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**TOPOGRAPHIC CONTROLS ON ROOT PARTITIONING PATTERNS  
IN A TEMPERATE FOREST**

A Thesis in  
Ecology  
by  
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## **Abstract**

While increased efforts to understand the impact of climate change on ecosystem processes has elevated the importance of accurately estimating ecosystem carbon allocation, belowground carbon estimates remain uncertain. Optimal Partitioning Theory and fixed proportion allocation are often incorporated into models to estimate biomass partitioning to root systems. While some experiments do support these types of allocation models, scaling them to the landscape level is challenging because complex topographic variation may drive spatial and temporal patterns of resource availability. We examined patterns of variation in soil inorganic nitrogen, organic matter, rock content, volumetric water content and above- and belowground carbon partitioning across a topographically diverse first-order catchment (Shale Hills CZO). In order to test both fixed proportion and optimal partitioning at the site, we compared leaf area with absorptive root surface area (RSA) and leaf litter production with simulated absorptive root production at each slope position and across an elevation gradient.

Both Optimal Partitioning Theory and fixed proportion allocation were moderately supported by the data. Fractional allocation analysis revealed no significant relationship between partitioning and elevation or slope position, so in general a simple scaling exponent or fixed ratio may be acceptable. However, while soil properties and aboveground growth patterns showed strong relationships with both elevation and slope position, root distribution varied widely across the catchment and followed a less clear pattern. Only soil depth correlated with increased RSA. While belowground patterns did not support optimal partitioning, aboveground patterns did indicate an increase in tree height in increased light competition, despite smaller variations in leaf production.

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# CHAPTER 1

## INTRODCUTION

### Belowground Carbon Partitioning

In the context of global change, understanding the relationship of above- to belowground carbon partitioning is extremely important in creating accurate carbon budgets. Because forests represent nearly 77% of global vegetative carbon (Dixon et al. 1994), understanding this relationship in forest ecosystems is particularly important. Compared to aboveground measurements, belowground measurements remain challenging because of its destructive nature as well as the level of monetary and labor costs associated with their implementation (Cairns et al. 1997; Mokany et al. 2006). To circumvent this challenge, several methods exist for estimating belowground allocation from aboveground measurements including allometric analysis, fractional biomass analysis and the inclusion of optimal partitioning theory.

Allometric analysis, a very common method in determining the relationship between above- and belowground allocation, determines an absolute relationship between the size of a particular plant organ to the whole plant or another plant organ (Poorter et al. 2015) and is neither plant size nor time dependent (Poorter et al. 2011). Oftentimes these relationships utilize a root to shoot ratio to estimate belowground biomass (Gilmanov et al. 1997; Levis et al. 2004 Smithwick et al. 2014). A common format for an allometric equation is

$$(1) \quad Y = aX^b$$

with, for example,  $Y$  representing root biomass,  $X$  representing aboveground biomass,  $a$  representing an allometric constant and  $b$  representing a scaling exponent. Metabolic Scaling Theory integrated both plant and animal allometric analyses into one unifying theory that

assumes that vascular transport is the limiting factor in metabolic rate capacity and predicts a constant scaling exponent of metabolic rate to size (West et al. 1997). This theory further developed into plant-specific allometric relationships with scaling exponents of  $\frac{3}{4}$  for leaf to stem mass,  $\frac{3}{4}$  for leaf to root mass and 1 for stem to root mass (Enquist & Niklas, 2002a; Niklas, 2004; McCarthy et al. 2007). While universal scaling exponents are useful, controversy surrounds their application because they not only prevent the possibility of plasticity in partitioning, they also assume no interspecific variation (Poorter et al. 2015; Poorter & Sack, 2012; Packard & Boardman, 1988).

In a forested system, the most common method for determining aboveground biomass is to use dimensional analysis which relies on the tenant that there is an allometric relationship between tree size, typically tree diameter at breast height (DBH), and biomass (Whittaker & Woodwell, 1968). Jenkins et al. (2003) sorted through the isolated and scattered allometric studies that existed and combined that data with the USDA's Forest Service's Forest Inventory and Analysis data to generate a consistent and generalized biomass equation set for species groups that were determined by taxonomy and geography. Recently, species-specific allometric equations for many North American temperate forest tree species have been developed (Chojnacky et al. 2014). These equations take the form of

$$(2) \quad bm = \text{Exp}(\beta_0 + \beta_1 \ln dbh)$$

with  $bm$  representing aboveground biomass and  $\beta$  parameters being species specific. To estimate biomass of a particular plant part (foliage, coarse roots, stem bark, stem wood) a ratio can be determined using the equation

$$(3) \quad ratio = \text{Exp}[\beta_0 + (\beta_1 / \ln dbh)]$$



that can be applied to the aboveground biomass value (Jenkins, 2003). This helps to remove some of the assumptions made by using a universal scaling exponent,  $b$  in equation 1.

While allometry is a common and relatively easy method for estimating belowground biomass, there are very few studies that actually test these relationships by measuring both above- and belowground biomass simultaneously (Smithwick et al 2014). In studies that did examine the accuracy of allometric equations across 12 hardwood species in New Hampshire, results indicated that allometric equations were accurate with on average 24-30% error in estimating lateral root (<10 cm in diameter) biomass for stands greater than 20 years of age (Kashian et al., 2013; Santantonio et al., 1977; Vadeboncoeur et al. 2007). In fact, in young forest stands, allometric equations may underestimate root biomass by up to 60%. (Robinson, 2004). Oftentimes smaller, understory trees are ignored in biomass and productivity calculations, which could have led to this bias in accuracy towards older stands. However when canopies allow enough light penetration to support understory growth, this understory growth can add substantially to allocation and productivity measurements, particularly belowground. In a maritime pine plantation in the southwest of France, for example, understory species accounted for 6.8% of total aboveground biomass but over 27% of total root biomass (Gonzalez et al. 2013).

Another common method for determining the relationship between above- and belowground biomass is clasmometry or fractional biomass analysis. This analysis looks specifically at the biomass of an individual plant part as a fraction of total plant biomass at a given time (Poorter et al, 2015; Poorter & Sack, 2012; Packard & Boardman, 1988). Common measurements are leaf mass fraction or root mass fraction. Fractional biomass measurements can lend insight into the plants ability to assimilate carbon and take up resources and thus can be

used to estimate potential growth rates (Evans, 1972). By plotting these fractions against plant size, an allometric analysis is essentially performed (Poorter & Sack, 2012). Fractional biomass is often interpreted in the context of functional equilibrium and optimal partitioning theory.

The functional equilibrium theory predicts that plants maintain a balance between roots and shoots in size and surface area (Brouwer, 1962). Given the opposite roles of roots and shoots in uptake and use of resources, one would expect a functional balance between these two components (Reich, 2002). The first experiments to support this functional equilibrium theory revealed that trimmed foliage or roots would quickly regrow to match the same root to shoot ratio as before the trimming (Brouwer, 1962). However, because resources are not uniformly available in a natural environment, one might expect that this root to shoot ratio may shift to reduce allocation costs. In fact, experiments have proven that allocation can shift toward the part of the plant responsible for the uptake of the most limiting resource in order to maximize plant growth. This shift in allocation has been coined the Optimal Allocation or Optimal Partitioning Theory (Wilson, 1988; Bloom et al., 1985; Thornley, 1969; Johnson & Thornley 1987). Despite the popularity of this model, there is mixed empirical evidence that supports optimal partitioning theory as a general model for predicting plant biomass allocation (Reich, 2002).

Many studies have tested Optimal Partitioning Theory in response to variations in light, nutrients and water availability. The majority of these studies test for optimal partitioning on potted seedlings, so confounding factors such as ontogenetic drift as well as scaling issues from pots to the landscape are common. In particular, most studies that reported higher leaf mass fraction under low light conditions (Callaway, 1992; Latham, 1992; Lei & Lechowicz, 1998), oftentimes showed little or no such relationship once ontogenetic drift and plant size were accounted for (Reich, 2002). Other studies found stronger support of a shift in allocation toward

stem mass rather than leaf mass under low light conditions (Walters et al. 1993a; Reich et al. 1998a). This shift toward stem mass has also been supported in data from many stable forest stands (Dybzinski et al. 2011). Additionally there is compelling evidence supporting plant adaptation to light level through plasticity of tissue morphology, rather than shifts in allocation, with plants grown in low light conditions exhibiting greater specific leaf area and lower specific root length (Walters et al. 1993a; Reich et al. 1998a).

In contrast to light, there is stronger evidence of optimal partitioning to belowground resources, particularly nitrogen. There are many studies that have observed increased root biomass independent of plant size with decreasing levels of nitrogen (McConnaughay & Coleman, 1999; Gedroc et al. 1996). However, the support for a similar trend with decreasing levels of phosphorus is controversial and may be species-specific (Eissenstat et al. 1993; Nielson et al. 1998). Of the studies that did account for plant size, there is also evidence that in woody plants, allocation will shift to roots in low soil moisture regimes (Tomlinson & Anderson, 1998; Ledig et al. 1970).

Dybzinski et al.'s (2011) Evolutionary Stable Strategy model found some major counter points to Optimal Partitioning Theory when looking at data from 152 primarily temperate deciduous and evergreen stands. The model based allocation on nitrogen and light availability in conjunction with allometric equations. Optimal Partitioning Theory interprets allocation in fractional rather than absolute biomass even though absolute biomass determines resource uptake. For example, a higher root mass fraction may not indicate higher nitrogen uptake but a higher total root biomass most likely will increase rates of resource acquisition. Additionally, there are upper limits for this resources acquisition that varies substantially between above- and belowground allocation. While root biomass may be a good predictor of nitrogen uptake

potential, mineralization rates occur independently of root biomass and set the limit at which this uptake can be maximized. For leaves, this upper limit is the height and level of closure in the upper canopy. In a closed canopy, increases in leaf biomass will not necessarily augment light uptake due to self-shading, so shifting allocation to stem mass may be a more competitive strategy. Therefore, in a stable forest system, a root to stem ratio may be more appropriate than a root to leaf ratio.

While some shifts in partitioning between shoots and roots have been observed with overall evidence supporting a shift toward stem rather than leaf biomass in low light conditions and a shift toward root biomass in soils with low moisture and nitrogen levels, these shifts are not consistent across plant species (Dybzinski et al. 2001; Reich, 2002). This is possible due to the fact that there are multiple strategies beyond biomass allocation that can increase resource uptake. In addition to morphological changes, metabolic or chemical strategies can also be employed. While Optimal Partitioning Theory bases competitiveness on maximum growth rate, the most competitive strategies do not maximize growth rate in monoculture but ensure that in competition, no other competitive strategy produces higher growth rates (Falster & Westoby, 2003). Interspecific variation in morphology and resource acquisition strategies may counter any evidences for Optimal Partitioning Theory in a mixed species habitat. Accounting for species variation, resource heterogeneity and the complexity at which these are expressed on a landscape level could lead to an overly complicated model. On the other hand, are simple allometric equations accurate enough in predicting belowground carbon budgets? Perhaps with increasing studies that combine both above- and belowground carbon measurements and new technologies that allow for easier or more accurate belowground research, we can be more certain in our estimates of belowground allocation.

## Fine Root Distribution

Carbon budgeting and ecosystem models tend to allocate carbon to the root system by using both allometric equations with a fixed scaling exponent between either NPP or leaf area and root biomass and optimal partitioning to account for environmental conditions (Smithwick et al. 2014). In order to improve the dynamics of roots in models, it is important to understand how roots actually distribute in the soil profile.

Fine roots are a chief mediator of soil carbon storage and cycling through both direct contribution of carbon from root turnover and indirect mediation of carbon cycling via water and nutrient acquisition (Leppälampi-Kujansuu et al. 2014; McCormack & Fernandez, 2011; Kuzyakov & Schneckenberger, 2004; Matamala et al. 2003; Joslin & Henderson, 1987; Cox et al. 1978). In a temperate, hardwood forest fine root lifespan can range from 0.6-2.5 years depending on tree species and site conditions (Withington et al. 2006; McCormack et al. 2014). Due to their relatively short lifespan, fine roots contribute substantially to soil carbon storage. There is evidence that carbon originating from roots is the main source of mineral soil carbon and a major fraction of the labile carbon pool (Kramer et al. 2010; Brassard et al. 2009; Mendez-Millan et al. 2010; Kalyn & Rees 2006).

Because soil is a habitat that exhibits strong spatial and temporal heterogeneity (Harper et al. 1991), estimating fine root distribution is arduous at best. There is a complex interplay between biotic and abiotic factors as well as inter- and intraspecific variations that control where roots develop and when they die (Hodge, 2010; Brassard et al. 2009; Fort, 2013; McCormack & Guo, 2014). Variations in root distribution and turnover can result from variation in resource availability, species composition, stand age, tree size and soil physical and chemical properties (Hendricks et al. 1993; McCormack et al., 2014; Yuan and Chen, 2012; Hodge, 2004; Brassard

et al., 2009). Due to the complex nature of making such estimations, scale is extremely important in understanding which factors are most critical. At the landscape scale, allocation to roots is expected to increase in soils with limited resources under the assumptions of optimal partitioning theory (Brassard et al., 2009; Johnson and Thornley, 1987; Poorter and Nagel, 2000). At a localized scale, the opposite could be expected. Many studies have shown a localized response of increased fine root production and growth in patches of water, nitrate, ammonium and phosphate (Drew, 1975; Gross et al. 1993; Pregitzer et al. 1993; Hodge et al. 1999b, 2000d). However, in comparison to responses in natural environments with mixed signals between competition, stresses and resource supply, these types of manipulation experiments show the most exaggerated response of root foraging (Hodge, 2004). The diversity and magnitude of signals in natural, forest environments will likely produce different results than simplified fertilization experiments, which hinders our ability to scale data to the ecosystem level.

Predicting vertical root distribution is also scale dependent. The majority of roots are distributed within the top 30-50 cm of soil due to decreased nutrient availability at greater depths (Jackson et al., 1996; Brassard et al., 2009). Local vertical root distribution is often strongly affected by soil physical properties and nutrient and water gradients along the soil profile (Schenk & Jackson, 2005; Zhou & Shangguan, 2007). At the regional and global scale, deep roots are found in seasonally dry or semiarid regions as well as tropical regions that experience greater water infiltration depths and higher potential evapotranspiration demands (Schenk & Jackson, 2005; Schenk & Jackson, 2002a; Meier & Leuschner, 2008). Valverde-Barrantes (2015) showed positive trends between vertical fine root biomass and soil fertility on a landscape scale in a temperate forest. These studies suggest that vertical distribution may be driven by resource foraging and acquisition. Despite the clear evidence that soil resources availability influences

rooting depth and distribution, ecosystem models typically ignore site conditions and simply base vertical distribution on empirical data of vegetation type (Smithwick et al. 2014). In fact some models still use the simplest method that involves a uniform pool of roots in the soil column (Budyko, 1974; Manabe, 1969).

### Conclusions

While numerous studies investigate fine root length and biomass distribution, there seems to be no common consensus on how to accurately predict these measures. In estimating total belowground allocation, allometric equations that incorporate optimality with light and nitrogen competition may be the simplest method. However, heterogeneous distribution of belowground resources can complicate where fine roots actually develop. Whether this variation in resource availability is dampened when looking at landscape averages has not clearly been tested. More investigation into the impact of resource competition across a landscape or ecosystem scale may lend insight into the necessity of incorporating this level of complexity into belowground models.

## CHAPTER 2

# TOPOGRAPHIC CONTROLS ON ROOT PARTITIONING PATTERNS IN A TEMPERATE FOREST

### Introduction

Ecosystem carbon allocation is of particular interest due to the uncertainty in the response of carbon processes to rising levels of CO<sub>2</sub> and fluctuations in precipitation patterns caused by climate change [Intergovernmental Panel on Climate Change (IPCC), 2013]. Forests account for over three quarters of global stored vegetative carbon and thus are critical in worldwide carbon budgeting (Dixon et al. 1994). Roots are estimated to account for over 20% of total forest biomass, but due to the challenges of taking belowground measurements, create uncertainty in predicting allocation estimates (FAO 2010; Cairns et al. 1997, Smith et al. 2014). Few studies examine the contribution of topography in forest carbon dynamics despite evidence that topography strongly influences temporal and spatial patterns of soil water content (Beven and Kirkby, 1979; Tromp-van Meerveld & McDonnell, 2006; Lozano-Parra et al. 2016; Lin et al. 2006; Crave & Gascuel-Odoux, 1999), which may be critical in determining both rates of organic matter decomposition (Janzen, 2015; Davidson & Janssens, 2006; Davidson et al. 1998) and fine root distribution and turnover (McCormack & Guo, 2014; Hodge, 2010). This study examines how belowground carbon allocation varies within a topographically diverse temperate forest at the Susquehanna Shale Hills Critical Zone Observatory.

Fine roots are a chief mediator of soil carbon storage and cycling through both direct contribution of carbon from root turnover and indirect mediation of carbon cycling via water and nutrient acquisition (Leppälammı-Kujansuu et al. 2014; McCormack & Fernandez, 2011;



Kuzyakov & Schneckenberger, 2004; Matamala et al. 2003; Joslin & Henderson, 1987; Cox et al. 1978). Fine root production and total root production can represent 30 to 50% of net primary production, respectively. There is evidence that carbon originating from roots is the main source of mineral soil carbon and a major fraction of the labile carbon pool (Kramer et al. 2010; Brassard et al. 2009; Mendez-Millan et al. 2010; Kalyn & Rees 2006). Despite the important role that roots play in ecosystem processes, our knowledge of fine root dynamics remains limited (Rewald et al. 2014; Pregitzer 2002) and roots remain one of the most simplified and poorly understood components of current Earth System Models (Smithwick et al. 2014; Warren et al. 2015).

Because soil is a habitat that exhibits strong spatial and temporal heterogeneity (Harper et al. 1991), estimating fine root distribution is arduous at best. Variations in root distribution and turnover can result from variation in resource availability, species composition, stand age, tree size and soil physical and chemical properties (Hendricks et al. 1993; McCormack et al., 2014; Yuan and Chen, 2012; Hodge, 2004; Brassard et al., 2009). Due to the complex nature of making such estimations, scale is extremely important in understanding which factors are most critical. At the landscape scale, allocation to roots is expected to increase in soils with limited resources (Brassard et al., 2009; Johnson and Thornley, 1987; Poorter and Nagel, 2000). At a localized scale, the opposite could be expected. Many studies have shown a localized response of increased fine root production and growth in patches of water, nitrate, ammonium and phosphate (Drew, 1975; Gross et al. 1993; Pregitzer et al. 1993; Hodge et al. 1999b, 2000d). The diversity and magnitude of signals in natural, forest environments will likely produce different results than simplified fertilization experiments, which hinders our ability to scale data to the ecosystem level.

At the landscape level, models often allocate carbon belowground by determining a fixed proportion of ANPP that is either directly proportional to aboveground biomass or an aboveground plant component, typically leaves (Smithwick et al. 2014). To account for environmental conditions, models can incorporate optimal partitioning, which favors growth of the plant component responsible for the uptake of the most limiting resource in order to maximize plant growth (Wilson, 1988; Bloom, Chapin & Mooney, 1985; Thornley, 1969; Johnson & Thornley 1987, Poorter and Nagel, 2000, Brassard et al., 2009). For example, the Community Land Model (CLM) allocates a fixed proportion of NPP that maintains a dynamic ratio between fine roots and foliage, where fine root allocation increases when water becomes limiting (Levis et al. 2004). There is evidence that supports optimization theory for many types of plants in various conditions (Shipley & Meziane, 2002; Portsmouth & Niinemets, 2007; McCarthy & Enquist, 2007); however, landscape-level experiments are limited and differences in allocation patterns among species (Nie et al. 2016) creates barriers to scaling this theory accurately. Additionally, in resource-limited environments, optimization to maximize growth may not overcome the carbon cost of growth if resource acquisition diminishes with increased growth. Therefore, optimal partitioning may not be the most competitive strategy (Dybzinski et al. 2011). Despite uncertainty in the universal application of optimal partitioning theory (Reich, 2002; Schmid & Weiner, 2000), the theory plays a key role in classic evolutionary and ecological models (Grime, 1979; Tilman, 1988).

The Susquehanna-Shale Hills Critical Zone Observatory (SSHCZO) includes the Shale Hills catchment, an 8-ha mixed-hardwood temperate forest dominated by northern red oak and chestnut oak. The site is a first-order catchment that exhibits diverse topography with slope positions including ridge tops, planar midslopes, midslope swales and a valley floor (Figure 1).

The SSHCZO has been studied intensively and there is ample data on the topographic patterns of soil water content, tree species distribution, ANPP and soil carbon (Meinzer et al. 2014; Andrews et al. 2011; Lin et al. 2006; Smith et al. 2016). Soil depths range from <0.3 m on the ridgetop to >2 m deep in the swales and valley floor (Lin et al. 2006). Topographic wetness index also indicates that the swale and valley floors exhibit the highest levels of soil water content at the site (Lin et al. 2006) so may be less affected by periods of drought. Tree size and species distribution also vary throughout the catchment with the tallest trees in the valley floor, the largest diameter trees in the valley floors and midslopes, and tree growth fastest on south facing slopes and swales (Meinzer et al. 2013; Smith et al. 2015, in review; Brubaker data). Oaks (*Quercus* spp.) dominate most midslopes with pines (*Pinus*) common on the ridgetop and hemlocks (*Tsuga*) common on the valley floor,

In order to test both fixed proportion and optimal partitioning at the site, we compared leaf area with fine root surface area, leaf litter production with simulated absorptive root production, and aboveground NPP with belowground NPP at each slope position and across an elevation gradient. If fixed proportion allocation is supported, a similar ratio of above- and belowground measures should be seen at all slope positions. If optimal partitioning is supported, the ratio of above- to belowground partitioning may vary depending on resource availability.

## Methods

### *Site Description and Experimental Design*

The Shale Hills catchment is located near State College, Pennsylvania, USA (Lat. 40°39'N, Long. 77°54'W). Fifty macro-sites were sampled across the catchment (Figure 1) with five

micro-sites nested within each. The sampling design was crafted to optimize analysis of variation in topography, which included a wide range in tree species, soil types and depths (Figure 2).

### *Soil Core Sampling*

Between June and October of 2014, 250 soil cores, 5cm in diameter, were taken at an 60-degree angle from the soil surface to a depth of 165 cm or maximum depth that could be cored with a gas-powered coring auger (Rhino GPD-40, Giddings Machine Company, Windsor, CO). The O<sub>a</sub> horizon was removed from the top of each soil core, so that 0 cm in the core began at the O<sub>e</sub> horizon. Each soil core was divided into depth increments of 0-20 cm, 20-40 cm, 40-80 cm, 80-120 cm, 120-165 cm unless rocks prevented reaching full coring depth. Each coring increment was homogenized and split so that each half contained equal amounts of soil and root constituents.

### *Soil Physical and Chemical Properties*

All soil samples were air dried in a greenhouse and sieved to 2mm. Rocks (greater than 2mm) were power washed and oven dried at 105°C for 24 hours to determine total rock content, the ratio of oven-dried rock weight to dry, sieved soil weight (g g<sup>-1</sup>). Percent soil organic matter content (SOM) was determined by oven drying one-gram soil samples at 105°C for 24 hours, reweighing these soil samples then determining loss on ignition at 450°C (Nelson & Sommers, 1996). Inorganic nitrogen was extracted by shaking  $5 \pm 0.2$ g soil samples with 50ml of 2M KCl in specimen cups for one hour. Samples were allowed to settle overnight in a refrigerator then were filtered with Whatman #1 filter papers. Approximately 15mL of each filtered extraction were stored in 20mL scintillation vials in a freezer. Samples were brought to room temperature before using a Vanadium(III) Chloride reagent and Citrate, Salicylate-nitroprusside and

Hypochlorite reagents for spectrophotometric determination of nitrate and ammonium concentrations respectively in parts per million (Doane & Horwath, 2003).

#### *Soil Volumetric Water Content*

Between May and October of 2015, weekly measurements of soil volumetric water content ( $\text{cm}^3\text{cm}^{-3}$ ) were taken with a ThetaProbe model ML2x (Delta-T Devices, Cambridge, UK) at a 5cm depth in four locations within each macroplot one meter away from where the soil core was taken. To take into account seasonal variations in soil moisture levels, the average was taken over the entire season to determine seasonal average macroplot soil volumetric water content.

#### *Root Length, Biomass and Surface Area*

Roots were washed from soil cores with water then separated with forceps into absorptive or woody roots using an order-based classification similar to a stream classification system.

Absorptive roots were defined as being 3<sup>rd</sup> order or less, with first order roots being the most distal roots with no other roots branching from them (Pregitzer et al. 2002). An order-based rather than diameter-based classification system allowed us to classify roots based on function and account for variations in root diameter (McCormack et al. 2015). Once classified, roots were then scanned and analyzed for root length and diameter using WinRHIZO software. Absorptive root surface area (RSA) was determined from length and diameter measurements, assuming roots had cylindrical geometry. Total RSA to ground area ( $\text{m}^2\text{m}^{-2}$ ) within each core sample was determined by summing RSA from all depth intervals within a soil column. We assumed that any roots below the depth of coring did not contribute appreciably to the total RSA. Fine root biomass (woody and absorptive) was determined from root core samples. These samples were oven dried at 60°C for 24 hours and weighed.

### *Biomass and Species Composition*

In the summer of 2015, all trees greater than 2.5cm in diameter within a 10m radius of the center of the macroplot were surveyed for species or genus identification and diameter at breast height (DBH). Aboveground woody biomass was calculated for all trees using an allometric equation (Eq. 1) designed from data on hard maple, oak, hickory, and beech species in temperate forests of the United States (Jenkins et al. 2003).

$$(1) \quad bm = \text{Exp}(-2.0127 + 2.4342\ln\text{DBH})$$

Data collected in 2008 on all trees in the catchment over 20cm in DBH were used to calculate aboveground woody increment (AGWI) for larger trees within macroplots. The difference in biomass between 2015 and 2008 was multiplied by 0.48 to get carbon content and divided by seven to determine total amount of carbon gained in wood annually (Smith, et al. 2016). Because the smaller trees had not been previously surveyed, we could not determine AGWI for trees less than 20cm in diameter.

Coarse root biomass was determined by calculating a ratio (Eq. 2) that was multiplied by aboveground biomass (Jenkins et al. 2003).

$$(2) \quad \text{ratio} = \text{Exp}[-1.6911 + (0.8160/\ln\text{DBH})]$$

Total root biomass was calculated by adding fine root and coarse root biomass. Average percent increase in aboveground biomass was applied to coarse root biomass to estimate annual belowground woody increment (BGWI)

### *Leaf Area Index and Tree Height*

LiDAR data was used to calculate average tree height per macroplot (Brubaker, 2013). Ten random trees were averaged within each macroplot to determine an average tree height. An LAI-2200 leaf area index (LAI) analyzer (LI-COR Biosciences, Lincoln, NE) was used to take monthly measurements of LAI at peak leaf-out between June and September of 2015. Average LAI was estimated for each macroplot from the four monthly measurements.

### *Leaf Litter Production and ANPP*

Two leaf litter traps of 0.152 m<sup>2</sup> area were suspended 0.5 m off the ground were used to estimate litter fall from each macroplot (g m<sup>-2</sup>). Leaves were dried at 60°C for 48 hours then weighed to determine biomass. Litter C content was assumed to be 48% (Bowden et al. 1992). ANPP was calculated by adding AGWI and leaf litter C produced.

### *Absorptive Root Production and BNPP*

Absorptive root turnover estimates were modeled based on tree importance values (IV) using the following equation obtained from the DISTRIB model (Prasad et al. 2006; Iverson et al. 2008)

$$(3) \quad IV(x) = \frac{50 \times BA(x)}{BA(All\ spp)} + \frac{50 \times NS(x)}{NS(All\ spp)}$$

where x is the species, BA(x) is total basal area for a particular species, BA (All spp) is the total basal area for all species, NS (x) is the total number of stems for a given species and NS (All spp) is the total number of stems for all species. The importance value equally weights relative area contributed by a species (basal area of a given species/total basal area of all species) and relative number of trees (number of trees of a given species/number of trees of all species) per macroplot.

Root lifespan estimates (Appendix) were estimated from previous data for dominant trees in each macroplot (McCormack et al. 2014).

Macroplot averages of absorptive root lifespan was determined using IV values of tree species and their associated absorptive root life span. There was not enough previous data on root turnover rates for understory species such as Eastern Hophornbeam (*Ostrya virginiana*), Serviceberry (*Amelanchier sp*), and Witch Hazel (*Hamamelis sp*) so could not directly contribute to lifespan estimates. Average macroplot absorptive root lifespan was adjusted to account for these missing tree species by dividing by the proportion of IV value that contributed to each macroplot by these understory trees (Equation 4).

$$(4) \quad \text{Avg. Root Lifespan} = \text{Proportion IV Covered} \times \sum \left[ \left( \frac{IV^{sp}}{100} \right) \text{Abs. Root Lifespan} (sp) \right]$$

Annual absorptive root biomass production per square meter ( $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) was determined from total macroplot absorptive root biomass and average absorptive root lifespan (Equation 5).

$$(5) \quad \text{Abs. Root Production} = \frac{(\text{Abs. Root Biomass} \times 0.43) \times (365 / \text{Avg. Root Lifespan})}{0.001963 \text{ m}^2}$$

A subset of 50 absorptive root samples were combusted in an elemental analyzer to determine an average carbon content (43%).

Total carbon cycled annually was calculated from absorptive root biomass production estimates and carbon content of fine root biomass. BNPP was calculated by adding BGWI and fine root C turnover.



### *Statistical Analysis*

One-way ANOVA tests were performed to determine differences in the averages for each slope position using JMP Version 12. Simple linear regression was used to test the relationship of the response variable (e.g., BNPP) with elevation for the ridgetop, planar midslope and valley floor using Sigmaplot 13.0 and JMP Version 12. Midslope swales were excluded from this analysis because most data collected such as soil depth, tree height, and soil properties did not show any relationship with elevation. Factors other than elevation were assumed to play a larger role in the midslope swales. randomForest was performed in R to initially look into contributions of belowground factors on root growth patterns, but only depth reduced mean squared error by margins of less of 20% (Liaw & Wiener, 2002). Additionally, geospatial analysis in R revealed no spatial pattern to our data (Diggle & Ribeiro, 2007).

### Results

#### *Resource Availability*

Light availability was estimated using a LAI meter which measures the incident radiation under a canopy relative to incident radiation with no canopy (open sky) to arrive as an estimate for LAI ( $\text{m}^2\text{m}^{-2}$ ). The LAI estimated with the LAI meter is an excellent proxy for light availability where an increase in LAI represents a reduction in light availability. Leaf area index decreased with elevation ( $p < 0.0001$ ) with ridgetop sites having moderately lower LAI ( $P = 0.076$ ) than all other slope positions, suggesting higher light availability with increased elevation (Fig. 3). In addition to having the lowest light level reaching the forest floor, due to the bowl shape of the overall catchment, day length may also be shorter in the valley floor, especially in the winter

months when the sun's zenith point is much lower in the sky. In addition to light availability varying predictably with elevation and slope position, so too did belowground resources.

Soil depth exhibited a strong relationship with elevation. The mean soil depth (cm) in the valley floor was three times that of the ridgetop (Fig 2). Soil physical and chemical properties in the top 20cm of the soil profile, the depth where 70-80% of root length occurred, also varied in relation to elevation and slope position (Fig 2). Rock content ( $\text{g}^{-1}\text{g}^{-1}$ ) increased with elevation with mean ridgetop rock content four times that of the valley floor. Extractable N concentration (ppm) also increased with elevation with the ridgetop soils nearly twice as N-rich as the valley floor and midslope sites. Volumetric water content ( $\text{cm}^3\text{cm}^{-3}$ ), however, decreased with elevation. Mean valley floor soil water content in the top 5cm of soil averaged over the entire 2015 season was approximately 30% greater than ridgetop soil water content (0.34 and 0.24  $\text{cm}^3\text{cm}^{-3}$  respectively). Soil organic matter (%) did not show a significant relationship with elevation ( $P=0.2104$ ); however, sample mean estimates of ridgetop soil organic matter was approximately 25% greater than corresponding estimates at all other slope positions (10% versus approximately 7.5%).

Despite higher extractable nitrogen concentration at higher elevations in the catchment, tree growth rates (AGWI) decreased with elevation ( $p=0.0027$ ), which could be evidence of resource limitation.

#### *Aboveground Growth Patterns*

Tree height (m), LAI ( $\text{m}^2\text{m}^{-2}$ ), leaf litter production ( $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) and ANPP ( $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) all decreased with elevation (Fig 3). However, aboveground biomass, estimated using allometric equations, was not correlated with elevation. Tree height in the valley floor was approximately

30% taller than tree height on the ridgetop. LAI was 20% higher in the valley floor compared to the ridgetop. However, aboveground biomass, leaf litter production and ANPP were roughly similar at all slope positions.

### *Belowground Growth Patterns*

Within the top 20 cm of soil (Appendix A2), where roots were most abundant, absorptive root length density ( $\text{cm}^3\text{cm}^{-3}$ ) varied widely across the catchment both within and between macroplots. Neither slope positions nor elevation significantly affected root length density and geospatial analysis determined there was no spatial structure to the data (Fig 4). In fact, measurements taken 1m apart varied as much as measurements taken between slope positions. Additionally, absorptive RSA ( $\text{m}^2/\text{m}^2$ ), belowground biomass ( $\text{kg m}^{-2}$ ), simulated absorptive root production ( $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) and BNPP ( $\text{gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) did not correlate with elevation. However, absorptive RSA tended to be approximately 29% lower on the ridgetop and planar midslope compared to the swales and valley floor ( $P=0.098$ ). Simulated absorptive root production was also tended to be 20-30% lower on the planar midslope than all other slope positions ( $P=0.078$ ).

### *Partitioning Ratios*

Partitioning ratios of absorptive RSA with LAI, simulated absorptive root production with leaf litter production and BNPP with ANPP were not affected by either elevation or slope position (Fig 5;  $P=0.22$ ).

## Discussion

While many soil properties and aboveground growth patterns varied predictably with elevation and showed differences among slope positions, root growth and belowground partitioning patterns did not show any relationship with elevation and only moderate differences

among slope positions. Belowground resource availability was somewhat contradictory. While both soil water content and soil depth decreased with elevation, extractable soil nitrogen concentration increased with elevation. Despite having the shallowest, driest and rockiest soils, the ridgetop also had the most N-rich soils and tended to have the highest level of organic matter. These mixed signals in belowground resources may complicate clear relationships between belowground partitioning and resource availability.

Aboveground growth including tree height, litter production and ANPP decreased with elevation while belowground growth showed wide variation at a one-to-two meter scale and no relationship with elevation. However, mean absorptive RSA per unit ground area and simulated absorptive root production tended to be lower on the planar midslope and ridgetop than the valley floor and midslope swales. While midslope planar and swale sites had similar aboveground growth patterns, root growth measurements tended to be higher in swales compared to the planar midslope.

These results support the use of a fixed ratio between aboveground and belowground carbon partitioning. However, due to wide variation in root growth and distribution patterns, regression analysis of above- to belowground measures may not prove to be significant.

Our results suggest that optimal allocation may come into play more aboveground than belowground. LAI exhibited a stronger relationship with slope position and elevation than leaf litter production, which suggests that absolute allocation towards leaves did not correlate strongly with increased light competition. Fractional allocation between root and leaf surface area and production also was not significantly different between the ridgetop and valley floor positions. However, similar to LAI, tree height exhibited a strong relationship with elevation and slope position. Our data agrees with other studies that predict an allocation shift toward stem

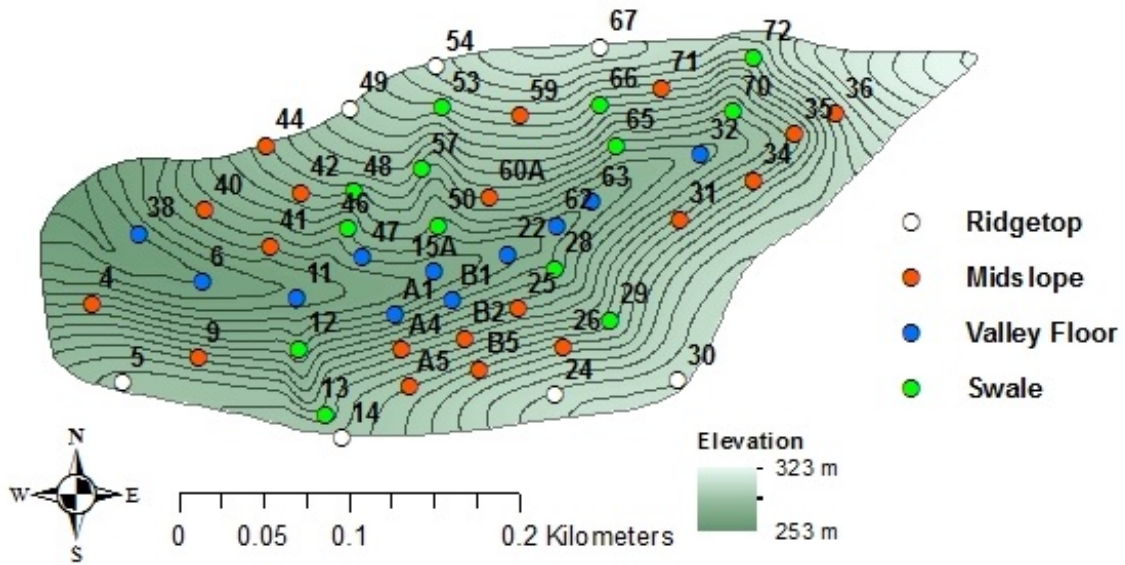
rather than leaf biomass in a closed canopy (Dybzinski et al. 2011). On the ridgetops and higher elevations of the midslope, the canopy becomes more open, which reduces the cost of allocating carbon to leaves because self-shading is less important. This suggests that areas on the midslope may benefit more from allocating carbon to leaves than lower elevation sites like the valley floor and swales, which could be a possible explanation for the common pattern of lower below to aboveground partitioning patterns on the planar midslope.

Optimal allocation was not supported belowground. While there was no clear relationship between slope position and total root biomass or absorptive RLD, RSA and estimated root production was lowest on the planar midslope and ridgetop, where nitrogen levels were highest. This may have been a function of soil depth. RSA correlated significantly with soil depth ( $P < 0.0001$ )

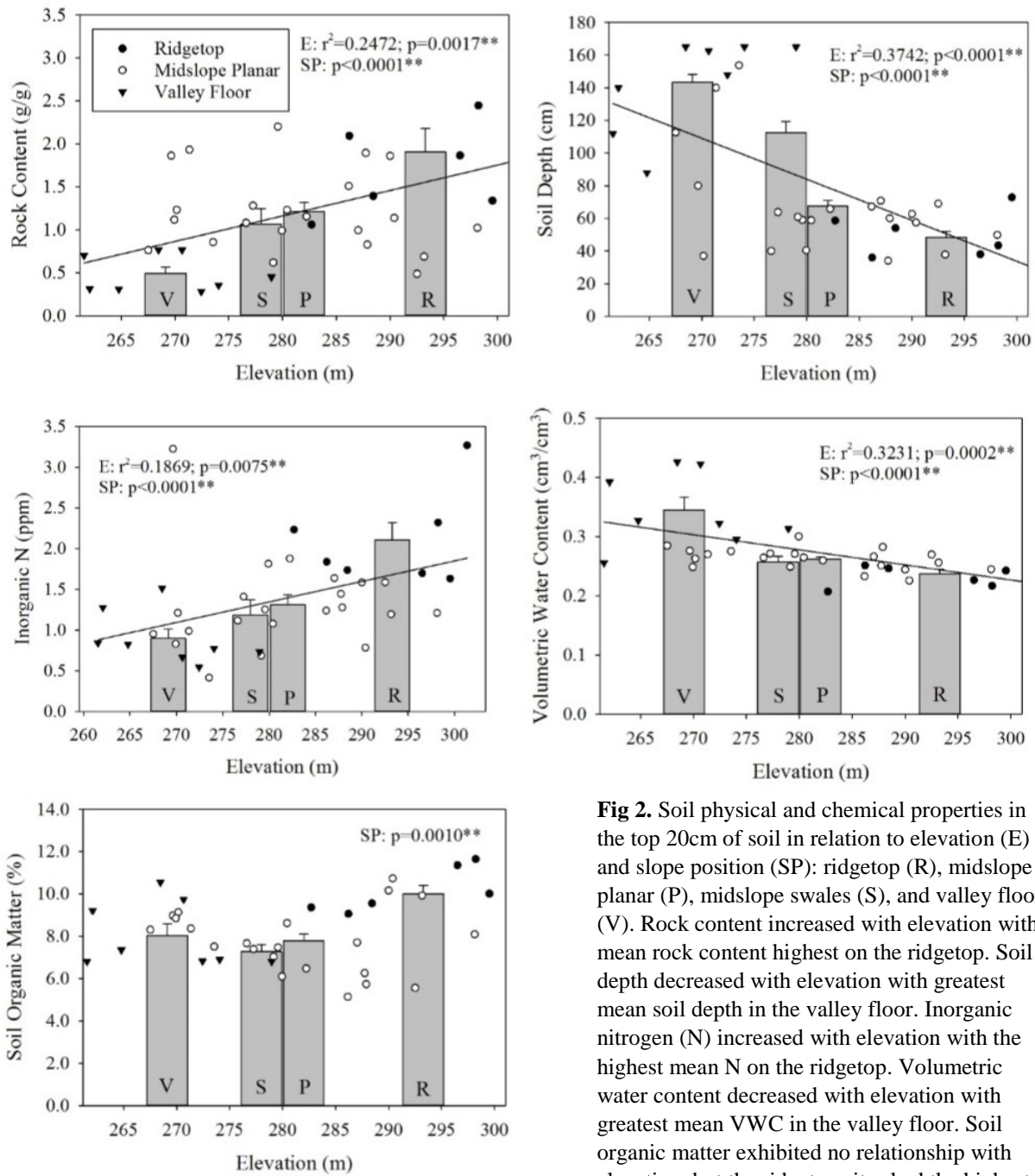
### Conclusions

In conclusion, our results suggest that aboveground resource availability and growth follow a more clear topographic pattern than belowground resource availability and growth. Trees at lower elevation sites experience greater light limitation and may allocate more carbon to stemwood to increase tree height. While there are many belowground factors that could potentially influence root growth, including all of these factors in carbon models of temperate forests may not be necessary. Mixed resource signals and high spatial variation may muddle clearly defined patterns exhibited in laboratory experiments. A fixed proportion of above- to belowground allocation may be the best approach. A model that incorporates decreasing soil depth as limiting root growth and decreasing light availability as limiting leaf growth and increasing stem growth may be an appropriate model for determining above- and belowground partitioning in a topographically diverse, temperate forest.

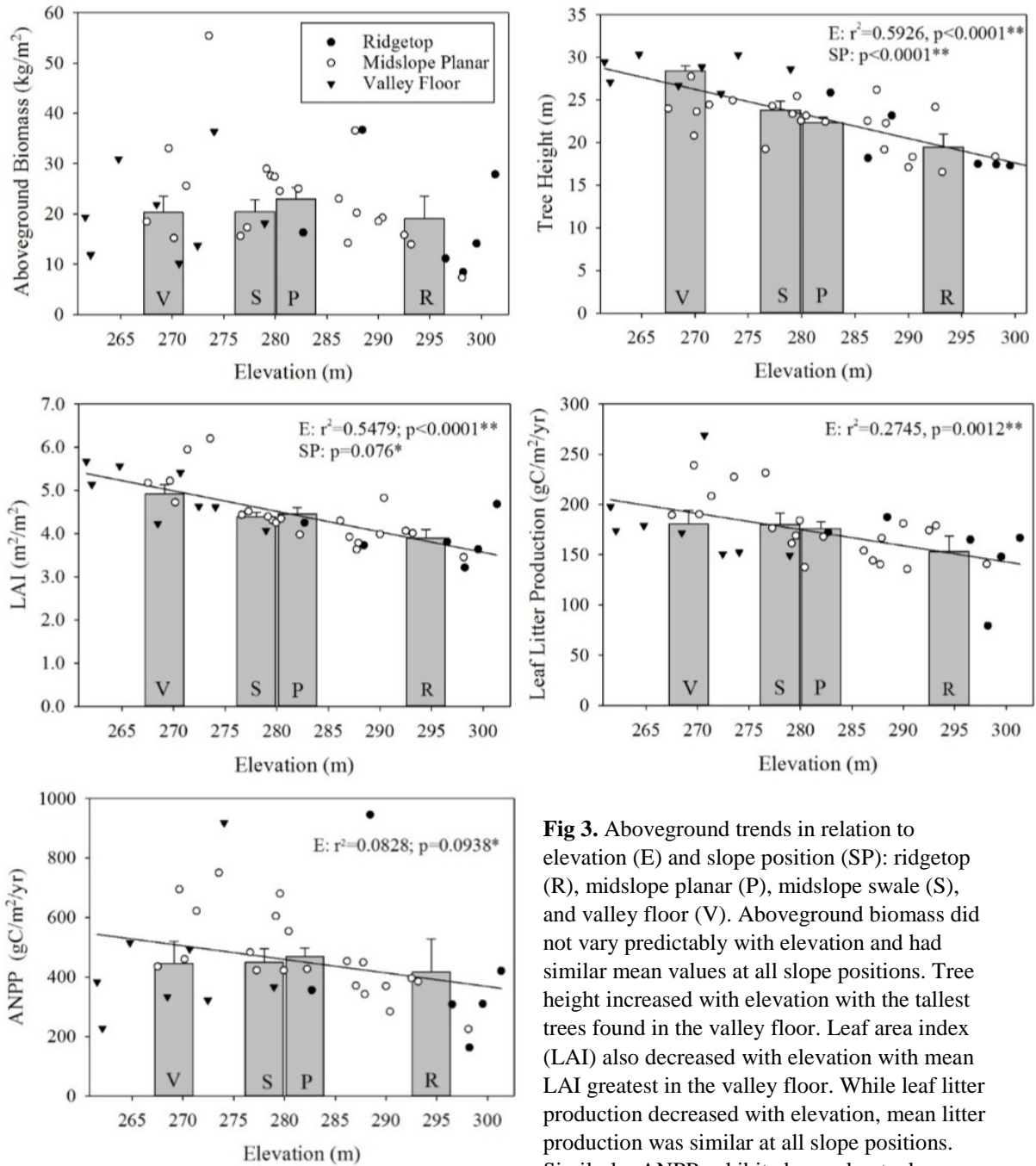
Figures



**Fig. 1** Topographic site map of the SSHCZO. 50 macroplots were sampled throughout the catchment to encompass all slope positions (ridgetop, midslope planar (midslope), midslope swale (swale), and valley floor).

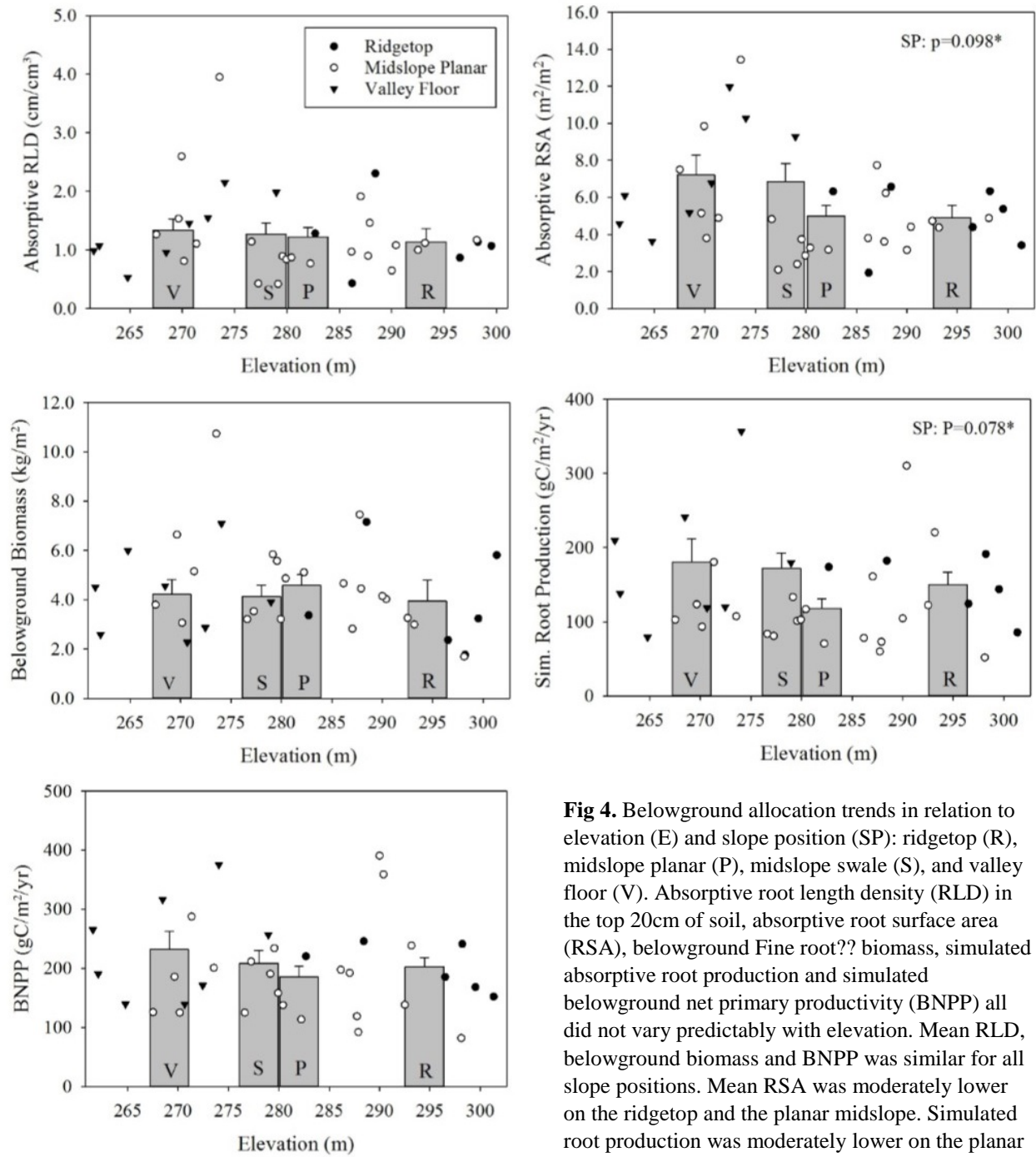


**Fig 2.** Soil physical and chemical properties in the top 20cm of soil in relation to elevation (E) and slope position (SP): ridgetop (R), midslope planar (P), midslope swales (S), and valley floor (V). Rock content increased with elevation with mean rock content highest on the ridgetop. Soil depth decreased with elevation with greatest mean soil depth in the valley floor. Inorganic nitrogen (N) increased with elevation with the highest mean N on the ridgetop. Volumetric water content decreased with elevation with greatest mean VWC in the valley floor. Soil organic matter exhibited no relationship with elevation, but the ridgetop sites had the highest mean soil organic matter content.

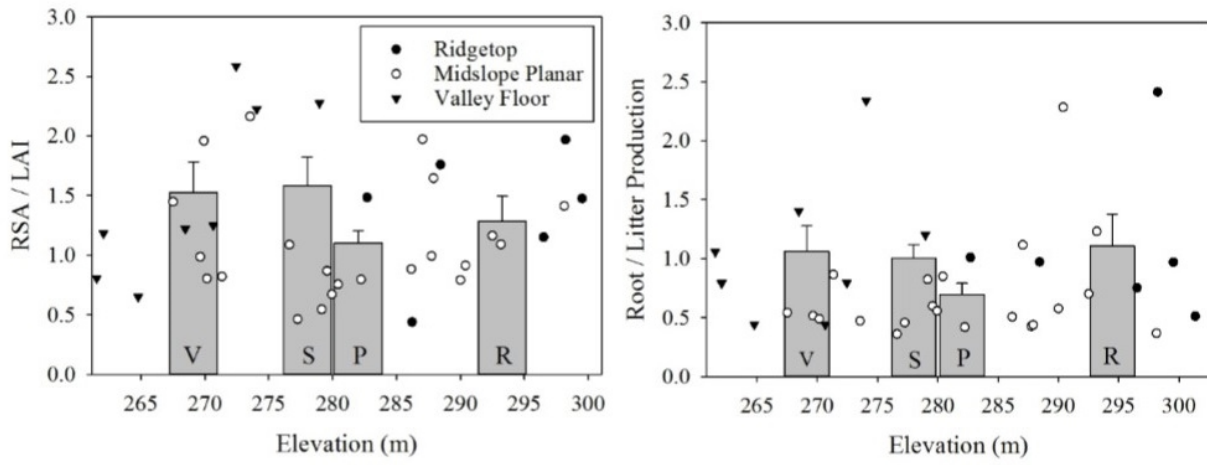


**Fig 3.** Aboveground trends in relation to elevation (E) and slope position (SP): ridgetop (R), midslope planar (P), midslope swale (S), and valley floor (V). Aboveground biomass did not vary predictably with elevation and had similar mean values at all slope positions. Tree height increased with elevation with the tallest trees found in the valley floor. Leaf area index (LAI) also decreased with elevation with mean LAI greatest in the valley floor. While leaf litter production decreased with elevation, mean litter production was similar at all slope positions. Similarly, ANPP exhibited a moderate decrease with elevation but had similar mean values at all





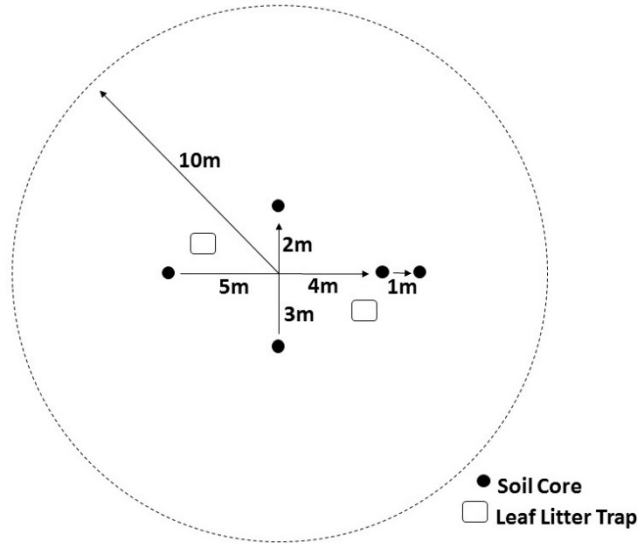
**Fig 4.** Belowground allocation trends in relation to elevation (E) and slope position (SP): ridgetop (R), midslope planar (P), midslope swale (S), and valley floor (V). Absorptive root length density (RLD) in the top 20cm of soil, absorptive root surface area (RSA), belowground Fine root?? biomass, simulated absorptive root production and simulated belowground net primary productivity (BNPP) all did not vary predictably with elevation. Mean RLD, belowground biomass and BNPP was similar for all slope positions. Mean RSA was moderately lower on the ridgetop and the planar midslope. Simulated root production was moderately lower on the planar midslope.



**Fig 5.** Partitioning trends in relation to elevation (E) and slope position (SP): ridgetop (R), midslope planar (P), midslope swale (S), and valley floor (V). Partitioning ratios between absorptive root surface area (RSA) and leaf area index (LAI) and simulated root production and leaf litter production showed no relationship with elevation or slope position.

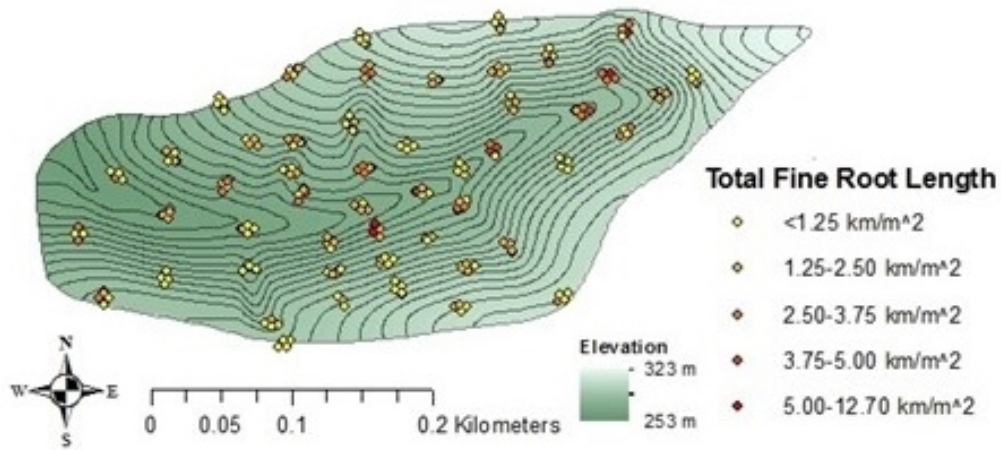
## Appendix A

**Fig A1.** Macroplot sampling was designed to maximize variation in distance between five soil core samples. Two leaf litter traps were placed randomly in the plots within 1m of a soil core. Tree surveys were conducted within a 10m radius of the center of the plot.



**Table A1:** Dominant tree species found at the Shale Hills CZO with corresponding absorptive root lifespans (days)

Tree Genus and/or Species	Absorptive Root Lifespan (days)
<b>Red Maple (<i>Acer rubrum</i>)</b>	259
<b>Sugar Maple (<i>Acer saccharum</i>)</b>	324
<b>Eastern Hemlock (<i>Tsuga canadensis</i>)</b>	400
<b>Hickory (<i>Carya sp</i>)</b>	247
<b>Red or Black Oak (<i>Quercus rubra or velutina</i>)</b>	235
<b>White Oak (<i>Quercus alba</i>)</b>	336
<b>Chestnut Oak (<i>Quercus prinus</i>)</b>	336
<b>White Pine (<i>Pinus strobus</i>)</b>	296
<b>Virginia Pine (<i>Pinus virginiana</i>)</b>	283
<b>Ash (<i>Fraxinus sp</i>)</b>	330
<b>American Basswood (<i>Tilia americana</i>)</b>	230
<b>American Beech (<i>Fagus grandifolia</i>)</b>	200
<b>Tulip Poplar (<i>Liriodendron tulipifera</i>)</b>	323



**Fig A2.** Spatial distribution of total fine root length ( $\text{km/m}^2$ ) for all soil cores taken within each macroplot (5/macroplot) across the catchment. Soil cores were taken to a maximum depth of 165 cm. Each soil core was divided into depth increments of 0-20 cm, 20-40 cm, 40-80 cm, 80-120 cm, 120-165 cm or unless mechanical obstruction prevented reaching full coring depth. Total fine root length from each coring increment was summed to get a total fine root length per ground area for each core. If mechanical obstructions prevented deep coring, we assumed roots present past that depth would not contribute substantially to total root length.

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