. The relationship between above and below ground biomass for 13 yr old loblolly pine stands in Waycross, GA (1999). An index of above ground leaf area, wood biomass, and wood volume per unit of root length and/or mass.

Site	LAI: FR mass ($m^2\ g^{-1}$)	LAI: FR length ($m^2\ m^{-1}$)	Woody volume: FR mass ($m^3\ kg^{-1}$)	Woody mass: FR mass (tons kg^{-1})
C	0.023	0.0008	0.0487	0.298
F	0.058	0.0018	0.1454	0.896
H	0.059	0.0021	0.1403	0.859
HF	0.147	0.0039	0.3576	2.207

Table 4.4. Tradeoffs between above and below ground biomass for 13 yr old loblolly pine stands in Waycross, GA (1999). An index of the percent increase in above ground volume (m^3 ha^{-1}) per decrease of fine root mass (ton ha^{-1}) relative to control (C).

Site	Fine root mass % Δ	Above ground volume % Δ	% Δ above ground : % Δ below ground
C	---	---	---
F	- 24	+ 128	5.3
H	- 50	+ 45	0.9
HF	- 66	+ 153	2.3

Table 4.5. Ratio of fine root mass (g m^{-2}) to coarse root mass (g m^{-2}) for 13 yr old loblolly pine stands in Waycross, GA (1999). Root diameter size classes include very fine roots = <0.5 mm, fine roots = 0.5 – 1 mm, coarser roots = 1 to 3 mm and >3 mm.

Site	Root diameter	
	<.5 mm: >.5 mm	0-1 mm: 1- >3 mm
C	0.22	1.45
F	0.22	0.89
H	0.11	0.64
HF	0.10	0.58

Table 4.6. Minirhizotron data. Annual rates of fine root length production and mortality (mm mm^{-2} yr^{-1}, 0-30 cm) for 13 yr old loblolly pine stands in Waycross, GA (1999-2001). Standard deviations in parentheses.

Site	C	F	H	HF
Production	0.129 (0.045)	0.085 (0.040)	0.085 (0.029)	0.045 (0.018)
% Δ		- 34	- 34	- 65
Mortality	0.134 (0.041)	0.079 (0.038)	0.082 (0.028)	0.043 (0.020)
% Δ		- 41	- 39	- 68

Table 4.7. Depth distribution of annual fine root length production and mortality (mm mm^{-2} year^{-1}, obtained from minirhizotrons) for 13 yr old loblolly pine stands in Waycross, GA (1999-2001). Depth increments are: 0-10, 10-20, 20-30, 30-40, and 40-50 cm. Percent total depth in parentheses.

Site	**Production**					**Mortality**				
	0-10	**10-20**	**20-30**	**30-40**	**40-50**	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**
C	0.042 (21.5)	0.055	0.032	0.039	0.025	0.032 (15.4)	0.058	0.044	0.048	0.028
F	0.024 (21.4)	0.037	0.024	0.014	0.013	0.027 (26.5)	0.032	0.020	0.013	0.009
H	0.029 (21.9)	0.026	0.030	0.025	0.021	0.027 (21.0)	0.027	0.028	0.027	0.018
HF	0.018 (25.3)	0.010	0.016	0.013	0.014	0.020 (31.3)	0.010	0.012	0.011	0.012

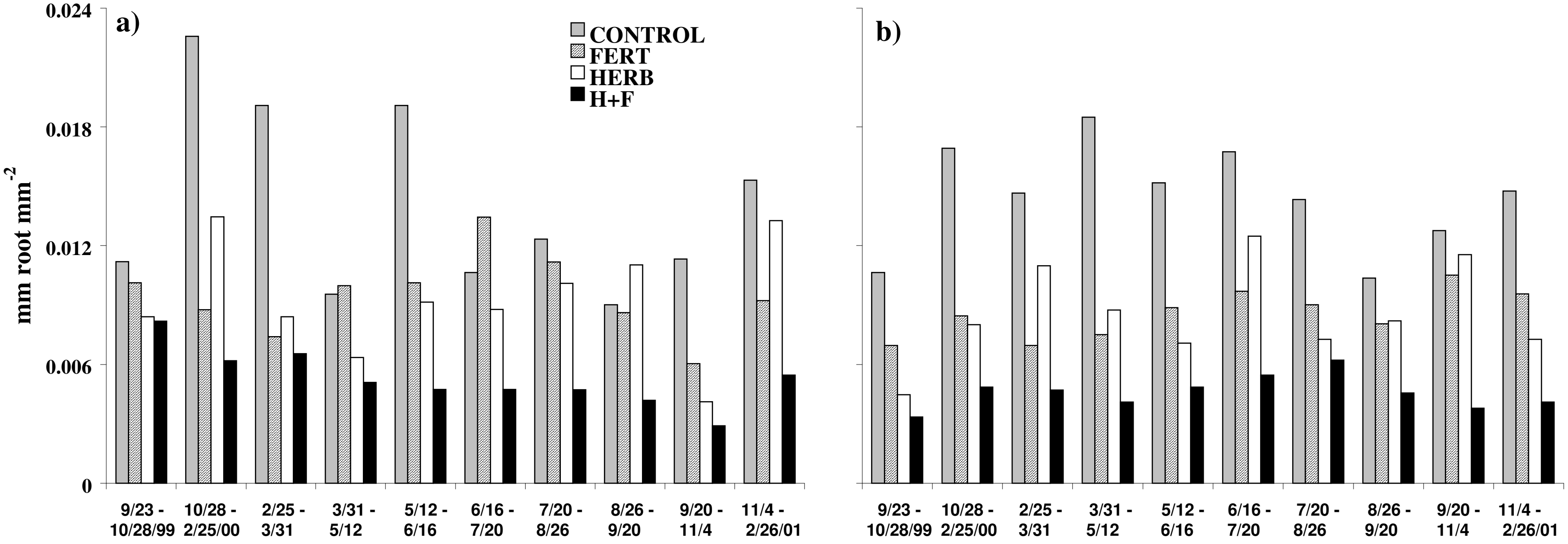

Figure 4.1. Monthly minirhizotron fine root length (mm root m^{-2}) a) production (P) and b) mortality (M) for 13 yr old loblolly pine stands in Waycross, GA (1999-2001). Values represent root length for the 0-30 cm depth class.

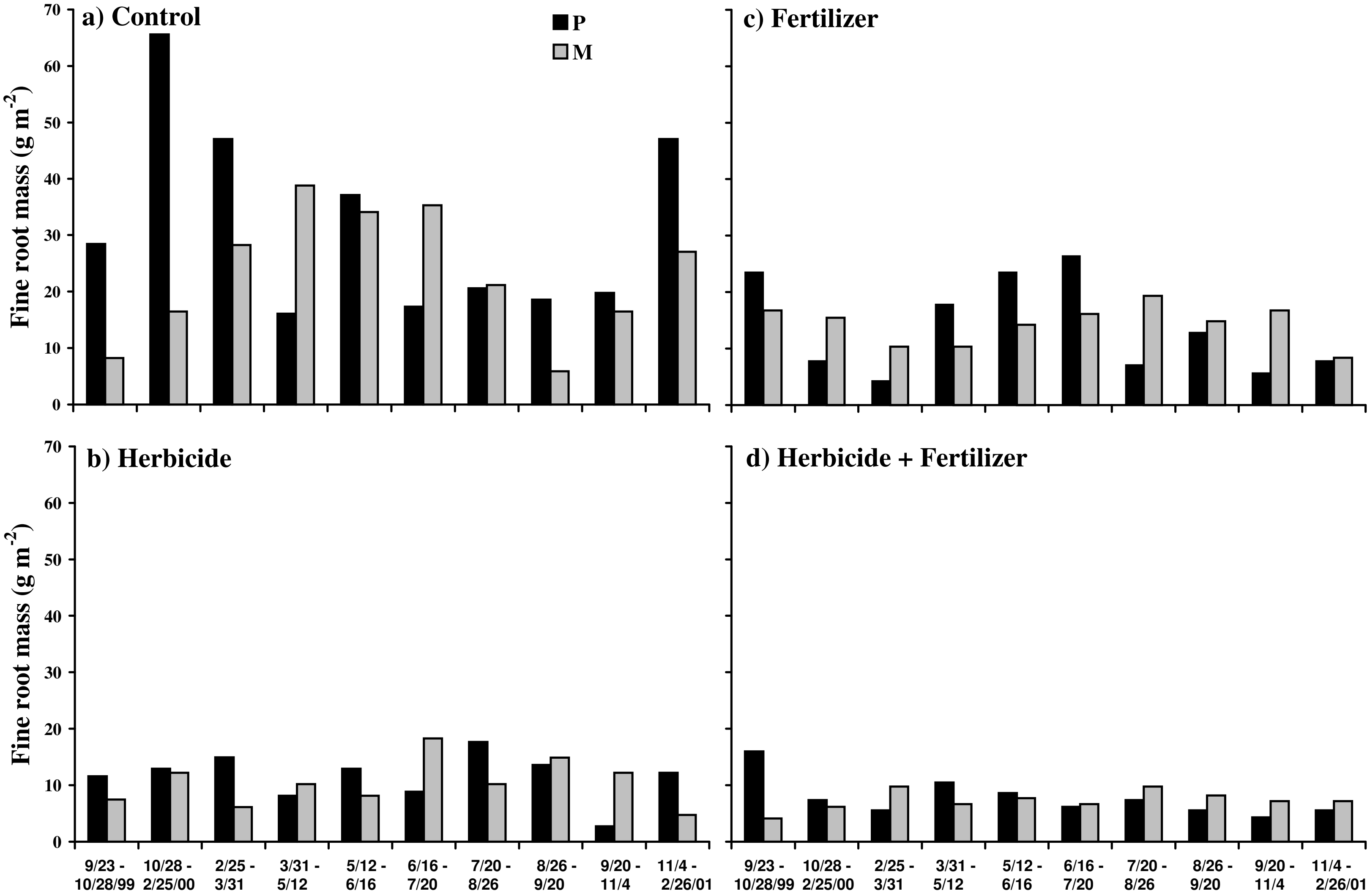

Figure 4.2. Monthly minirhizotron fine root mass (g m^{-2}) production (P) and mortality (M). Values represent root mass for the 0-10 cm depth class.

CONCLUSIONS

1. Freeing up resources through competition control and adding resources through fertilization both have similar effects but differ in magnitude and direction.

2. Both fertilizer and competition control reduce root mass and length relative to the control, increasing above ground growth allocation.

3. Fertilizers are most effective at increasing above ground growth while retaining a relatively large root mass. The result is bigger trees overall (root +shoot) relative to herbicide alone. Herbicides are most effective at decreasing root mass and length and especially reduced the amount of very fine roots and ectomycorrhizae relative to the rest of the root system.

4. In combination (herbicide plus fertilizer), trees retain the low root mass and length associated with competition control with further enhancement of above ground growth associated with fertilization.

5. The treatment effects appear to be complimentary and somewhat additive with HF plots supporting two times or more the leaf area, stem mass, or wood volume per unit root mass of the single factor treatments.

6. Allocation effects are due largely to reductions in root production and mortality, and apparent increases in root longevity.

7. Fertilizer and competition control, alone and especially in combination, dampen the natural periodicity of root growth, probably due to less pronounced shortages of resources (nutrients and water) during the growing season. These effects are likely to be less dramatic in more seasonal environments or during significant rain events.

8. In general, effects of fertilizer and competition control on loblolly pine root dynamics and patterns of growth allocation appear to be similar to those of slash pine (Shan et al. 2001). This suggests that response mechanisms, if not magnitudes, are similar across these species.