

Relationships between fine root productivity and aboveground forest metrics

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ABSTRACT

Understanding pools and fluxes of belowground living plant C in most ecosystems is a global priority (Clark et al. 2001). There is a pressing need for studies that address the variability of fine roots and to accurately describe the causes for variability of belowground plant C. This study addressed variability in fine root productivity as it is influenced by overstory productivity, overstory diversity, and variation of canopy height. We use imagery from a minirhizotron optical scanning device for estimates of fine root productivity, while overstory productivity and overstory diversity were assessed with traditional field-based methods. Aerial LiDAR was used for estimates of variation of canopy height, which provided an estimate of the standard deviation of upper canopy height. Estimates of fine root productivity were related to estimates of overstory productivity, overstory diversity and standard deviation of canopy height with the goal of finding the best predictor of variation in fine root production. We prioritize this research in terms of three hypotheses: 1) There is a relationship between overstory productivity and fine root productivity; 2) There is a relationship between overstory diversity and fine root productivity; 3) There are relationships between the standard deviation of canopy height and fine root productivity. A better understanding of relationships between aboveground plant metrics and variability of belowground plant C could allow for an increased understanding of causes for variation of belowground plant C, especially as there is a pressing need to accurately estimate whole system C in forest ecosystems (Toan et al. 2004; Hese et al. 2004; Boudreau et al. 2008).

Keywords: fine root productivity (FRP), carbon (C), remote sensing, minirhizotron, LiDAR, buffer, canopy, temperate forest, diversity, productivity, GIS, zonal statistics

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Chapter 1: Introduction

1.1 Introduction

Understanding forest carbon (C) dynamics remains one of the major frontiers in ecosystem ecology (Lindner and Cramer 2002), largely because forests store the vast majority of aboveground terrestrial C (Dixon et al. 1994) and forest C dynamics respond so heavily to enhanced levels of atmospheric carbon dioxide (CO₂) (Van der Meer 2002; Jackson et al. 2009). In the near future a change in global climate could alter CO₂ uptake and decomposition rates of forests, changing C flux and pools both above- and belowground in these ecosystems (Jackson et al. 2009). Due to the uncertainty and concerns of the effects of climate change on forests, there is a pressing need to accurately estimate whole system C and C-flux in forest ecosystems (Toan et al. 2004; Hese et al. 2004; Boudreau et al. 2008). Understanding relationships between above- and belowground processes in forests are particularly important since aboveground attributes are so much easier to assess. For example, aboveground forest C is located in the easily visible aboveground plant structures, while belowground C exists in a complex matrix of soil and parent material (see below).

Understanding how C cycles aboveground in forests has been the focus of numerous studies over many years in forest ecology (Gholz 1982; Field et al. 1998; Carey et al. 2011). There is no shortage of studies that estimate aboveground C in ecosystems, and these studies explore the variables that influence how aboveground C cycles through forest ecosystems. Studies typically require relatively simple field tools to measure parameters, such as the girth and height of trees. These measurements are then input into biomass equations to calculate a tree's aboveground biomass (e.g., Means et al. 1994; Jenkins et al. 2003). These techniques are used to quantify stand level biomass and

productivity and are relatively straightforward, quick, reliable and non-destructive. Because of the ease and repeatability of these methods, studies measuring aboveground C are done quite frequently. Some studies have also shown widespread consistency in the percent of tree mass belowground, and so estimates of tree mass belowground might also be estimated using a multiplier of 0.25-0.26 times aboveground mass, where 0.26 is the global average for root to shoot ratios in temperate forests (Jobagy and Jackson 2000). Empirical, studies on belowground C flux are not done as frequently as aboveground forest C pool and flux studies, because they are both time consuming and destructive, and with results that exhibit a high amount of variability.

There is a clear disparity between the abundance of studies measuring aboveground C and the lack of studies measuring belowground C and C flux. Specifically studies estimating belowground C in the form of roots are poorly represented in the biogeochemistry and global C model literature (Jackson et al. 1997, Clark et al. 2001). This is because estimations of belowground C pools and fluxes are typically labor intensive, require weekly or monthly measurement intervals over annual cycles (for fluxes) and are inherently destructive, as it is difficult to directly observe the rhizosphere without disturbance. Because of these obstacles, root studies have been referred to as representing one of the most difficult problems in terrestrial ecosystem studies (Cheng et al. 1991). Despite the difficulty in obtaining accurate estimations of belowground C pools, belowground systems are vitally important to understand, and studies estimating belowground C are critical. One of the least understood fluxes of C in forests are fine-root dynamics (Strand et al. 2008), and despite several decades worth of work and developing methods to estimate belowground fine root C flux (e.g., Johnson et al. 2001,

Iverson et al. 2012), a more complete understanding of this important variable in forests C cycling remains a major frontier in ecology (Gordon and Jackson 2000; Clark et al. 2001).

Accurately estimating rhizosphere C flux and storage is an important component of whole system C cycling (Clark et al. 2011). The rhizosphere is an ecological zone where there is an abundance of nutrient cycling and water uptake, these processes are vitally important for understanding how C moves through an ecosystem (Jackson et al. 2009). However, understanding how roots behave is difficult since directly measuring them often requires destruction of their habitat (Joslin and Wolfe 1999; Johnson et al. 2001). While coarse roots (roots >2mm in diameter) are important for C storage and anchorage of plants, fine roots (<2mm) are the major pathway for water and nutrients to enter the plant and often have an association with bacteria and fungal bodies which allow them to absorb nutrients more efficiently. Their turnover, the growth and death of roots, can be responsible for up to 33% of annual net primary productivity (NPP), where unlike the more static coarse roots, fine roots are constantly growing and dying back. This assimilated C to fine roots is eventually added back to the soil (Jackson et al. 1997), making fine root productivity an important component of belowground C cycling, largely because a significant amount of annual photosynthate is transported belowground to produce fine roots (Vogt et al. 1996).

While roots play major roles in plant anchorage, nutrient uptake, water acquisition, and carbon storage, little is known about how fine root dynamics are related to overstory productivity, overstory diversity, and structural variation in canopy height. Recent studies in Northwest forests have shown a relationship between forest plot

aboveground net primary productivity (ANPP) and diversity, whereas tree diversity increased so did plot ANPP, this suggests that forest plots that absorb more CO₂ from the atmosphere are also more diverse (Kirsch et al. 2012). While these patterns have been observed at landscape scales it is unknown how these patterns relate to belowground C flux. Although, fine roots are typically smaller in diameter than coarse roots, fine root production (FRP) can consume up to 33-75% of annual photosynthate (Jackson et al. 2009; Vogt et al. 1996; Meinen et al. 2009), and are considered an important part of biogeochemical cycling and the carbon cycle (Jackson et al. 1997). Understanding how fine roots respond to changes in aboveground metrics is an important component of understanding whole system forest C dynamics.

Due to the deficit of fine root studies in forests, very little is known about how fine roots are influenced by aboveground metrics such as overstory productivity, overstory diversity (Meinen et al. 2009) and standard deviation of canopy height. For instance, Konopka and Lukac (2009) found a linkage between the upper crown and fine root productivity, where plots with less healthy crowns tended to have decreased FRP. Vogt et al. (1987) found that fine root biomass reached a peak in conifer sites at canopy closure, and that fine root biomass tended to be lower in low productivity sites with canopy closure. Lei et al. (2012^a) showed that FRP was related to light availability. Wilson et al. (2007) found that soil was more nutrient rich under the tree canopy, suggesting a relationship between soil biogeochemistry and canopy structure. While Wilson et al. (2007) did not look at the relationship between canopy density or canopy roughness, this study still suggests a possible linkage between soil (which houses roots) and the upper canopy. Jackson et al. (2009) showed that fine root biomass was shown to

increase under increased ambient CO₂. A variety of other patterns between tree canopies and FRP have also been found in other studies. Vogt et al. (1987) found that plots with lower productivity had fewer fine roots than more productive plots, suggesting a linkage between overstory productivity and FRP. Lei et al. (2012^b) showed that tree diversity and FRP relationships may not have been apparent in young stands, and such relationships may be age dependent, while Lei et al. (2012^a) showed that FRP was higher in more diverse stands than in monocultures. However, the mechanisms for these patterns are unclear. Are diverse assemblages inherently more productive belowground (see Tilman et al. 2001), or do heterogeneous canopies result in more diverse soils with implications for root proliferation? Addressing causes for variation in fine root dynamics in natural systems is an important step to better understand whole system forest C cycling.

Because of the difficulty in accurately estimating fine root dynamics, studies estimating belowground C fluxes are still underrepresented in the literature despite nearly half a century of continual study (Lyr and Hoffman 1967). Thus the amount, productivity, and variation of belowground living plant C in most ecosystems is poorly understood (Clark et al. 2001). Additionally, how fine root C flux varies in response to aboveground factors such as overstory productivity, overstory diversity and SD of canopy height are less well understood. Fine roots are difficult to observe and their growth can be sensitive to variations of numerous abiotic and biotic factors. As a result their growth and productivity do not always reflect changes in aboveground metrics. For example Lei et al. (2012^a) and Lei et al. (2012^b) found conflicting results on FRP and overstory diversity relationships. For example, in one study FRP responded to changes in diversity (Lei et al. 2012^a) and in another study FRP and overstory diversity were not shown to be related

(Lei et al. 2012^b). Rather they exhibited a high amount of variability between FRP and overstory diversity relationships. Fine roots have also been shown to have more total biomass in low productivity stands than in high productivity stands (Vogt et al. 1987) and have also been shown to vary in total annual biomass when comparing differently aged and productive stands. It is evident that further study is needed to understand the causes of variation of FRP in response to aboveground forest metrics.

Various root studies have attempted to address variation in FRP using a variety of root sampling methods. Understanding the causes for variation in FRP is a major challenge in understating the nature of the global carbon cycle (Lefsky et al. 2002). There are numerous ways to measure fine roots, all with unique strengths and limitations. Because one cannot see into or measure objects in the soil directly without disturbance, measuring roots is inherently destructive. No matter which method is used arriving at a large enough sample size for accurate estimation of fine roots and causes for variation of FRP is expensive and time consuming. Various methods to measure fine roots have been used over the years: ingrowth cores (Konopka and Lukac 2009 (ingrowth bags), Jackson et al. 2009; Lei et al. 2012^a, 2012^b), the min-max method, sequential coring (Konopka and Lukac 2009), and minirhizotrons (Cheng et al. 1991, Johnson et al. 2001, Tierney and Fahey 2002; Fischer et al. 2006; Fischer et al. 2007). With the exception of the minirhizotron method, all of these methods require fine roots to be repeatedly disturbed upon measurement; these roots are often excavated and weighed. Additionally there are assumptions inherent in these destructive methods:

- 1) That all samples represent the same area - a problem because one cannot measure a repeat area over time

2) That cores reflect individual fine root growth and death and not just a net loss or gain

One of the major strengths of these methods is that one is able to use analytical analysis of the materials to estimate nutrients as well as the ability to identify species. Most, if not all, ways to estimate FRP are not only destructive, but also require a large number of assumptions already listed above (Vogt et al. 1996; Nadelhoffer et al. 2000).

One technique, the minirhizotron method, allows for the repeat non-destructive measurement of fine roots in the same area over time while also measuring the life span of individual roots. A minirhizotron is a small transparent viewing window or surface (usually a tubular PlexiglasTM acrylic) installed in the soil and shielded from light so that an optical imaging device can be inserted belowground and used to repeatedly image fine roots. In the most common minirhizotrons (and the instruments used in the current study), a clear plastic tube is used, and an optical imaging device is inserted belowground to capture images. While many imaging devices used with minirhizotrons have been small cameras (typically producing images 1-2mm² – 1-2cm²), recent advances have taken advantage of digital scanner technology to capture high-resolution, large format (~400 cm²) images of the soil interface through minirhizotrons (Johnson et al. 2001, Fischer et al. 2006; Fischer et al. 2007, Iverson et al. 2012). The minirhizotron method is a non-destructive remote sensing technology, which is regarded as the best way of repeatedly observing roots (Johnson et al. 2001, but see Taylor et al. 2013 *in review*).

Similarly, new advances in remote sensing technology have created the potential for less impactful measurement of aboveground forest stand structure using remotely sensed data. Remote sensing technologies are innovative ways to measure ecological

phenomena, often with the ability to estimate parameters that traditional field based methods cannot provide. Remote sensing is a way to measure an object by not measuring it directly. The classic definition from Lillesand et al. (2007) is: "...the science and art of obtaining information about an object, area, or phenomena through the analysis of data acquired by a device that is not in contact with the object, area, or phenomenon under investigation." Recently, remote sensing has gained popularity as a tool to measure forest C and canopy structure (Lefsky et al. 1999, 2002; Feng et al. 2010). Specifically, the active remote sensing tool light detection and ranging (LiDAR) has been used extensively over the last 10 years to measure forest structure, biomass, productivity (Bortolot and Wynne 2005), canopy height (Erdody and Moskal 2009), and leaf area index (LAI) (Richardson et al. 2009). This is primarily because LiDAR has the ability to provide three-dimensional information regarding vegetation and can be acquired for large areas (Levick and Rogers 2006). It has become a critical tool in estimating canopy structural variables (Lim et al. 2003) such as canopy structure (Lefsky et al. 1999; Dial et al. 2011) and variability in height, or roughness, of forest canopies (Kane et al. 2010). LiDAR produces a three dimensional point cloud that can be calibrated to existing field data, providing a more accurately estimation forest biomass and productivity (Nakajima et al. 2008). While the traditional way to estimate forest biomass was derived by measuring individual trees for height and diameter and then applying an allometric equation to them, these field-based estimates can vary by a factor of 2 (Houghton et al. 2002) and can be inaccurate estimations of forest biomass. One of the strengths of LiDAR is that it has the ability to equal or exceed the accuracy of field-based measurements (Bortolot and Wynne 2005). For example, Popescu et al. (2002) used

LiDAR-derived tree crown diameter measurements and was able to improve on volume and biomass estimations by 25%, suggesting a linkage between the upper canopy and total biomass (though belowground biomass was not measured). Since remotely sensed data can provide predictable estimates of aboveground mass, it seems likely that such data would be related to belowground C flux since belowground C derives from aboveground photosynthesis. Linking remotely sensed aboveground structure to patterns in belowground C flux, and especially fine root C flux, could significantly improve our ability to estimate forest belowground C cycles at landscape scales. Further, no study as of yet has examined potential correlations between remotely sensed canopy structure and belowground fine root C dynamics. While the mechanisms for such relationships could be diverse, an important first step in combining cutting edge aboveground and belowground technologies is the simple examination of covariance between data sets in a system where high resolution LiDAR, FRP and plot level data are simultaneously available.

1.2 Goals and objectives

The main objective of this research, estimating relationships between FRP and aboveground forest metrics, can be outlined by two distinct goals:

- 1) To understand the variation in FRP as it relates to standard measures of forest structure, function, and diversity including overstory productivity and overstory diversity.

2) To understand how the estimation of FRP data vary with remotely sensed SD of canopy height (a three-dimensional measure of variation in the upper forest canopy). Currently, this is the first known study to combine these measures of belowground function and aboveground structure. Increased understanding of the correlations between above- and belowground plant C could allow for more accurate estimations of FRP across landscapes, and provide better comprehension of the landscape-scale importance of canopy structure for ecosystem functions in Northwest forests.

These research goals each have their own unique benefits for the advancement of root research by explaining how fine roots respond to aboveground forest metrics. Understanding how roots respond to these variations may provide additional understand of belowground carbon pools and fluxes. This research will be conducted in a forested ecosystem where there are known positive relationships between overstory diversity and overstory productivity where more diverse plots tended to be more productive (Kirsch et al. 2012).

1.3 Expected research applications

There are a number of expected research applications arising from this research, these include but are not limited to:

- 1) Increased understanding of relationships between aboveground forest metrics and FRP
- 2) Prediction of FRP using field-based and LiDAR measurements
- 3) Baseline study for development of equations for prediction of FRP

- 4) Improved total carbon budget estimates, benefits land managers, stewards, and researchers estimating the effect of climate change on the global carbon cycle
- 5) Improved estimate of the effect of loss of biodiversity on the carbon cycle, benefits conservationists attempting to resist removal or thinning of forest

These research applications will benefit ecologists, land managers and environmental stewards attempting to use non-destructive methods for the development of allometric biomass equations for quantification of belowground C. Further, these results provide a baseline study showing a linkage between fine roots and the upper canopy. Remote sensing scientist may benefit from non-destructive studies such as these to quantify relationships between fine roots and aboveground forest structure with remote sensing technologies.

Chapter 2: Study overview, area and methods

2.1 Study overview and hypotheses

This study takes advantage of a single permanent plot network where such high-resolution remotely sensed LiDAR data and closely monitored FRP data are available for the same time period. Using these data, and data from the broader permanent plot network, we address how variability in FRP in a second-growth temperate rainforest is influenced by overstory productivity, overstory diversity and SD of canopy height. The central aim of this work is to use non-destructive remote sensing techniques to address the causes of variation of FRP using minirhizotron and LiDAR in combination with field based measurements to estimate relationships between FRP and aboveground metrics. I use three distinct, but simple hypotheses:

- 1) There is a relationship between FRP and overstory productivity
- 2) There is a relationship between FRP and overstory diversity
- 3) There is a relationship between FRP and SD of remotely sensed canopy height

2.2 Study area

This study was conducted adjacent to the Puget Sound, Washington, USA in the Evergreen Ecological Observation Network (EEON), a long-term permanent plot network of 44 permanent ecological monitoring plots located throughout a 380 ha forest reserve owned and managed by The Evergreen State College (**Figure 1**; Kirsch et al. 2012). The ecosystem is a second-growth temperate forest that was clear-cut in 1937-39 using cable techniques. Our site has an average temperature of 10 °C and receives approximately 100 cm of annual rainfall (TESC weather station). For this study we used plots, with similar disturbance histories, located on similar Alderwood gravelly loam soils (Web Soil Survey USDA).

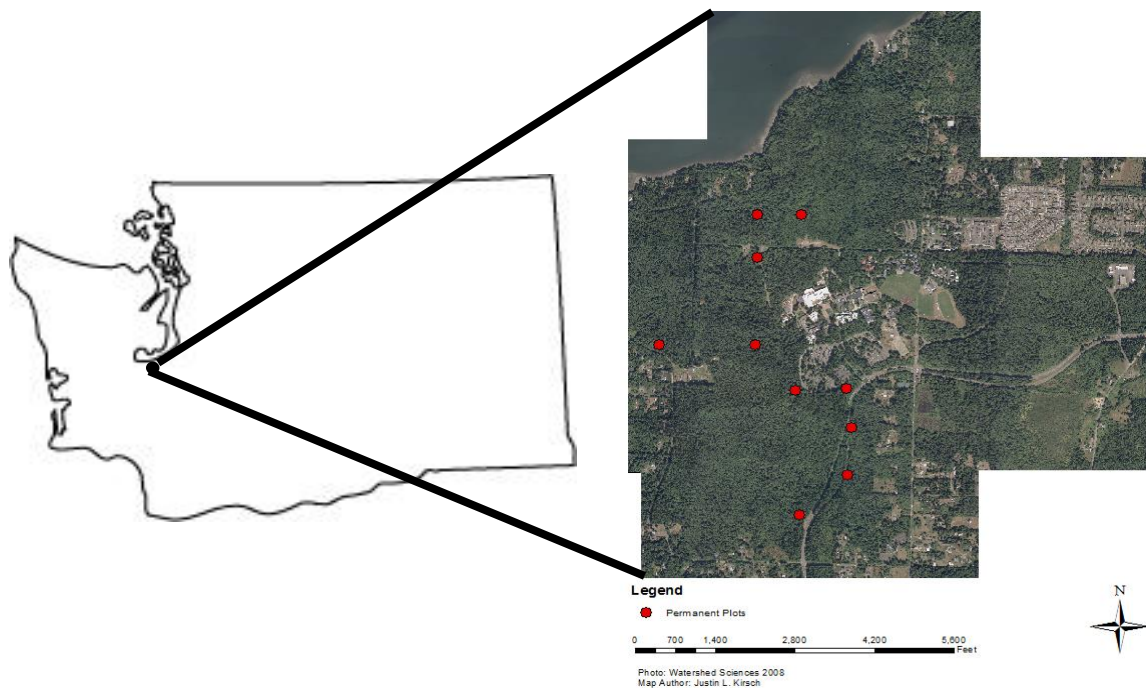


Figure 1. Map of Washington State and the study area (Evergreen Ecological Observation Network (EEON)) located in the forest surrounding the Evergreen State College in Olympia, WA. Red dots represent plots used this study.

The forest overstory was variable across plots, and dominated by a mixed canopy of *Pseudotsuga menziesii* and four primary codominant species: *Acer macrophyllum* Pursh, *Alnus rubra*, *Tsuga heterophylla* and *Thuja plicata*, with an understory dominated primarily by *Polystichum munitum* (Kaulf.) C. Presl and *Gaultheria shallon* Pursh. The plot network was established in 2005 using a systematic 250 m spaced grid placed with a random start point using circular 20 meter diameter plots.

For this study we utilize 10 plots for estimates of overstory productivity (measured as aboveground net primary productivity of trees - $ANPP_{tree}$ - as described in Kirsch et al. 2012) and overstory diversity. From 2006-2008 10 plots were measured for overstory productivity and overstory diversity. Based on data from an on-site weather station (TESC weather station) these years were expected to be average growth years. Similar site histories of forest clearing were used as a criteria to haphazardly choose plots from a 1939 orthophoto. We used a subset of 38 plots to estimate FRP and SD of canopy height. A maximum of four subplots were installed in cardinal directions four-meters from plot center in each of the 10 permanent plots (see section 2.2.1; **Figure 2**).

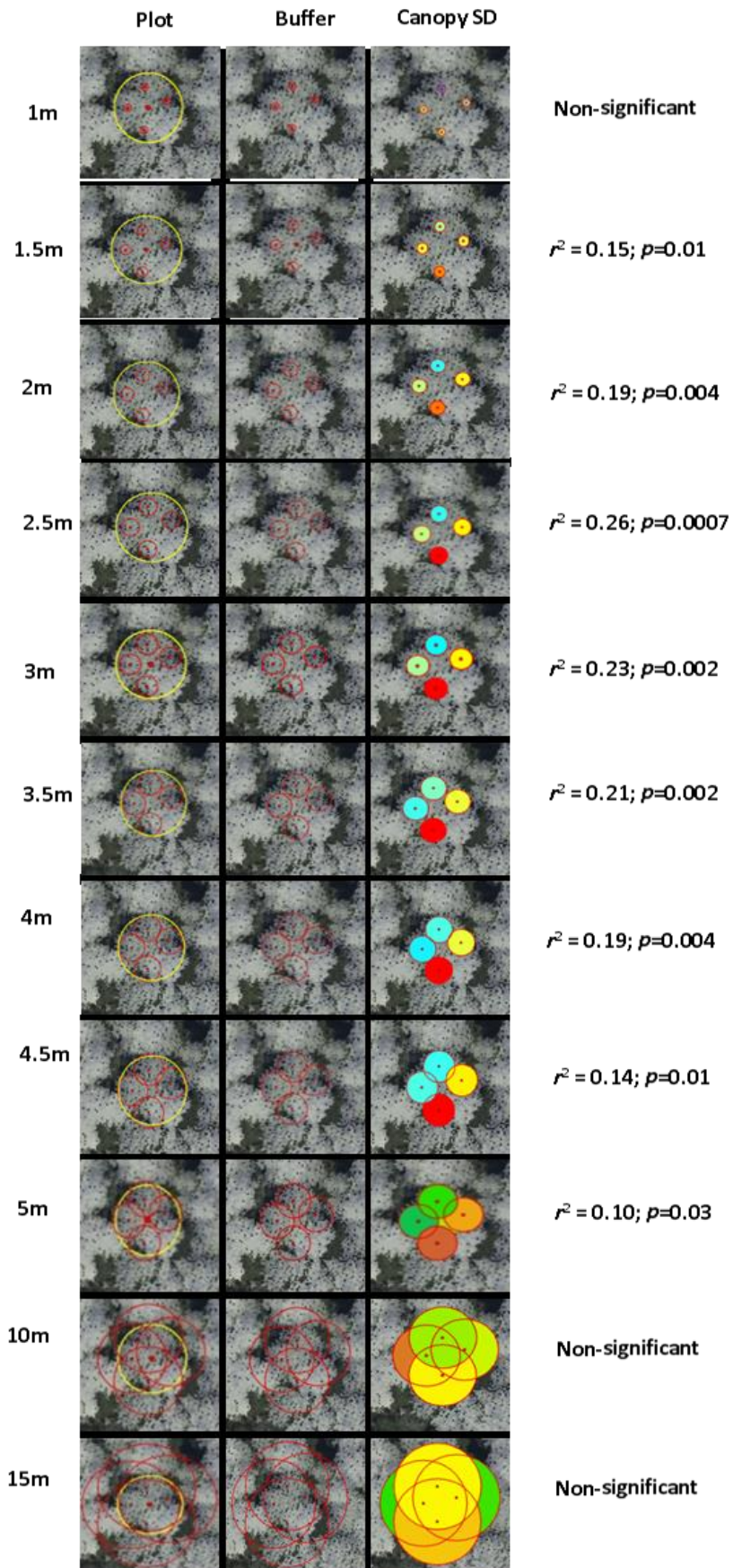


Figure 2. Depiction of variability of canopy height by buffer class for a single plot

2.3 Methods

2.3.1 Fine root measurements

2.3.1.1 Minirhizotron

Minirhizotrons are clear plastic tubes installed below the soil surface that allow for repeated measurements of fine roots (fine roots are any root <2mm in diameter). They are currently one of the best tools available for directly measuring fine roots (Johnson et al. 2001, but see Taylor et al. 2013 *in review*). Minirhizotrons have been used to measure the life span of roots, or their longevity, and to estimate the turnover of individual fine roots (Strand et al. 2008). Unlike most other destructive fine root sampling methods, use of minirhizotrons only require a one-time disturbance of the soil upon installation of the tube belowground. The tube is then allowed to ‘dwell’ for 6 months to a year before use (see Joslin and Wolfe 1999).

In the minirhizotrons we used in this study, a scanner is placed inside a transparent tubular Plexiglas™ acrylic tube which produces a 75-1200 dpi colored digital image of all roots impacting the tube’s surface (Fischer et al. 2006). Acrylic tubes are the least impactful material (outside of glass which breaks easily) to use in minirhizotron studies (Withington et al. 2003). Specifically, we used a rotating scanner head CI-600 minirhizotron (CID Inc., Vancouver, WA, USA) to collect all root images. The fine root image processing software RooTracker™ (Duke University, Durham, NC, USA) was used for tracing and analyzing all images. Images were hand traced for all roots in the image (<2m in diameter) to quantify fine root length-productivity based on differences between images over time. Dead roots were identified if they were absent from the image for two months or if they appeared to have changed color and died (**Figure 3**). In total, thirty eight 6.5 cm diameter minirhizotron tubes were utilized for this study for the

estimation of FRP, turnover, and fine root C. Minirhizotron tubes were allowed to ‘dwell’ for over 1 year before measurement (as recommended by Joslin and Wolfe 1999). We measured tubes once monthly at a fixed depth of 21.59 cm for one calendar year from April 2010 –April 2011.

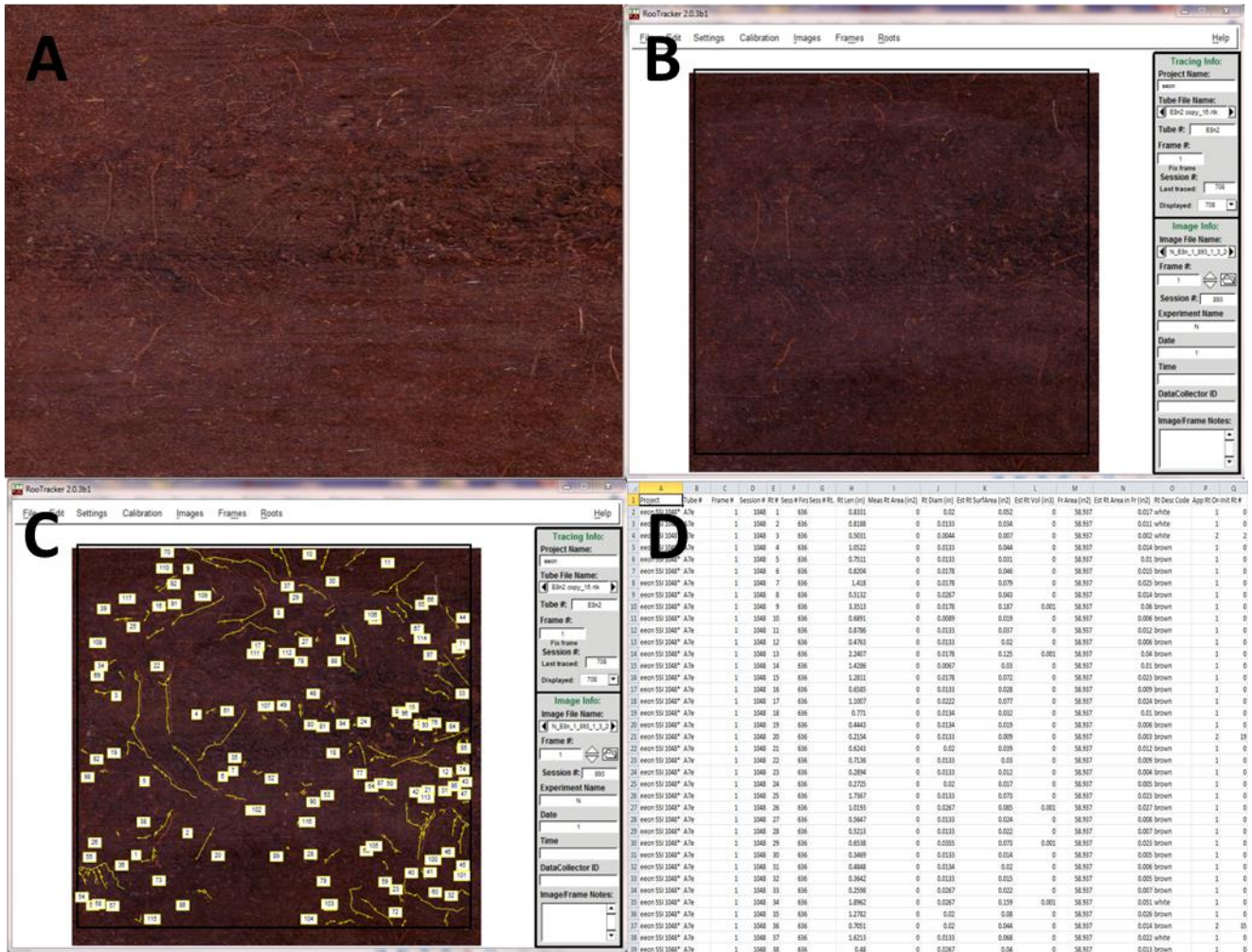


Figure 3. Steps of minirhizotron image collection and data processing. Panel A: minirhizotron image; Panel B: Image imported into RootTrackerTM for tracing; Panel C: traced roots with ID numbers; Panel D: Exported results

There are both strengths (Johnson et al. 2001; Taylor et al. 2013 *in review*) and limitations (Crocker et al. 2003; Tierney and Fahey 2002; Joslin and Wolfe 1999) to the

minirhizotron method. However, we were confident the minirhizotron method was the best approach for this study, where minirhizotron disturbance decreased spatial heterogeneity with our monthly measurements of fine root production in repeat locations over one calendar year.

2.3.1.2 Fine root productivity, turnover and carbon

Annual fine root productivity was calculated by taking the total length of new roots for a set of minirhizotron images for each of 38 minirhizotron tubes. Fine root data was collected in inches and converted to FRP ($\text{g m}^{-2} \text{y}^{-1}$) and biomass ($\text{g C m}^{-2} \text{y}^{-1}$) as in Fischer et al. (2007) using the equation:

$$\frac{L_i \times D_i}{\text{SRL} \times A_i \times \text{DOF}}$$

where i is a minirhizotron tube ID if numerous minirhizotron tubes were used, these totals would then be summed for each tube; L is the length of new root growth per tube (m y^{-1}); D is the maximum depth a tube measures into the soil, or the vertical depth (m); SRL is the median specific root length (m g^{-1}), here we calculated SRL by taking the length, diameter and weight of a representative sample of roots that were excavated from cores in close proximity to minirhizotron tubes. This value was estimated as 10.4 g m^{-1} ; A is the measurement area of each minirhizotron tube (m^2). This value was adjusted if areas of the tube were not able to be measured because of areas of condensation or holes in the soil that inhibited tracing of fine roots; DOF is a value that represents how deep into the soil you are viewing in root images. This value was assumed to be 0.002 m as in Johnson et al. (2001) and Fischer et al. (2007). Fine root turnover was calculated by

dividing FRP by the maximum standing root length. Fine root carbon was calculated by taking 50% of FRP (Fischer et al. 2007).

2.3.1.3 Soils

Variation in soil nutrient status could underlie any observed co-variation in forest diversity and C flux. In order to address potential variation in plot nutrient status, we analyzed cation exchangeable pools of mineral soil PO_4^{3-} , K^+ , Ca^{2+} , NH_4^+ , NO_3^- from a spring 2011 survey of the intensively measured plots (see Kirsch et al 2012).

Previous studies have shown that soil nutrients may alter fine root biomass (Vogt et al. 1983) as well as aboveground tree productivity (Vogt et al. 1983) may also influence the diameter and nutrient concentration of fine roots (Gordon and Jackson 2000). For example, plants will allocate more C to fine root production when nitrogen and water are deficient (Tingey et al. 2005), and while we did not test for water availability in soil next to minirhizotron tubes this is likely a limitation in our study and our results should be interpreted with caution. Vogt et al. (1983) also found that differences in site productivity and fine root biomass were largely caused by available soil nutrients, where more productive sites had higher available soil nutrients, but had fewer fine roots. Gordon and Jackson (2000) found an inverse relationship between fine root diameter and the nutrient concentration in fine roots for available soil nutrients nitrogen, phosphorus, and magnesium. These studies suggest that soils play a large role in determining variation in fine root biomass and productivity and although soil biogeochemistry was beyond the scope of this study we do expect soils at the Evergreen Ecological Observation Network (EEON) to play a large role in determining variation in FRP.

2.3.2 Overstory biomass and productivity

Aboveground tree biomass was estimated using independent allometric relationships based on stem diameter at 1.37 meters (DBH) and tree height (HT). All methods for aboveground measurements were previously described in Kirsch et al. (2012). Briefly though, all trees within 10m radius plot boundaries with $DBH \geq 5\text{cm}$ were tagged and measured. Tree DBH was measured in 2006 and again in 2008 at a tagged location on the tree trunk. Tree HT measurements were taken in 2007 and were applied to both 2006 and 2008 allometric biomass equation estimates of tree mass. Measurement of tree HT was obtained by using a laser range finder and clinometer, and validated using estimates of tree HT generated from aerial LiDAR and processed using the program FUSION (McGauhey et al. 2004; USDA Forest Service 2010). For mass estimation, we used widely available biomass estimation equations from published studies compiled in the BIOPAK software package (Standish et al. 1985; Means et al. 1994; **Table 1**), a collection of species specific allometric biomass equations using field measurements (i.e. DBH, HT, diameter and percent cover) to estimate aboveground biomass.

Changes in aboveground tree biomass were estimated using independent allometric relationships based on repeated measures of DBH and HT, as mentioned previously. We primarily used biomass equations from Standish et al. (1985) with the exception of the equation for *A. macrophyllum* biomass. For this species we compiled an equation from Gholz (1982) using a summation of individual equations for five separate components of the tree: total foliage biomass, stem wood biomass, live branch biomass, dead branch biomass, and stem bark biomass. In instances where a tree species did not have an associated biomass equation, the biomass equation for *A. rubra* (Standish et al. 1985) was substituted since it produced allometric predictions intermediate to other

equations. This substitution was applied to the species *Salix scouleriana* Barratt ex Hook. *Frangula purshiana* (DC.) Cooper, *Corylus cornuta* Marsh. *Cornus nuttallii* Audubon ex Torr. & A. Gray, and *Ilex aquifolium* L. Across all species, aboveground C was assumed to be 50% of plant biomass, which is a common assumption (Clark et al. 2001) (**Table 1**).

	Species	BAT Equation	R ²	Original Source
Hardwood	<i>Acer macrophyllum</i> ¹	(EXP(3.14276+1.617*LN(DBH))) ^a	0.87 ^a , 0.99 ^b ,	Gholz et al. 1979
		+EXP(3.4148+2.723*LN(DBH)) ^b	0.88 ^c , 0.15 ^d ,	
		+EXP(2.67176+2.43*LN(DBH)) ^c	0.98 ^e	
		+EXP(4.7918+1.092*LN(DBH)) ^d		
		+EXP(2.3338+2.574*LN(DBH)) ^e		
	<i>Alnus rubra</i>	4800 + 0.2065 * (DBH)2 * HT	0.99	Standish et al. 1985
	<i>Rhamnus purshiana</i> ²	4800 + 0.2065 * (DBH)2 * HT	0.99	Standish et al. 1985
	<i>Salix scouleriana</i> ²	4800 + 0.2065 * (DBH)2 * HT	0.99	Standish et al. 1985
	<i>Corylus cornuta</i> ²	4800 + 0.2065 * (DBH)2 * HT	0.99	Standish et al. 1985
	<i>Cornus nuttallii</i> ²	4800 + 0.2065 * (DBH)2 * HT	0.99	Standish et al. 1985
Softwood	<i>Ilex aquifolium</i> ²	4800 + 0.2065 * (DBH)2 * HT	0.99	Standish et al. 1985
	<i>Thuja plicata</i> ²	40400 + 0.0969 * (DBH)2 * HT	0.97	Standish et al. 1985
	<i>Tsuga heterophylla</i> ²	29800 + 0.1558 * (DBH)2 * HT	0.98	Standish et al. 1985
	<i>Abies grandis</i> ²	30200 + 0.1469 * (DBH)2 * HT	0.96	Standish et al. 1985
	<i>Picea sitchensis</i> ²	17600 + 0.1721 * DBH ² * HT	0.96	Standish et al. 1985
	<i>Pseudotsuga menziesii</i> ²	37300 + 0.1393 * DBH ² * HT	0.99	Standish et al. 1985

Table 1. Biomass equations used for calculating tree mass and growth

1, Biomass equation for *Acer macrophyllum* is the summation of 5 biomass equations each accounting for a separate component of the tree. Separate components for the equation are listed here: a: total foliage biomass, b: stem wood biomass, c: live branch biomass, d: dead branch biomass, and e: stem bark biomass.

2, Associated biomass equation for tree species could not be found, biomass equation for *Alnus rubra* was substituted (see Changes in Aboveground Standing Carbon section)

*BAT = biomass aboveground total, DBH = diameter at breast height (see Changes in Aboveground Standing Carbon section), HT = tree height

For the 10 plots measured for plot productivity we estimated aboveground net primary productivity of trees (ANPP_{tree}) by summing estimates of aboveground biomass increment (see Kirsch et al. 2012), with estimates of litterfall from litter traps. This metric provides a combined estimate of ANPP in trees through estimates of changes in aboveground tree woody increment, new foliar production, and foliar production that replaced foliage lost through litterfall. We collected litterfall using 50 cm diameter litter traps suspended 20 cm above the forest floor at plot center. Litterfall was collected monthly from November 2006 through November 2007. Following collection, litter was

immediately dried at 70 °C for 72 h, sorted by species, and weighed to the nearest 0.001 g. While aboveground biomass increment was calculated as the average over two years (2006–2008), litterfall was estimated based on the 2006–2007 collection. Thus, $ANPP_{tree}$ estimates represent aboveground biomass increment averaged over two years and litterfall from the single year it was measured.

2.3.3 Overstory diversity

We classified species diversity (as in Kirsch et al. 2012) based on the presence of species within a plot in three ways:

- 1) Using the total amount of trees within a plot, called plot richness
- 2) Using Shannon's diversity indices (H') and (3) using Simpson's diversity indices

Only the 10 macro plots were included in estimates of diversity vs. FRP, since diversity estimates were not available at the sub-plot scale. We included all occurring species for estimates of diversity. While the five most dominant overstory species comprise 95.5% of all tagged trees and account for 99% of total tree biomass, we still include all 12 occurring species for estimates of diversity. This was done to classify true plot tree diversity so data could be analyzed with respect to the influence of rare species. Any patterns related to richness or diversity in this study can be assumed to be based on random sampling, since this plot network is located throughout an even-aged forest using a stratified-random plot design. Shannon's (H') and Simpson's (D) diversity indices were calculated using the program PC-Ord (McCune et al. 2002).

2.3.4 Forest canopy

2.3.4.1 LiDAR

The application of aerial LiDAR on quantifying aboveground biomass has been used extensively over the past two decades (Lefsky et al. 1999; Patenaude et al. 2004; Boudreau et al. 2008), and provides data sets in the form of three dimensional point clouds where various metrics can be extracted. One of the strengths of LiDAR is that the cost is expected to decline in the coming years (Li et al. 2008), making its use in future studies more feasible. Here we use aerial LiDAR for estimation of standard deviation of forest canopy height.

To quantify standard deviation of canopy height we used a 2008 aerial LiDAR acquisition for the City of Olympia, WA (Watershed Sciences, Inc. May 23, 2008). This 2008 survey used an Optech 3100 sensor mounted inside of a Cessna Caravan 2088. The survey acquired over 71,000 pulses per second and was flown at 900 meters aboveground. The system acquired data at a 14 degree scan angle which allowed for the acquisition of over 6 points per square meter. Data are delivered in North American datum 1983 (NAD83) Washington State Plane South (FIPS 4602 in units of feet) (**Table 2**). For this study we used only the highest-hit surface delivered with a 0.5-meter resolution above ground highest-hit surface ESRI GRID.

Sensor	Optech 3100
Survey Altitude (AGL)	900 m
Pulse Rate	>71 kHz
Pulse Mode	Single
Mirror Scan Rate	46 Hz
Field of View	28° ($\pm 14^\circ$ from nadir)
Overlap	100% (50% Side-lap)

Table 2. LiDAR specifications for 2008 LiDAR survey for the City of Olympia

2.3.4.2 Standard deviation of canopy height

Standard deviation of canopy height was calculated using the highest-hits of the forest canopy from the aerial LiDAR 2008 acquisition of Olympia, WA using the zonal statistics tool in ArcMap 10. Using the highest-hit data, a surface raster was created where every 0.5m pixel has an associated highest-hit x, y, and z value; where x is the longitudinal value, y is the latitudinal value, and z is the height value in a NAD83 Washington State Plane South datum and a FIPS 4602 in units of feet projection. For each of the 38 subplots measured for FRP we took the SD of the highest-hit values of the canopy. The minirhizotron tubes served as plot center for the 38 subplots. For these subplots we used the SD of the canopy using various circular buffer sizes originating from each minirhizotron tube in order to determine if different buffer extents produced different strength relationships with belowground metrics. The 11 circular buffer sizes were: 1m, 1.5m, 2m, 2.5m, 3m, 3.5m, 4m, 4.5m, 5m, 10m, and 15m (**Figure 2**). The SD of the highest-hits was calculated using all pixel values falling within each unique buffer class.

To calculate the standard deviation of canopy height we used the zonal statistics tool in ArcGIS 10 using the highest hit raster from the 2008 Olympia LiDAR acquisition. SD was calculated for the pixels which fell inside of each buffer class (**Figure 2**). This method gives an estimate of the variability in height of the upper canopy height.

2.3.4.3 GPS

In order to best match belowground and remotely sensed data, high-accuracy GPS readings are essential since the belowground data has no inherent geographic reference. Plot centers of all 10 plots were surveyed with a high accuracy JAVAD GPS device. The JAVAD was placed above the center pole at plot center for 1 hour. Sampling with a

JAVAD for this duration achieved sub 1m accuracy when comparing GPS and plot locations with aerial photos. The distance and azimuth from plot center was applied to all 4 sub-plots so minirhizotron tube locations could be extracted. Points were differentially corrected in the Pinnacle software using real time data from two CORS base stations which sample every second. The base stations used for this study are Thurston and Chehalis. Both stations are within 30 miles of the Evergreen Ecological Observation Network and with a 1 second sampling interval.

2.3.5 Statistics

This study estimating relationships between fine root production (FRP) and aboveground forest metrics can be summarized by three sets of analyses:

- 1) We conducted linear regression analyses between FRP and the productivity measure $ANPP_{tree}$ (n=10)
- 2) We conducted linear regression analyses between FRP and five species diversity indices (overstory richness all species, overstory richness 5 most dominant species, Shannon's and Simpsons' diversity, and evenness) (n=10)
- 3) We conducted linear regression analyses between FRP and the SD of canopy height for 11 unique buffer sizes (1m, 1.5m, 2m, 2.5m, 3m, 3.5m, 4m, 4.5m, 5m, 10m and 15m) (n=38)

We used a single factor small sample size Akaike's Information Criterion (AICc) model in selecting the most appropriate model for FRP and SD in canopy height for the 11 unique buffer sizes. This approach is considered less biased and less prone to error compared to stepwise regression (Burnham et al. 2002). We were only interested in

comparing single factor models in these analyses because the estimates of SD among different buffer sizes were inherently non-independent.

Chapter 3: Results

3.1 Fine root productivity, turnover and carbon

We present individual tube data for fine root productivity, turnover, and C (**Appendix B**) as well as average values and SD for plots (**Table 3**). Mean FRP at the plot level varied significantly (**Table 3**) with values ranging from 336.8 to 1507 g m⁻² y⁻¹. Standard deviation of FRP (**Table 3**) also exhibited a high amount of within plot variability with a range of values among plots from +/- 84.1 to +/- 725.8 g m⁻² y⁻¹. Mean turnover values did not vary largely among plots (**Table 3**) with values ranging from 0.75 to 1.24 y⁻¹ but did exhibit a high amount a variation within plots with values ranging from 0.07 to 0.92 y⁻¹.

Plot	Mean FRP (g m ⁻² y ⁻¹)	SD FRP (g m ⁻² y ⁻¹)	Mean C (g C m ⁻² y ⁻¹)	SD C (g C m ⁻² y ⁻¹)	Mean Turnover (y ⁻¹)	SD Turnover (y ⁻¹)
A7	336.8	192.8	168.4	96.4	0.95	0.31
C4	573.3	164.0	286.6	82.0	1.19	0.92
C5	519.5	84.1	259.7	42.1	0.75	0.07
C7	824.3	198.4	412.1	99.2	1.24	0.44
D4	667.3	370.6	333.7	185.3	0.97	0.08
D8	761.3	476.9	380.6	238.4	0.78	0.19
D11	454.2	282.5	227.1	141.2	0.96	0.22
E8	739.1	295.8	369.6	147.9	1.09	0.26
E9	1507.0	407.8	753.5	203.9	1.13	0.16
E10	998.9	725.8	499.4	362.9	1.00	0.22

Table 3. Plot means and standard deviations of fine root productivity, turnover and carbon (C)

3.2 Fine root productivity and overstory productivity

Despite the initial hypothesis that there would be a predictable relationship between aboveground productivity and belowground FRP, we found no significant

relationship between FRP and our measure of overstory tree productivity $ANPP_{tree}$ (**Figure 4**; $p = 0.48$). Thus, even though FRP varied significantly (the values described above span the magnitude of average FRP reported for temperate forests systems – Chapin et al. 2006), this variation was not coincident with variation in plot-level tree productivity.

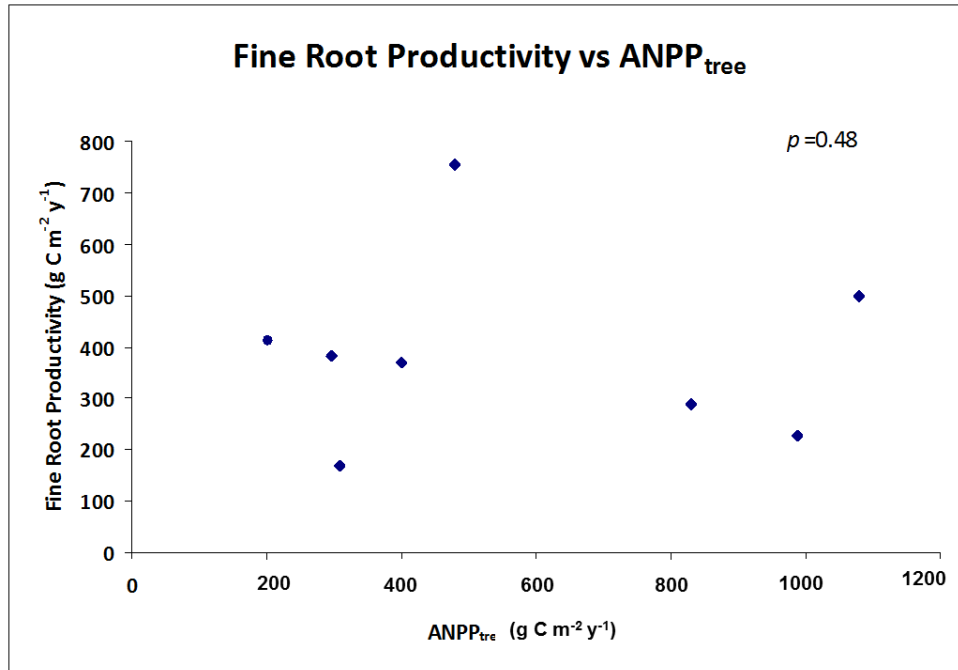


Figure 4. Relationship between annual fine root productivity and $ANPP_{tree}$.

3.3 Fine root productivity and overstory diversity

Despite our initial hypothesis, and previous patterns in aboveground C flux, we also found no significant relationship between FRP and overstory richness for all overstory species (**Figure 5A**; $p = 0.78$) or the 5 most dominant species (**Figure 5B**; $p = 0.92$) in the 10 plots measured for overstory richness in 2010. Additionally we found no significant relationships between FRP and overstory evenness (**Figure 5C**; $p = 0.76$) Shannon's (**Figure 5D**; $p = 0.65$) or Simpson's (**Figure 5E**; $p = 0.68$) diversity indices in

the same 10 plots measured for diversity in 2008. FRP did not vary in response to any measure of overstory diversity.

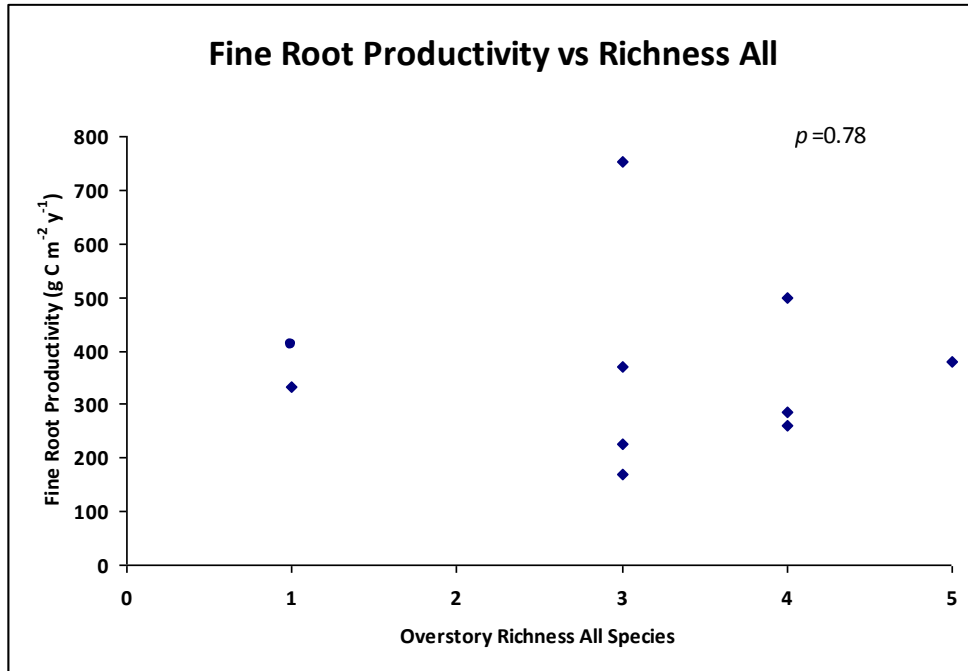


Figure 5A. Relationship between annual fine root productivity and overstory richness of all species

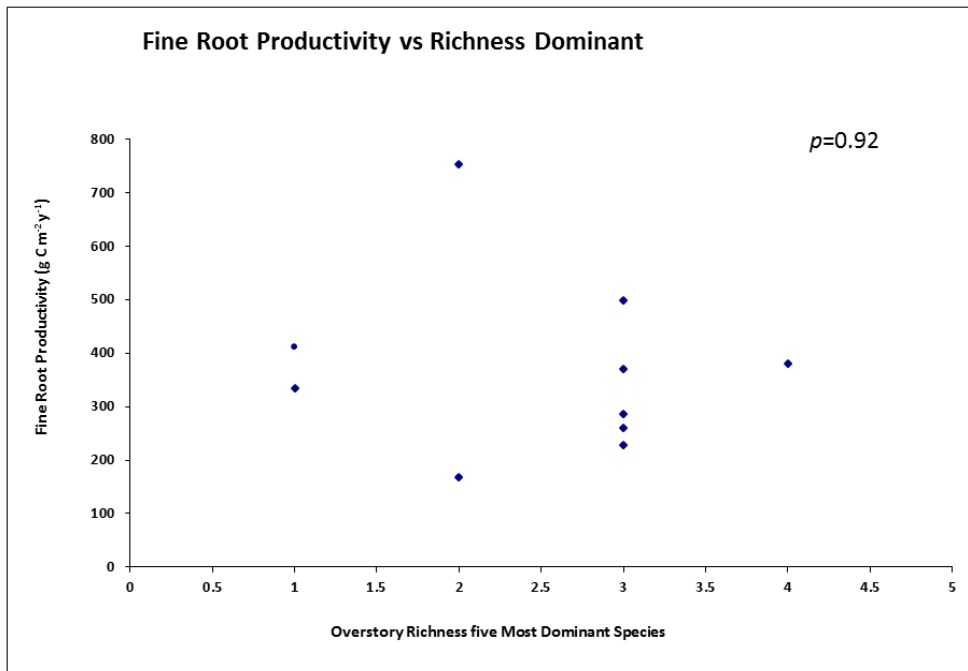


Figure 5B. Relationship between annual fine root productivity and overstory richness of the five most dominant species

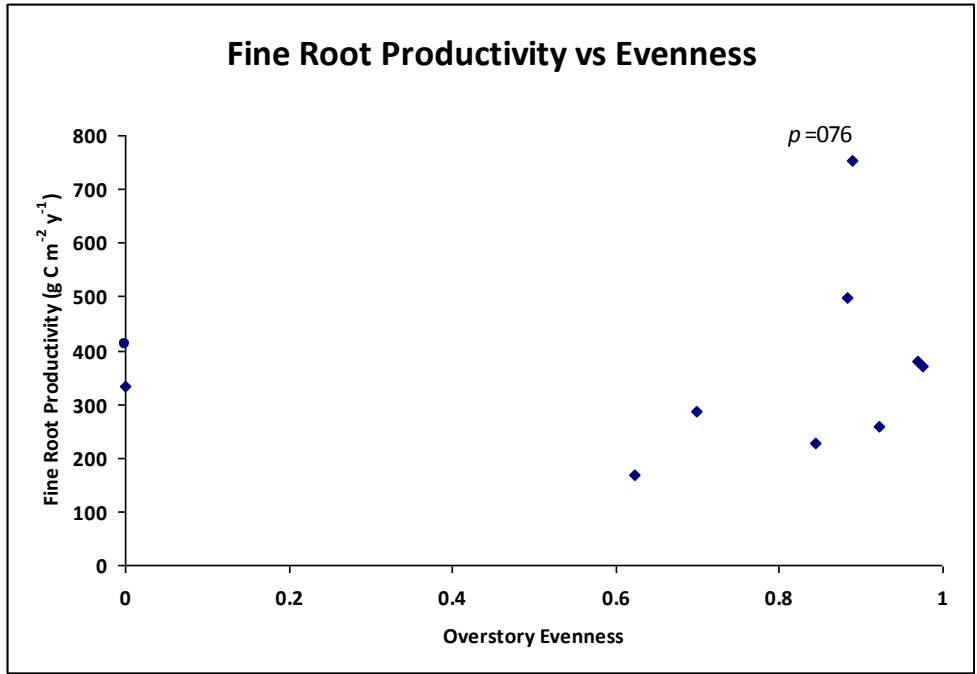


Figure 5C. Relationship between annual fine root productivity and overstory evenness

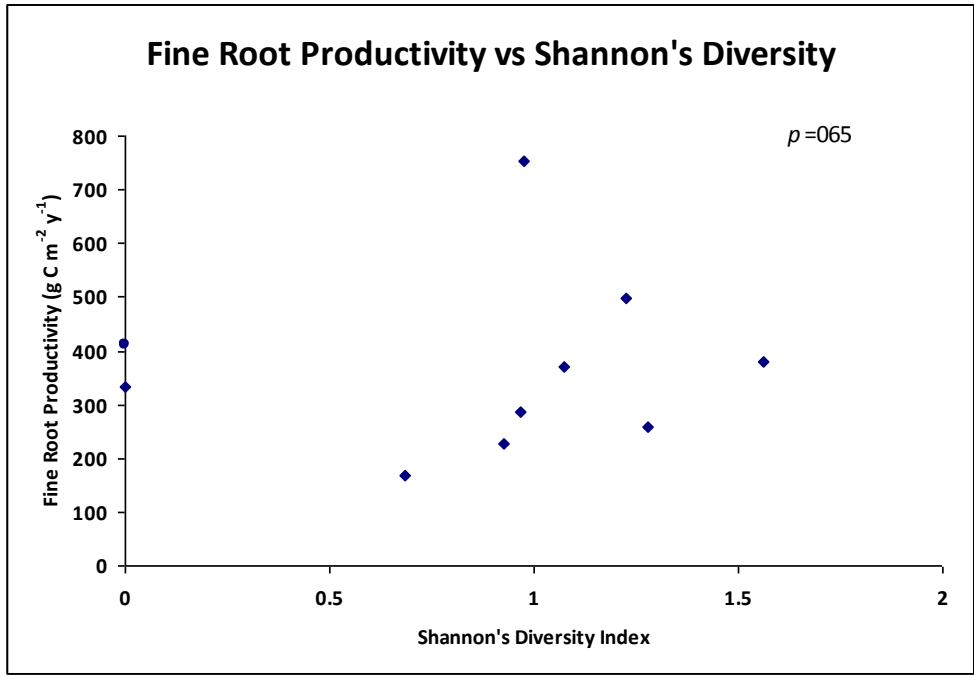


Figure 5D. Relationship between annual fine root productivity and Shannon's diversity of the overstory

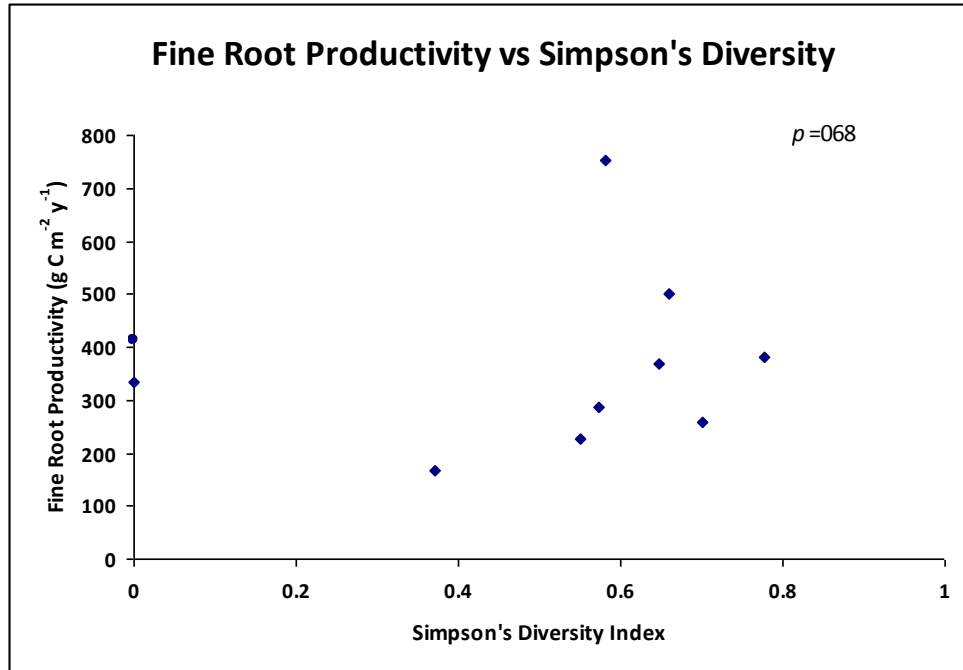


Figure 5E. Relationship between annual fine root productivity and Simpson's diversity of the overstory

3.4 Fine root productivity and standard deviation in canopy height

We initially hypothesized that variability in the SD of canopy HT would be associated with changes in FRP. Accordingly, we found significant negative relationships between the SD of canopy height and FRP for the 1.5m, 2m, 2.5m, 3m, 3.5m, 4m, 4.5m, and 5m buffer sizes (**Figure 2; Table 4; Figures 6B-6I**), where FRP tended to decline with an increase in the SD of canopy height. Specifically, relationships between FRP and SD peaked at the 2.5 m buffer size, and were weaker at both smaller and larger buffer sizes (**Figure 7**), suggesting that at the 2.5m extent, roots respond most heavily to variation in canopy height (**Table 4, Figure 6D**). Specifically, a 0.5m increase in standard deviation of canopy height was related to a 29.1 decrease in FRP ($\text{g C m}^{-2} \text{y}^{-1}$) for the 2.5m buffer class, which responded most heavily to variation in canopy height. FRP did not respond to SD of canopy height at the 1m buffer (**Figure 6A; $p = 0.17$**), 10m buffer (**Figure 6J; $p=0.17$**) and the 15m buffer (**Figure 6K; $p=0.98$**) sizes. For significant

buffer results the r^2 values were lowest at the 1.5m buffer ($r^2=.15$; **Figure 6B**) and increased steadily until they peaked at the 2.5m buffer ($r^2=.26$ **Figure 6D**) and then fell steadily until the 5m buffer ($r^2=.10$; **Figure 6I**; **Figure 7**; **Table 4**). Overall these results show that as canopy height becomes more variable FRP tends to decline. Additionally, these results show that this relationship may be spatially dependent, where there may be an optimal distance away from a fine root sampling point that is most closely related to the forest canopy (**Figure 7**).

Buffer	Adjusted r^2	p -value	$F_{(2,37)}$	AICc
1m_SD	---	0.18	1.86	577.2
1.5m_SD	0.15	0.01	7.70	571.7
2m_SD	0.19	<0.01	9.52	570.2
2.5m_SD	0.26	<0.01	13.89	566.7
3m_SD	0.23	<0.01	11.84	568.3
3.5m_SD	0.21	<0.01	10.83	569.1
4m_SD	0.19	<0.01	9.48	570.2
4.5m_SD	0.14	0.01	6.81	572.5
5m_SD	0.10	0.03	5.15	574.0
10m_SD	---	0.17	1.93	577.1
15m_SD	---	0.99	0.00	579.1

Table 4. Relationship between fine root productivity and standard deviation of canopy height by buffer class

Fine Root Productivity vs. a 1m Buffer

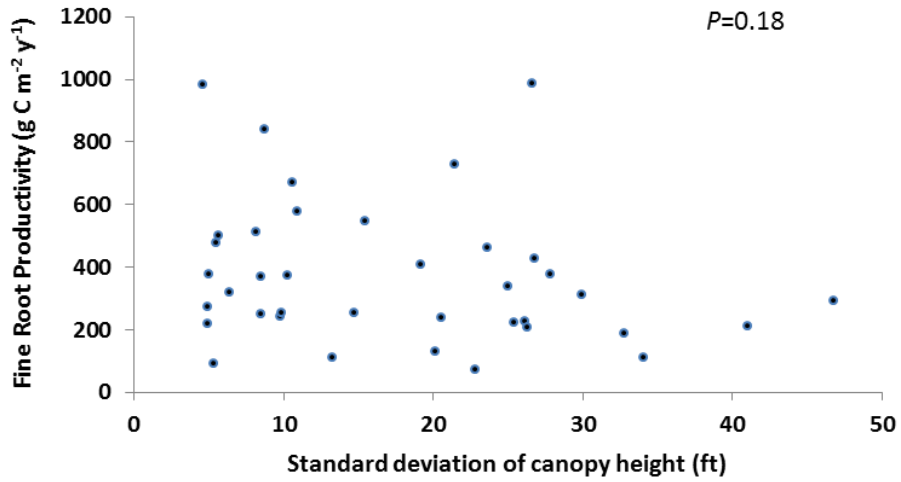


Figure 6A. Relationship between annual fine root productivity and variation of overstory canopy using a 1m buffer

Fine Root Productivity vs. a 1.5m Buffer

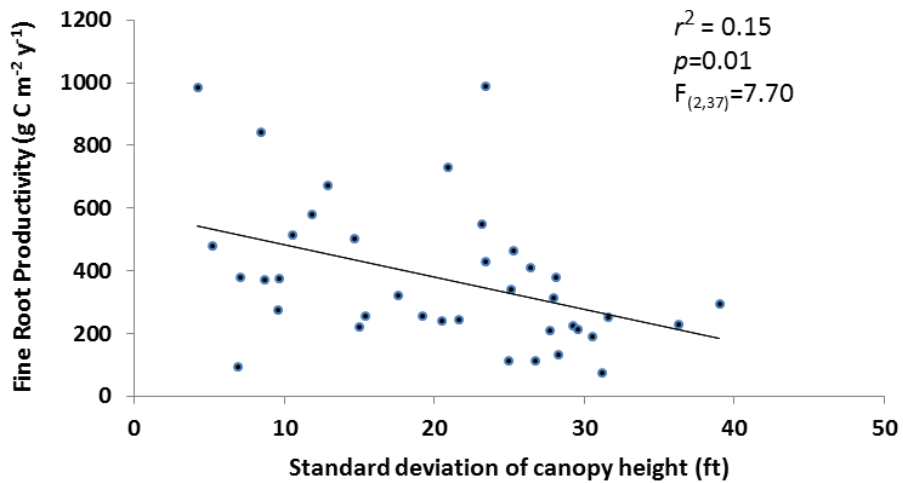


Figure 6B. Relationship between annual fine root productivity and variation of overstory canopy using a 1.5m buffer

Fine Root Productivity vs. a 2m Buffer

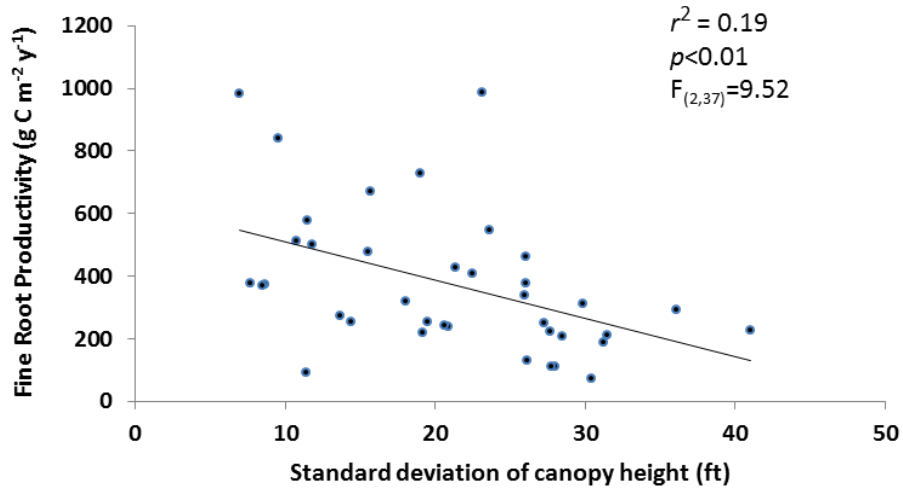


Figure 6C. Relationship between annual fine root productivity and variation of overstory canopy using a 2m buffer

Fine Root Productivity vs. a 2.5m Buffer

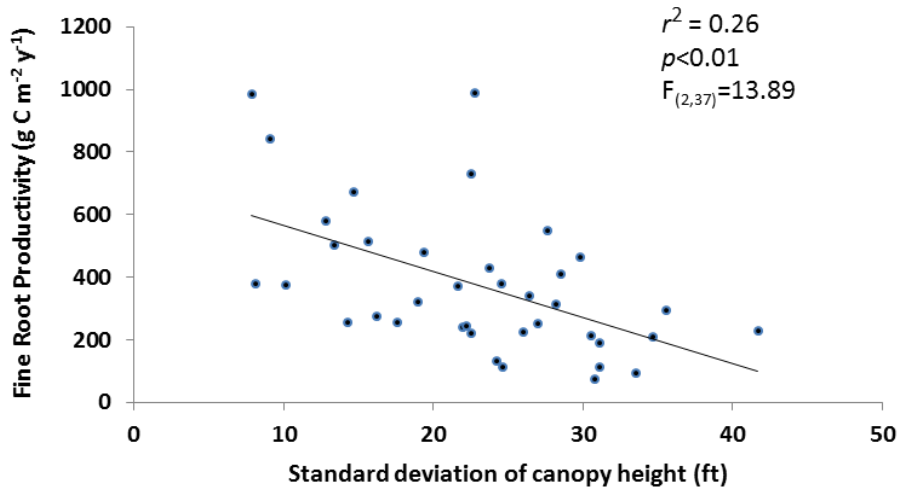


Figure 6D. Relationship between annual fine root productivity and variation of overstory canopy using a 2.5m buffer

Fine Root Productivity vs. a 3m Buffer

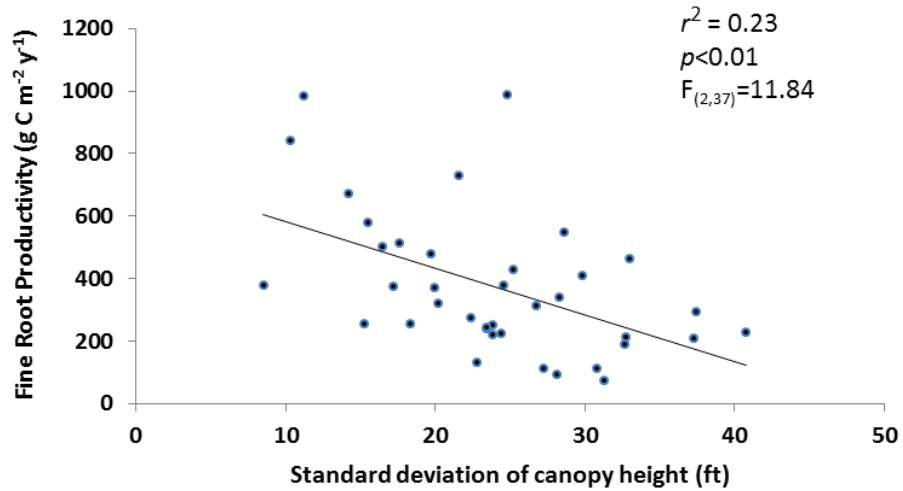


Figure 6E. Relationship between annual fine root productivity and variation of overstorey canopy using a 3m buffer

Fine Root Productivity vs. a 3.5m Buffer

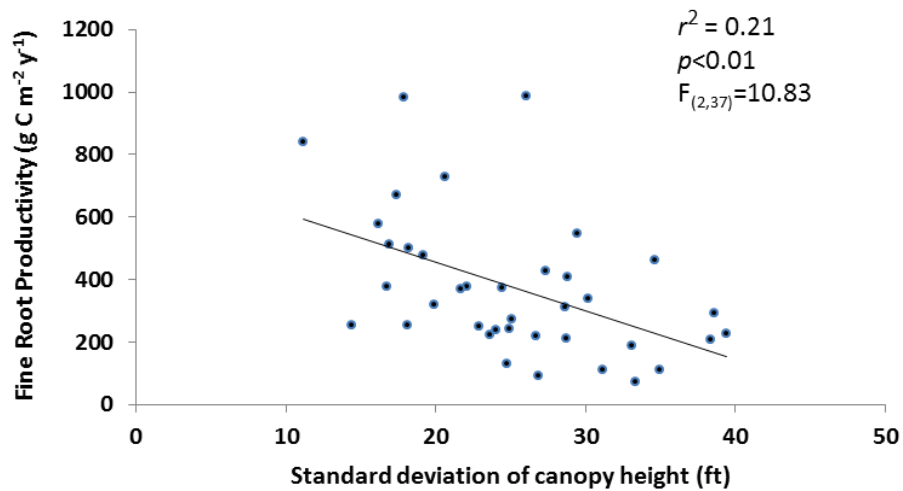


Figure 6F. Relationship between annual fine root productivity and variation of overstorey canopy using a 3.5m buffer

Fine Root Productivity vs. a 4m Buffer

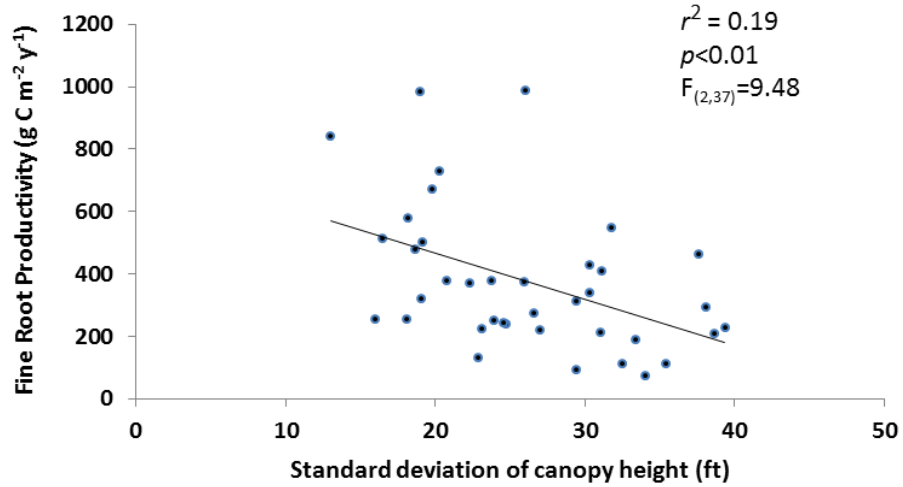


Figure 6G. Relationship between annual fine root productivity and variation of overstory canopy using a 4m buffer

Fine Root Productivity vs. a 4.5m Buffer

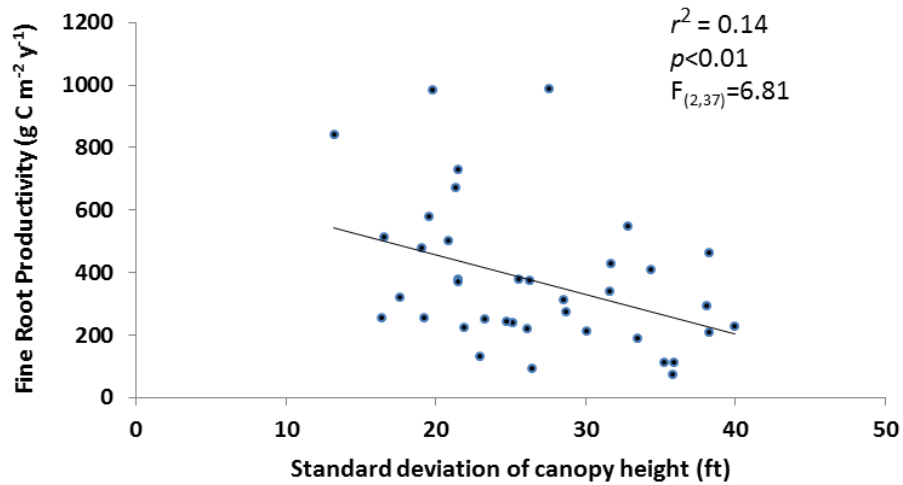


Figure 6H. Relationship between annual fine root productivity and variation of overstory canopy using a 4.5m buffer

Fine Root Productivity vs. a 5m Buffer

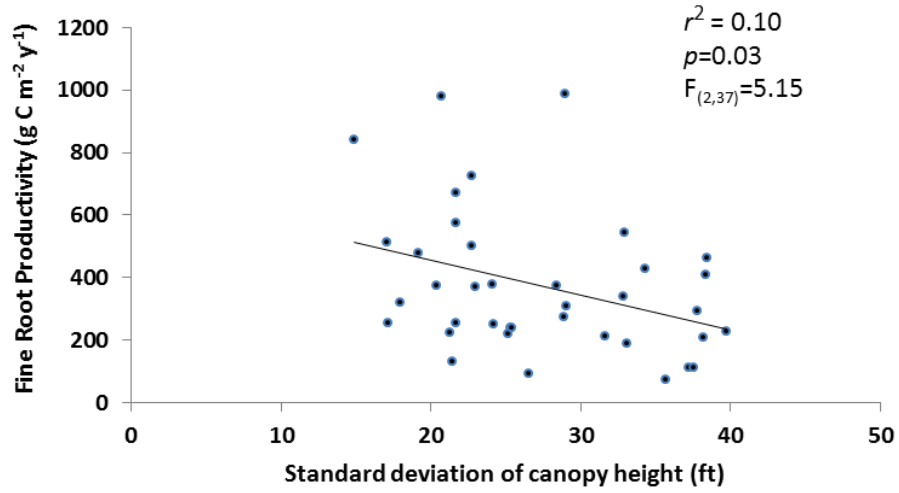


Figure 6I. Relationship between annual fine root productivity and variation of overstory canopy using a 5m buffer

Fine Root Productivity vs. a 10m Buffer

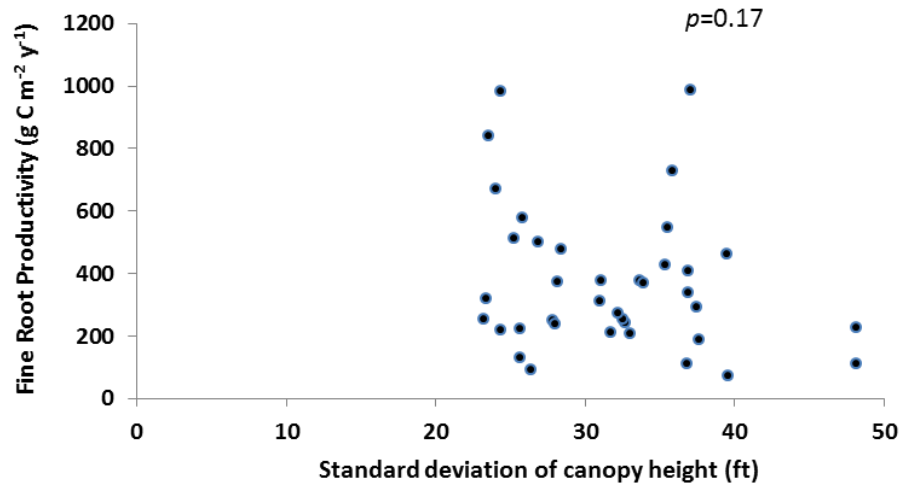


Figure 6J. Relationship between annual fine root productivity and variation of overstory canopy using a 10m buffer

Fine Root Productivity vs. a 15m Buffer

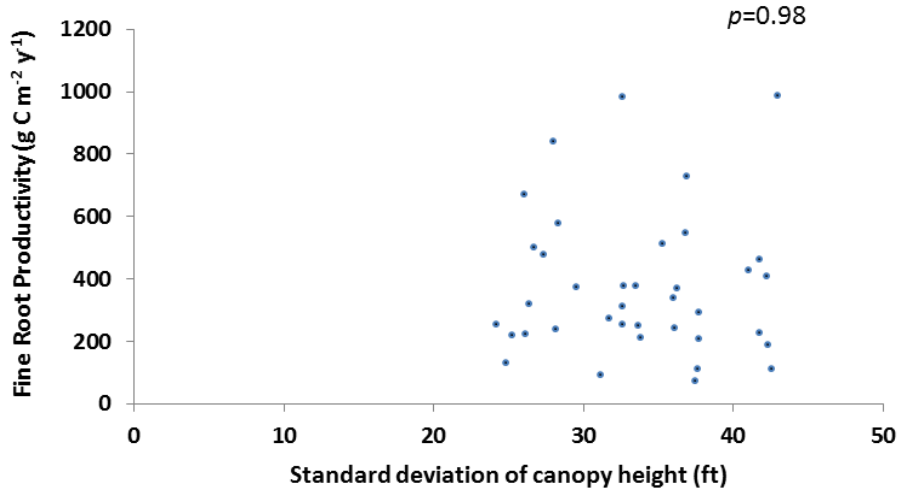


Figure 6K. Relationship between annual fine root productivity and variation of overstorey canopy using a 15m buffer

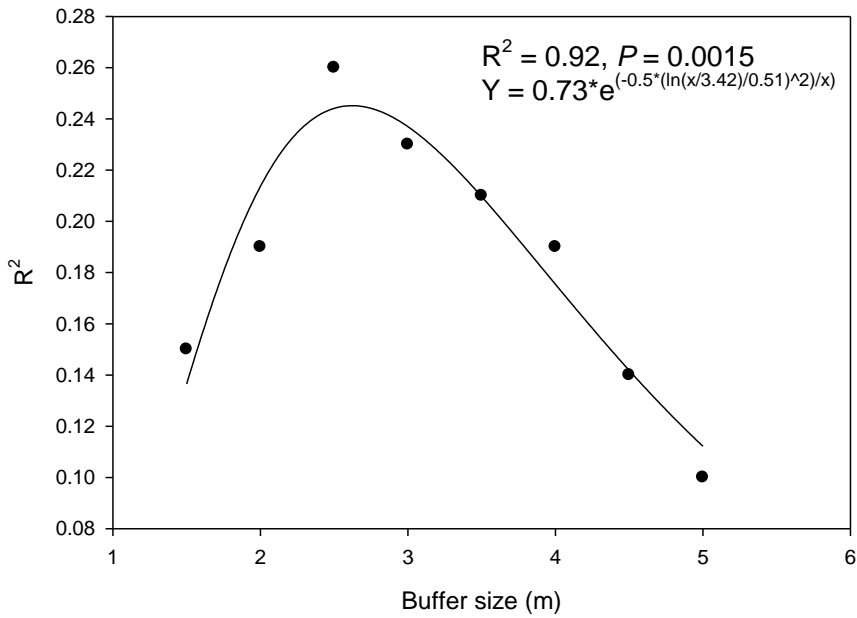


Figure 7: Depiction of relationships between buffer size and the r2 value for fine root productivity and standard deviation of canopy height by buffer classes

Chapter 4: Discussion

4.1 Fine root productivity, overstory productivity and overstory diversity: Dependent relationships?

Our initially hypotheses for this study were developed based on the expectation that highly diverse overstories were associated with high overstory aboveground and belowground productivity (Kirsch et al. 2012; **Figure 8**). Specifically, we hypothesized FRP would be related to both overstory productivity and overstory diversity (**Figure 9**). Fine roots are the pathway for nutrients and water to enter plants, and thus high FRP activity is essential for high photosynthesis and productivity. Thus, we hypothesized a linkage between fine roots and aboveground metrics at the plot scale, where FRP would increase with increases in overstory productivity and diversity (**Figure 9**). However, our data do not suggest clear patterns between increases in FRP and differences in either overstory productivity or diversity.

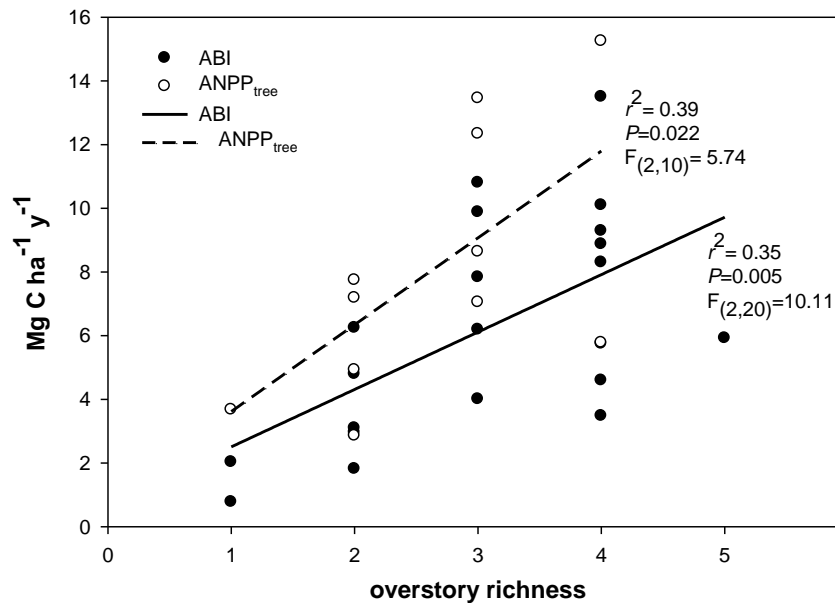


Figure 8. Relationships between overstory richness and aboveground productivity of trees as in Kirsch et al. (2012)

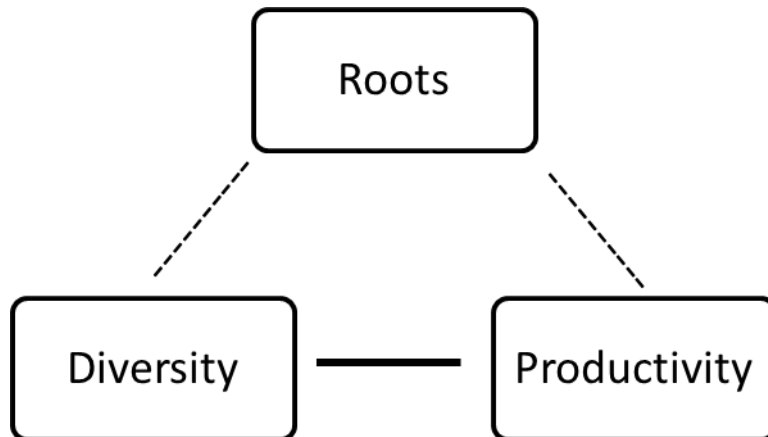


Figure 9. Depiction of existing (bold line) and predicted (hyphenated lines) relationships between fine root production, overstory diversity and aboveground productivity of trees

Despite our initial hypotheses, previous research has shown that fine roots and aboveground metrics may not be related to factors such as aboveground productivity (Vogt et al. 1983) or tree diversity (Lei et al. 2012^b) and relationships between FRP and some aboveground metrics may appear independent of each other. Here we discuss possible justifications for the observed variation in FRP in our study.

4.2 Fine root productivity and overstory productivity

We found a lack of significant relationships between FRP and overstory productivity, similar to Vogt et al. (1983), suggesting that this previously found relationship holds true at our site. The lack of any significant relationships between FRP and overstory productivity is not surprising since previous studies have shown that less productive plots can have lower fine root pools (Vogt et al. 1983), where the variation in overstory productivity may be attributed to available soil nutrients. Such findings might be similarly extended to FRP, where lower fine root pools result in lower FRP. However,

other studies have clearly demonstrated that low soil nutrients are associated with a higher proportional investment in FRP (e.g., see Nadelhoffer et al. 2000 and references therein). Such findings could cancel each other out across study plots, resulting in similar FRP despite differences in aboveground C uptake ($ANPP_{tree}$). While our plots show no significant relationship between FRP, and overstory productivity, our results are similar to other research that suggests that FRP and overstory productivity are not consistently related. FRP and overstory productivity relationships may be dependent upon a variety of factors such as stand age (Konopka and Tsukahara 2000), available soil nutrients (Vogt et al. 1983; Pregitzer et al. 1993), or water availability (Pregitzer et al. 1993). These effects and their interactions could result in no predictable pattern across diverse, but similarly-aged stands, of the same climate. Previous, work at the EEON, which was limited, show no significant differences in soil nutrient pools among plots (Kirsch et al. 2012). While we cannot attribute a lack of relationship between FRP and overstory productivity to differences in available soil nutrients among plots, further detailed analyses of nutrient pools and fluxes might reveal patterns that are obscured by our current data. Further two studies, Ammer and Wagner (2005) and Konopka and Tsukahara (2000) found a relationship between fine roots and tree biomass, an analysis we did not test for, but may be apparent in our data.

4.3 Fine root productivity and overstory diversity

We show no significant relationship between FRP and overstory diversity. FRP did not respond to any of the five measures of diversity: richness, Shannon's and Simpson's diversity indices, or evenness. While Lei et al. (2012^a) showed only a small diversity effect on FRP, where FRP was slightly higher in more diverse stands than in

monocultures, our study showed that not to be the case. However, Lei et al. (2012^b) did not show species richness levels and FRP to be significantly related. We formulated this hypothesis because of previous work at the EEON. In this study more productive plots tended to be more diverse, specifically diversity and productivity were positively related where productivity increased with increases in overstory productivity in positive linear relationships (**Figure 8**). Due to those findings we hypothesized that more diverse plots would also have higher FRP (**Figure 9**). However as mentioned above, FRP is determined by a variety of factors such as soil nutrients and stand age, and therefore diversity was not able to explain any amount of variation in FRP in this study.

Similar to Lei et al. (2012^a), Meinen et al. (2009) were able to show that fine root growth and tree species diversity were positively related, where more diverse stands had higher fine root growth after disturbance. Using ingrowth and sequential coring methods Meinen et al. (2009) hypothesized that after disturbance fine roots recover faster in presence of higher tree species richness. They also found that fine root biomass was higher in more diverse stands than in monocultures. They were able to show a threefold increase in fine root growth from monocultures to stands with richness up to 5. These results highlight the likelihood that diversity and fine roots are in some way connected, but that a variety of factors such as soil nutrients, light and water availability, and stand age may confound underlying relationships.

Additionally, while we did not detect any relationship between FRP and diversity, it is possible that this was due to the fact that some of the roots traced in the images were from the understory and not from the overstory. We make the assumption here that productivity-diversity and FRP are connected, however this assumption neglects the

understory and any understory roots that may appear in images. It is very likely that a portion of roots are from understory plants, however the minirhizotron method is non-destructive and we did not remove samples from the soil to identify them for species or vegetation type. This is likely a source of error in our study that may alter relationships.

4.4 Fine root productivity and standard deviation in canopy height

We showed spatially dependent negative linear relationships between FRP and SD of canopy height for eight out of 11 buffer classes (**Table 4; Figures 6B-6I**). Our results, although weak, show FRP declined as the SD of canopy height increased, where r^2 values rose sharply and fell steadily in relation to increases in buffer sizes (**Figure 7**). These results indicate a mild spatially dependent relationship between the upper canopy and FRP, where variation in canopy height was able to explain as much as 26% of the variation in FRP, this finding is supported by a range of studies which indicate that for all species a certain minimum proportion of root is needed to supply a given quantity of leaf (Atkinson and Fogel 1997).

Our results may indicate a weak linkage between canopy structure and the spatial distribution of fine roots that remote sensing technologies may be able to detect. Although only 26% of the variation in fine roots was explained by a canopy structural measure, these results are still promising as a variable to be used in a model attempting to predict FRP remotely, and this value is on-par with other studies relating aboveground structure and belowground function (Taylor et al. 2013 *in review*).

Although not tested for directly here, these results may indicate that light availability and leaf area index (LAI) may play a significant role in determining an amount of variation in FRP, where more closed canopies may tend to have lower FRP.

Our results may be interpreted that plots with a higher SD of canopy height have more leaf area and thus higher LAI. These plots tended to have lower FRP, suggesting a possible connection between LAI and FRP. While Jackson et al. (1997) do not support the possible connection we found, they did find that calculated root surface area is almost always greater than leaf area, so it may be likely that a connection between FRP and the forest canopy exist in varying degrees in forest ecosystems.

Our results may also be interpreted that more complex canopies are also older and thus there is a relationship between stand age and the amount of fine roots, a hypothesis supported by Konopka and Tsukahara (2000). Although these results may be interpreted as such, only as much as 26% of the variation in FRP was determined by SD of canopy height so our results should be interpreted with caution. Further Konopka and Lukac (2009) found a relationship between fine roots and stressed trees where annual fine root production decreased and root length increased in proximity to trees with visible crown damage. This study indicates it may be possible to use crown health as an indicator for fine root status and concluded that there appears to be a linkage between tree crowns and fine roots.

4.5 Soils

Previous work at the EEON (Kirsch et al. 2012) did not show significant differences in soil nutrients among plots. Since soil nutrient concentration was not central to the hypotheses in this study we did not explore how available soil nutrients may influence variability in FRP at the EEON. Because of the complexity of belowground systems, the plant soil interactions are expected to affect many different regulatory signals such as molecular interactions and associations with bacteria and fungi, These

measurements are beyond the scope of this study, but may describe an amount of variation in FRP that we were not able to detect (Hirsch et al. 2003; Phillips et al. 2003).

4.6 Conclusion

This study addressed the variations in FRP in response to overstory productivity, overstory diversity and SD of canopy height. We attempted to address the understudied relationships between belowground carbon fluxes and aboveground metrics, while using two non-destructive remote sensing techniques, LiDAR and minirhizotrons. Specifically we addressed patterns of association between FRP and the aboveground factors productivity, diversity, and canopy height. While our study showed only weak relationships between FRP and SD of canopy HT as spatial scales, the lack of patterns of association between above – and belowground factors may have occurred due to:

- 1) High rooting extent or deeper rooting activity, while we evaluated buffer sizes up to 10 m, and depths up to 24 cm, trees may either root farther or deeper than our study could measure
- 2) The most productive trees do not necessarily invest the most amount of resources into fine root production, however aboveground factors have been shown to be influential in determining causes for variation in FRP (Vogt et al. 1983; Lei et al. 2012^a)
- 3) Higher FRP allocation may occur in areas of lower site productivity. Thus low resource plots, with correspondingly low tree production, may invest in higher FRP to “forage” for nutrients and water

Our study did not elucidate any relationships between FRP and both overstory productivity and overstory diversity; results that are consistent with previous studies

examining relationships between fine roots and various aboveground factors (Vogt et al. 1983). Previous work on this site did not show differences in soil nutrients to be the cause for variation in FRP or aboveground productivity among plots. However, our study was successful in suggesting a peak in predictability of FRP in relation to remotely-sensed canopy structure at 2.5m buffer distances surrounding the minirhizotron tubes. This study showed that as FRP decreased there was an increase in SD of canopy height in relation to proximity of the root tube, suggesting a possible linkage between FRP and the upper canopy where more diverse canopies tend to have fewer fine roots at an optima scale (~2.5m).

These results are promising for researchers attempting to describe belowground carbon pools and fluxes at the landscape scale using non-destructive remote sensing tools such as aerial LiDAR. Future work will focus on using aerial LiDAR to address causes for variation in FRP influenced by the upper forest canopy to better elucidate relationships between aboveground forest metrics and belowground plant C.

4.7 Future Work

The findings in this study provide a baseline for additional hypotheses that address that causes for variation in fine root C flux in forested ecosystems. A refined methodology and reworked study design may provide the ability to elucidate relationships between above- and belowground plant C interactions. The methods outline below may allow future fine root C flux studies to address underlining patterns that were not entirely uncovered in this study.

The method used in the productivity and diversity section make use of FRP estimates by averaging 4 minirhizotron tubes for a 314m² plot area. This was a weakness as the area immediately surrounding the tube (as in the variation in canopy height related to buffer size

section) was not directly represented as it was influenced by overstory productivity and diversity. Additionally, productivity and diversity were not sampled spatially using a buffer size system, as was done with the forest canopy. Future studies should establish plots around the minirhizotron tubes and measure the trees for productivity and diversity which fall in various buffer sizes. This would test the effect of overstory productivity and diversity at a spatial scale in relation to FRP. This method would also allow for the combination of canopy diversity, overstory diversity, and overstory productivity to be combined in a model at various buffer sizes. This may strengthen future estimates of the influence of aboveground metrics on belowground carbon flux.

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Appendix A: List of terms and definitions

AICc- Small sample size Akaike information criterion. A measure of the relative goodness of fit of a statistical model using a small sample size, where lower values separated by a statistically significant difference are typically the best fit for the model.

ANPPtree = The aboveground net primary productivity of trees. Estimates represent aboveground biomass increment averaged over two years and litterfall from a single year.

BIOPAK – A collection of allometric biomass equations typically using the girth, height, or percent cover of vegetation to estimate biomass or productivity.

Canopy complexity – The variation in the upper most canopy height in relation to the ground height. See also rumple index or canopy roughness.

DBH – Diameter at breast height. A height off of the ground (1.37 meters or 4.5 feet) used to measure the girth of a tree for use in growth estimates and in biomass equations.

Fine root – Any root less than 2mm in diameter, in contrast to coarse roots that are greater than 2mm in diameter.

FRP – Fine root productivity. Calculated as the total net root increment measured over one year. Takes into account growth and death of fine roots.

GIS – Geographical information system, a system designed to capture, store, manipulate, analyze, manage, and present all types of geographical data.

GPS – Global positioning system. A collection of satellites used to locate unknown locations on the ground from known locations.

LiDAR – Light detection and ranging, an active remote sensing technique which measures the distance of objects using laser light to create point clouds of 3D data sets.

Minirhizotron - Clear plastic tubes installed below the soil surface that allow for repeat measurements of the rhizosphere.

NPP – Net primary productivity. The total annual net growth of organic compounds given as gross primary productivity minus respiration.

Zonal statistics – The tool used for calculation of standard deviation of canopy height in ArcGIS. This tool uses a defined area (i.e. a buffer size) to calculate a series of statistics for that area.

Appendix B. Fine root productivity (FRP), carbon (C), and fine root turnover by subplot

Plot	Subplot	FRP (g m ⁻² y ⁻¹)	C (g m ⁻² y ⁻¹)	Turnover (y ⁻¹)
A7	N	383.6	191.8	0.8
A7	E	586.5	293.2	1.4
A7	W	226.9	113.5	0.9
A7	S	150.0	75.0	0.8
C4	N	456.5	228.3	0.6
C4	W	760.8	380.4	2.2
C4	S	502.5	251.3	0.7
C5	N	509.2	254.6	0.7
C5	E	640.1	320.0	0.7
C5	W	448.6	224.3	0.8
C5	S	480.0	240.0	0.8
C7	N	1094.8	547.4	1.9
C7	E	624.1	312.1	0.9
C7	W	823.6	411.8	1.1
C7	S	754.6	377.3	1.0
D4	N	440.0	220.0	0.9
D4	E	960.6	480.3	1.0
D4	W	265.4	132.7	0.9
D4	S	1003.3	501.6	1.0
D8	N	484.6	242.3	0.5
D8	E	680.9	340.5	0.9
D8	W	1457.2	728.6	1.0
D8	S	422.3	211.2	0.8
D11	E	749.6	374.8	0.8
D11	W	186.7	93.4	1.2
D11	S	426.3	213.2	0.9
E8	N	1156.2	578.1	1.2
E8	E	510.5	255.2	0.9
E8	W	548.6	274.3	0.9
E8	S	741.2	370.6	1.4
E9	N	1027.8	513.9	1.1
E9	E	1966.9	983.5	1.0
E9	W	1686.2	843.1	1.4
E9	S	1347.1	673.5	1.0
E10	N	861.2	430.6	0.9
E10	E	1978.4	989.2	1.2
E10	W	226.2	113.1	0.7
E10	S	929.9	464.9	1.2