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ABOVEGROUND CARBON DISTRIBUTION ACROSS A TEMPERATE WATERSHED

A Thesis in

Ecology

by

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Abstract:

Aboveground net primary productivity varies across topographic position (which affects microclimate and plant species distribution) and in a watershed could be inaccurately quantified if data are limited by inadequate sampling of topographic position. My objective was to create a spatially explicit aboveground C budget in a small forested temperate watershed using C stored in trees and leaf litter C flux. The average ANPP at the watershed was 550 gC m⁻² yr⁻¹; however, interpolated maps suggest that the ANPP could vary from 223 to 3410 gC m⁻² yr⁻¹ across the watershed. The hypothesis was that the spatial variability in aboveground C could be explained by tree genera and topographic characteristics such as aspect, elevation, and slope angle. Trees on the south aspect stored more average gC m^{-2} yr⁻¹ than trees on the north, and more average gC m⁻² was stored in aboveground biomass on planar surfaces than plots located in swales. Leaf litter C flux (gC m⁻² yr⁻¹) was not correlated with any topographical feature due to the immense variation of litter contribution across the watershed. In addition, the common method of using elevated litter traps to predict C donated to the soil from leaf litter at the trap location was assessed by comparing collected leaf litter C of the elevated litter traps to C accumulated in litter in surrounding floor plots. The elevated traps collected 40 percent more litter than the forest floor; overestimating C donated to the soil. Future studies should incorporate spatially explicit C budgets and consider using floor plots in addition to elevated litter traps to determine accurate C distribution.

Key Words: Aboveground net primary production, aboveground carbon budget, carbon distribution, temperate watershed, aboveground biomass, litterfall

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Introduction

While many field studies have measured components of an aboveground carbon budget (Andrews and Schlesinger 2001, Savage and Davidson 2001, Davidson et al 2002, Ehman et al 2002), very few have looked at the spatial variability of carbon (C) and productivity across a temperate watershed. Most studied watersheds are represented by an average aboveground net primary productivity (ANPP) value; however, this value does not convey the potential variability across a dynamic landscape. Local environment, soils, and plant species drive productivity and even at the small watershed scale, microenvironment can significantly affect the magnitude and distribution of productivity (Houghton 2005, Sharma et al 2011). The objective of this research was to provide a spatially explicit aboveground C budget that would quantify spatial variation of productivity across a small temperate, forested watershed. As we still understand very little of the ecosystem-level production in temperate watersheds (Clark et al 2001), a spatially explicit aboveground C budget could provide helpful insight on how multiple ecosystem processes and topography affect productivity.

One method of creating an aboveground watershed C budget is to measure the leaf litter C flux and the vegetative C pool. While using litter traps to predict the total amount of leaf litter is added to the watershed is beneficial, some spatial studies use the litter collected in elevated traps as a proxy to determine what C is being donated directly to the soil underneath the trap; however, this assumes that the litter will not move once it drops to the ground. On a perfectly level surface with no wind or water, this may be the case, but in a small watershed with varying slope angles, high winds and rain, it is unlikely (Orndorff and Lang 1981, Lee et al 1999). Thus, a secondary objective of this research was to quantify the error in assuming that C collected from elevated litter traps will be incorporated into the soil at the trap location. Providing an error

prediction when using elevated litter traps to determine leaf litter C distribution could change the current methodology many researchers use to quantify leaf litter C.

To build an above ground C budget and estimate ANPP, C stored in trees ($gC m^{-2} yr^{-1}$) and leaf litter C flux (gC m⁻² yr⁻¹) were measured in a small oak-dominated temperate watershed located in Pennsylvania. In Chapter 1 the measurements of C stored in trees and leaf litter C flux are used to create a spatially explicit aboveground C budget and a watershed-scale estimate of aboveground net primary productivity. Chapter 2 quantifies the amount of error in collecting leaf litter from elevated traps as a proxy to predict the amount of C incorporated into the soil at that specific trap location by comparing litter collected in elevated traps and litter accumulated in adjacent forest floor plots. This watershed study was conducted in a second growth forest that is common throughout most of the mid-Atlantic and northeast United States. The forest history is representative of much of the northeast United States and measurements from this study can be generalized to other landscapes within the area. Future aboveground C research will find using a spatially explicit aboveground C budget useful in providing insight into how multiple ecosystem processes contribute to watershed productivity and should consider using forest floor plots, in addition to elevated litter traps, to predict spatial distribution of litter contributed into the soil to minimize error.

Chapter 1: Aboveground Carbon Distribution across a Temperate Watershed

Introduction:

Despite the many studies that have documented field measurements across many plots, the current understanding of ecosystem-level production in temperate forests remains limited (Clark et al 2001, Goodale et al 2002). Societies in the Northern Hemisphere may need temperate forests to sequester and offset more carbon (C) as the concentration of carbon dioxide in the atmosphere increases with climate change. It is estimated that forests in North America sequester 60% of the terrestrial C in the Northern Hemisphere, the United States being responsible for the majority (Gurney et al 2002, Woodbury et al 2007). Currently most forests in the United States are recovering from severe harvesting and land use change; and as forests age, more C can be stored in the vegetation. Northeast North America has the largest C gain and sink of 31 Tg yr⁻¹; which is expected to increase until 2040, (Birdsey et al 1993, Turner et al 1995, Smithwick et al 2002). However, this rapid C sink will not continue indefinitely (Schimel et al 2001). Although the Kyoto Protocol was not signed by the US government, voluntary cap-andtrade systems allow C emissions to be offset through forest initiatives (Fahey et al 2010). For offset projects there is potential to protect forested areas based on their C storage and identify where there may be some leniency in harvesting to fill wood product demands (Fahey et al 2010).

Forest ecosystems play a major role in the C cycle. They directly interact with the atmosphere while taking up CO₂ during photosynthesis, store C in wood production, and donate C through litter and root decomposition to the soil, contributing to soil formation (Ryan et al 2010). Thus, my research determines aboveground temperate forest C pools and rates; such as C

stored in the trees, leaf litter C flux, and aboveground net primary productivity (ANPP) to help understand potential future C storage in temperate forests.

On a smaller scale, a difference in local environment and soils across a landscape can drive forest species composition and carbon dynamics through shifts in temperature and water regimes. Across a landscape topography and tree species composition play large roles in determining C stocks and fluxes. Current studies do not consider where on the landscape and at what rates C is stored in vegetation and donated by leaf litter, failing to capture the true spatial and temporal variability of C stocks and flux (Powell et al 2010). The objective of this study was to provide spatially explicit predictions of C stored in trees, leaf litter C flux, and ANPP, which will improve the current understanding of aboveground C distribution in temperate forest watersheds.

Forest ANPP cannot be directly measured and must be estimated by using indirect methods (Clark et al 2001). Currently, most studied watersheds are represented by an average ANPP value predicted from on-the-ground measurements. While this value is ideal to compare ANPP across watersheds or ecosystems, it does not convey the heterogeneity of primary production within a watershed. Variability even at fine spatial scales is important when calculating total forest productivity because it may be as great between adjacent hectares as it is over thousands of kilometers (Houghton 2005). Adding spatial context to ANPP will be useful to expand current knowledge of C distribution across temperate watersheds and will also be valuable when calculating change in C sinks and fluxes over time (Houghton 2005).

ANPP has had several different definitions in many different studies (Clark et al 2001, Lovett et al 2006, Woodbury et al 2007). For this particular study I defined ANPP as the amount of organic matter that was produced in the trees and lost in leaf litter during a given time interval.

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An advantage of using this definition is that ANPP can be calculated by adding the amount of C stored annually by trees and carbon donated by leaf litter in a watershed. Both components, C stored and C flux, comprise an aboveground C budget and while time consuming, are relatively inexpensive to collect (Houghton 2005).

Spatial variability of an aboveground carbon budget and ANPP can be influenced by topographic factors such as aspect, elevation, and slope angle. In all forest types of the Northern Hemisphere, northern aspects have higher tree biomass (Sharma et al 2011). The south (or equatorial) aspect is warmer and drier due to longer sun exposure during the day and the north-facing aspect is cooler and wetter because it receives less sun exposure. The increased moisture and cooler temperature creates a favorable environment for most temperate tree species. In this study it was predicted that higher productivity would be found on the north aspect and lower elevations due to higher tree biomass on the north aspect and litter moving downslope with gravity to lower elevations.

Tree species composition is commonly different between north and south aspects and as elevation increases due to different microenvironments. As the climate changes, species compositions may change as tree species expand their ranges to higher latitudes and altitudes (Iverson and Prasad 1998). There have been many studies on how plant composition can affect carbon storage; however, most of these studies are performed in the tropics or grasslands (Wedin and Tilman 1996, Tilman et al. 2001, Kirby and Potvin 2007). Studying how species can affect carbon storage in the northeastern United States can provide more insight into the relationship between species and productivity (Turner, 1995). Trees grow at different rates inter-specifically between species and intra-specifically depending on topographic location and microenvironment, storing a range of C. Using a small watershed approach to study interspecific and intraspecific tree growth rates across a landscape is advantageous before scaling up to a regional carbon budget.

The Susquehanna Shale Hills Critical Zone Observatory (SSHCZO) was used as a study site to examine C distribution across a small, temperate watershed. The SSHCZO is located in Huntingdon County, Pennsylvania and is a small forested catchment of shale bedrock (Naithani et al 2013). It is an ideal study site because it has been extensively mapped and surveyed since the early 1950s, making it possible to perform in-depth spatial and temporal analyses. The oak-dominated second growth forest at the SSHCZO is a common forest type found throughout most of the mid-Atlantic and northeast United States. The primary purpose of the SSHCZO is to research the formation of Earth's critical zone layer (aboveground vegetation to the bedrock) over different time scales and observe how the multiple layers within the zone interact (Shale Hills CZO, 2013). While humans rely on the critical zone for many natural resources including food and clean water, very little is documented about how the layers of critical zone interact (Shale Hills CZO, 2013). The spatial distribution of C across the watershed can provide insight on other ecosystem functions including nutrient cycles, leaf area index, soil formation, net ecosystem productivity, as many of these functions are interrelated (Gower et al 1997).

While many C budgets and ANPP values have been calculated in temperate watersheds, very few have had the opportunity to use an area that is extensively mapped and surveyed. Defining the effects of local environments on C sequestration is pivotal in determining how long term climate changes will affect forest carbon storage (Simmons, 1996). My objective was to add spatial context to improve current C budgets and provide detailed data of C distribution across a small temperate watershed. The main research question was what aboveground factors contribute to areas of high C storage in trees and leaf litter C flux? It was hypothesized that high

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C storage and C flux would be found on the north aspect, lower elevations, and planar surfaces with less inclination; as less C should be stored at higher elevations due to decreased water availability and species composition because pines that grow slower occupy high, dry, elevations at the SSHCZO and litter moves downslope with gravity and settles on flat surfaces. More C should be stored in vegetation on planar surfaces because the water that runs down through the swales could create a difficult environment for vegetation to establish. To estimate the C stored in the trees, the radial growth of over 2000 trees was measured and allometric equations were used to estimate annual wood production. To estimate total biomass, including trees in the understory, vegetation in 35 biomass plots was measured. To estimate leaf litter C flux, litter was collected from 35 litter traps over a two year period. The C stored annually in the trees and leaf litter C flux were analyzed spatially across the watershed to create a spatially explicit aboveground C budget.

Materials and Methods:

Study Site:

The Susquehanna Shale Hills Critical Zone Observatory (SSHCZO) is located in Huntingdon County, Pennsylvania and is an 8 hectare, 110+ year old humid temperate forested catchment on shale bedrock. The watershed has a north- and south-facing aspect, with an elevation change of 60 meters from the lowest point to the highest point (240-300 meters above sea level) and several swales. The site is primarily oak dominated, with maple and hickory on the south aspect, hemlock at lower elevations, and pine found at upper elevations. There are 23 documented tree species with dominant species including oaks (*Quercus prinus* L. syn., *Q. rubra* L., *Q. alba* L., *Q. velutina* Lam.), maples (*Acer saccharum* Marsh., *A. rubrum* L.), hickories (*Carya tomentosa* (L.) Nutt., *C. glabra* (P. Mill.) Sweet, *C. ovata* (P. Mill.) K. Koch, *C. cordiformis* (Wangenh.) K. Koch), Eastern hemlock (*Tsuga canadensis* (L.) Carr.), and pines (*Pinus virginiana* P. Mill., *P. strobus* L.). The mean annual temperature is 11°C and the annual precipitation is 900 mm (Naithani et al 2013).

Data Collection:

To create a spatially explicit carbon budget and calculate ANPP at the SSHCZO leaf litter C flux and C stored annually in trees were measured. Leaf litter C flux was estimated from trap collections. Carbon stored annually in trees was estimated by change in radial growth and general allometric equations that estimate tree biomass based on diameter. By adding leaf litter C flux and C stored annually in the trees, ANPP was predicted for the watershed. To estimate the leaf litter C flux 35 litter traps were assembled out of plastic tubs (0.1518 m^2 area, 33 cm width x 46 cm length x 12 cm depth) with holes drilled in the bottom to allow water drainage. A suspended net was used to catch and hold the litter above the base to dry, as well as plastic rods for legs to keep the trap off of the forest floor at 0.5 meters (Fig. 1.1).



Figure 1.1. A sample litter trap from the Susquehanna Shale Hills Critical Zone Observatory. The traps were made using a plastic tub (0.1518 m^2 area, $33 \times 46 \times 12 \text{ cm}$), suspended net, and plastic rods to stabilize the trap 0.5 meters off of the ground.

The traps were placed on six transects that covered both the north and south facing slopes,

spanned an elevation gradient of 60 meters and alternated between planar slopes and swales (Fig.

1.2).



Figure 1.2. The locations of the 35 litter traps at the Susquehanna Shale Hills Critical Zone Observatory. The traps differ in elevation, aspect, and in the swales or planar slopes.

Litter was collected once a week from August 31st to November 28th, 2011 and September 4th to November 12th, 2012. Litter was collected from each trap and dried in a Binder Drying Oven at 57°C for a minimum of 24 hours. Foliage from each trap was then separated by tree species and mass determined. Leaf biomass was converted into g C m⁻² using 48% C content for all species, as was used in other studies (Bowden et al, 1992) and the area of the traps. An average watershed value of litterfall C flux per m² was calculated for 2011 and 2012 by averaging the gC m⁻² collected at each trap. An average value was then used to represent the leaf litter C flux at the site by averaging the 2011 and 2012 values.

Radial growth for ANPP estimates were measured with dendrobands that were constructed using 1 cm wide metal strips. Each dendroband had two punched holes to fit a metal spring that tightly fastened the band to the tree at breast height. A small loop of metal was fit around the dendroband and the band was scored next to the metal loop with a sharp object. As the tree grew, repeated diameter measurements were taken every two weeks and the radial growth was quantified by measuring the distance between the metal loop and score mark (Fig. 1.3).



Figure 1.3. A dendroband constructed at the Susquehanna Shale Hills Critical Zone Observatory. Constructed out of a metal band, metal spring, and metal loop to measure radial growth.

One hundred and ten trees of nine different species (A. Saccharum, C. glabra, C. tomentosa, P. virginiana, Q. alba, Q. prinus, Q. rubra, T. canadensis, P. strobus) were fitted with dendrobands in Winter 2012. Radial growth was measured May 9th to October 14th 2012 bimonthly. Subtracting the initial diameter-at-breast-height (dbh) measurement from the final dbh estimated annual radial growth. To estimate a watershed value of C stored annually for the SSHCZO 1,968 trees were used in addition to the trees with dendrobands, totaling 2,078 trees. In 2008 a tree survey was conducted of all trees with dbh larger than 8 inches (20.32 cm). All trees were mapped, identified by species, dbh measured, and given a unique identification tag. In 2012, each tree's dbh was re-measured. To estimate the annual change in biomass per tree, generalized allometric equations of ten tree genera groups were used that were developed from species-specific allometric equations (Jenkins et al 2004, Jenkins et al 2003). Total aboveground biomass was calculated for each tree by using the final and initial dbh. By subtracting the initial aboveground biomass in 2008 from the final aboveground biomass in 2012 the total biomass accumulated over the interval was estimated. For the trees without dendrobands, the total biomass accumulated was divided by four years (2008 to 2012) to estimate an average annual biomass accumulation. Trees with dendrobands did not have an average annual biomass accumulation because they were measured over one year (2012). Foliage for each tree was calculated using the initial and final dbh and allometric equations of biomass components for broad hardwood and softwood species from the Comprehensive Database of Diameter-based Biomass Regression for North American Tree species (Jenkins et al 2004). Change in foliage was subtracted from the total annual accumulated biomass to estimate total woody biomass

accumulated in each tree. Then using 48% C content of woody biomass the total amount of C stored annually by each tree was estimated. The watershed value in gC m⁻² yr⁻¹ stored at the watershed was predicted by adding all of the trees gC yr⁻¹ and dividing by the watershed area (85,318 m²). By adding the watershed values of gC m⁻² yr⁻¹ stored in trees and gC m⁻² yr⁻¹ leaf litter flux an ANPP value gC m⁻² yr⁻¹ was calculated for the watershed. Total stand biomass (gC m⁻²) was calculated by summing all of the trees final biomass in gC without foliage and then dividing by the watershed area.

To estimate unaccounted C stored in vegetation at the SSHCZO due to only using tree survey measurements, ten meter radius standing-biomass plots were made around each of the 35 litter traps. All vegetation with dbh greater than three centimeters was identified by species and had its dbh measured. Using the Jenkins et al. generalized allometric equations total aboveground biomass and gC stem⁻¹ was calculated using the methods mentioned above. For each plot the gC for each tree was summed and then divided by the plot area (314.159 m²) to get gC m⁻² for each plot. The total biomass in each plot was compared to the total biomass of the trees from the tree survey that were located in each plot. Because vegetation in the biomass plots was measured once there is no temporal component and the growth over time was not predicted, the units are in gC m⁻², compared to the tree survey that had repeated measurements with units of gC m⁻² yr⁻¹.

Spatial Modeling:

To display C spatial variability across the SSHCZO estimates of C stored annually in the trees and leaf litter C flux were used to make interpolated maps using ESRI ArcMap Desktop 10.1 geostatistical analyst (ESRI, 2012). To produce an interpolation of the C stored annually in

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the trees, all of the trees measured for radial growth (n = 2078 trees) were used. Each tree had a value of C stored annually in gC yr⁻¹ that was calculated by the general allometric equations. To normalize the data, all tree values (gC yr⁻¹) were log-transformed and then interpolated. Ordinary kriging from the geostatistical analyst was found to be the best interpolation method by using a cross-validation comparison. To convert gC yr⁻¹ to gC m⁻² yr⁻¹, the interpolated raster was exported to a filled contour (polygon) vector layer. Each filled contour polygon represented a gC yr⁻¹ interpolation value based on the previous interpolated raster layer. By selecting all of the trees located in each polygon and summing the gC yr⁻¹ stored in each tree then dividing by the polygon area, the average gC m⁻² yr⁻¹ stored was calculated for each polygon. The vector layer was then edited and each polygon interpolation value was changed to the average gC m⁻² yr⁻¹ storage value and converted into a final raster layer.

To produce an interpolation showing the spatial variability of the leaf litter C flux, the average gC m⁻² yr⁻¹ leaf litter flux at each of the 35 litter trap points was used. To normalize the litter data, the data was first log-transformed and then interpolated. Ordinary kriging was found to be the best interpolation method by using a cross-validation comparison. The interpolation was then exported to a final raster layer. The two final raster layers of the C stored annually in wood and the leaf litter C flux were added using the raster calculator tool with the same environment and a cell size of 1.04 to make an interpolated ANPP raster layer.

Statistical Analysis:

To model the influence of topography and tree genera on aboveground biomass and ANPP, elevation, slope angle, aspect, and the presence of swales were compared with linear regressions and one sample t-tests. All statistical analyses were conducted in Minitab with alpha 0.5 (Minitab 16 Statistical Software 2010). Linear regressions and regression lines were used to fit C stored in vegetation of the biomass plots and leaf litter C flux on each aspect over elevation and slope angle. A one sample t-test was used to compare C stored in vegetation of the biomass plots, C stored in the trees from the tree survey, and leaf litter C flux between aspects and the presence of swales. To compare the difference between leaf litter C flux in 2011 and 2012 a one sample t-test was used.

Results:

The standing biomass of the trees was 7900 gC m⁻² and the average annual C stored at the SSHCZO watershed was 230 gC m⁻² yr⁻¹. To provide a spatially explicit map of the C stored in the watershed a cross-validation comparison was used. Ordinary kriging, was found to be the best interpolation method for the data, as the model had the best unbiased predictions (mean = 0.006), accurate standard errors (root-mean-square standardized = 0.800), small root-mean-square and average standard error values (1.09 and 1.37, respectively), and the predictions did not deviate significantly from the measured values (Fig. 1.4a). These data are also illustrated in a map with each individual tree (Fig. 1.4b). The interpolated map showed values of C stored annually in the trees ranging from 16.5 to 3192.2 gC m⁻² yr⁻¹ with only 0.17% of the watershed storing C over 750 gC m⁻² yr⁻¹ (Fig. 1.4a and Fig. 1.5). Red areas have higher gC m⁻² yr⁻¹ and are located below a few hemlocks and oaks that are storing large amounts of carbon annually, areas with lower gC m⁻² yr⁻¹ are blue and have very few trees in the area (Fig. 1.4b).



Figure 1.4a. Aboveground C stored annually at the Susquehanna Shale Hills Critical Zone Observatory in woody biomass from the tree survey. The interpolated map uses the annual C

stored in gC m^{-2} yr⁻¹ from each tree, estimated by the change in DBH from 2008 to 2012. All of the 2078 trees from the tree survey had DBH greater that 20 cm.



Figure 1.4b. Aboveground C stored annually in tree biomass from the tree survey at the Susquehanna Shale Hills Critical Zone Observatory with each data point representing annual biomass accumulation (gC yr⁻¹) of a tree, separated into common genera of hemlock, hickory, maple, oak, pine, and other trees. The size of the data point is scaled to the amount of C stored by each tree annually in gC yr⁻¹. The bottom layer is an interpolated map of aboveground C stored annually in wood from the tree survey. The interpolated map uses the annual C stored in gC m⁻² from each tree, estimated by the change in DBH from 2008 to 2012. All of the 2078 trees from the tree survey had DBH greater that 20 cm.



Figure 1.5. The percent area of the watershed (8.5 hectares²) of the C stored annually in gC m⁻² yr⁻¹ at the SSHCZO. The average annual C stored at the SSHCZO was 230 gC m⁻² yr⁻¹. Not shown in this figure, 0.17% of the annual C stored fell between 3000 to 3250 gC m⁻² yr⁻¹

The average leaf litter C flux at the watershed was 220 gC m⁻² yr⁻¹. A cross-validation comparison showed that the best interpolation method for C donated was ordinary kriging (Fig. 1.6). The model had the best unbiased predictions (mean = 0.004), accurate standard error values (root-mean-square standardized = 0.982), small root-mean-square and average standard error values (0.088 and 0.090, respectively), and the predictions did not deviate from the measured values. The interpolated map had a range of 159 to 275 gC m⁻² yr⁻¹ leaf litter C flux across the watershed with a hotspot in the watershed donating 250 to 275 gC m⁻² yr⁻¹ on the southeast aspect around one trap that donated 288 to 383 gC m⁻² yr⁻¹ (Fig. 1.7 and Fig. 1.8).



Figure 1.6. An interpolated map of leaf litter C flux at the SSHCZO. Each data point represents a litter trap and the average gC m⁻² collected at the trap each year. Areas of high leaf litter flux C (orange) correspond with litter traps that had higher amounts of C collected annually (red).



Figure 1.7. The frequency distribution of leaf litter C in the watershed (8.5 hectares²). Leaf litter C flux in gC m⁻² yr⁻¹ at the SSHCZO ranged from 150 to 300 gC m⁻² yr⁻¹. The average leaf litter C flux at the SSHCZO was 220 gC m⁻² yr⁻¹.

Average annual aboveground net primary productivity at the watershed was 450 gC m⁻² yr⁻¹ (Fig. 1.8). ANPP at the SSHCZO ranged from 223 gC m⁻² yr⁻¹ to 3410 gC m⁻² yr⁻¹, with 89% of the watershed area ranging from 200 to 500 gC m⁻² yr⁻¹, 9% ranging from 500-800 gC m⁻² yr⁻¹, and 1% from 3200-3500 gC m⁻² yr⁻¹ (Figure A.A.1).



Figure 1.8. An interpolated map of ANPP in gC m^{-2} yr⁻¹ at the SSHCZO. C stored annually in trees and leaf litter C flux were added to estimate ANPP values. Areas of high ANPP are orange and areas of low ANPP are shown in blue.

Total aboveground C stored in the vegetation of the biomass plots (gC m⁻²) on the north and south aspect showed no trend over elevation (Fig. 1.9) or over slope angle (Fig. 1.10). There was no difference in C stored by aspect in the biomass plots (Fig. 1.11a); however, there was a significant difference between the average annual C stored in trees from the tree survey (gC yr⁻¹) in the south and north aspect, using trees from the tree survey (One sample t-test df 2025, p = 0.002) (Fig. 1.11b). More average gC m⁻² yr⁻¹ was stored on the south aspect (4.6 hectares²) than the north aspect (3.8 hectares²), which was contrary to the hypothesis. There was also a significant difference in C stored in the biomass plots (gC m⁻²) in swale and planar surfaces, with more C stored on planar surfaces (Fig. 1.12).



Figure 1.9. C stored (using 10m biomass plots) in gC m⁻² on an elevation gradient at the SSHCZO. Each point represents a 10m biomass plot around a litter trap, closed points represent plots on the north aspect, open points represent points on the south aspect. No relationship was found for north (N) (n = 18 biomass plots, p = 0.251) or the south (S) aspect (n = 17 biomass plots, p = 0.134).



Figure 1.10. Average C stored annually (using 10m biomass plots) in gC m⁻² on a slope angle gradient at the SSHCZO. Each point represents a biomass plot at that slope angle, closed point represent plots on the north aspect, open points represent points on the south aspect. No relationship was found for the north (N) (n = 18 biomass plots, p = 0.277) or the south (S) aspect (n = 17 biomass plots, p = 0.825).



Figure 1.11a. Total C stored annually (using 10m biomass plots) in gC m⁻² on both the north-facing (N) and south-facing (S) aspects at the SSHCZO. North aspect n = 18 biomass plots; South aspect n = 17 biomass plots, one sample t-test, 34 df, p = 0.442.



Figure 1.11b. Average C stored annually by the 2078 trees from the tree survey in gC yr⁻¹ on both the north-facing (N) and south-facing (S) aspects at the SSHCZO. South aspect n = 933 trees; North aspect n = 1093 trees, one sample t-test, 2025 df, p = 0.002.



Figure 1.12. Total C stored annually (using 10 m biomass plots) in gC m⁻² on a swale (S) or planar (P) surface at the SSHCZO. Swale n = 14 biomass plots; Planar n = 21 biomass plots, ANOVA single factor 34 df, p = 0.012.

Leaf litter C flux (gC m⁻² yr⁻¹) in the 35 litter traps on the north and south aspect showed no trend over elevation (Fig. 1.13), slope angle (Fig. 1.14), and there was no difference between the amount of C donated on the north and south facing aspect (Fig. 1.15) or swale and planar surfaces (Fig. 1.16).



Figure 1.13. Average leaf litter C flux over elevation at the SSHCZO. Each point represents the gC m⁻² yr⁻¹ donated at each litter trap, closed points represent traps on the north aspect, open points represent traps on the south aspect. No relationship was found for the north (N) (n = 17 biomass plots, p = 0.567) or the south (S) aspect (n = 18 biomass plots, p = 0.051).



Figure 1.14. Average leaf litter C flux over a slope angle gradient at the SSHCZO. Each point represents the average gC m⁻² yr⁻¹ collected at each slope angle, closed points represent traps on the north aspect, open points represent traps on the south aspect. No relationship was found for the north (N) (n = 18 traps, p = 0.229) or the south (S) aspect (n = 17 traps, p = 0.327).



Aspect

Figure 1.15. Average leaf litter C flux (gC $m^{-2} yr^{-1}$) by north (N) and south (S) facing slopes at the SSHCZO. North aspect n = 18; South aspect n = 17, one sample t-test 34 df, p = 0.190.



Figure 1.16. Average leaf litter C flux (gC $m^{-2} yr^{-1}$) on swale and planar surfaces at the SSHCZO. Swale n = 14; Planar n = 21, one sample t-test 34 df, p = 0.560.

There was a significant difference between the annual leaf litter C flux in 2011 and 2012, with 13% more total gC m⁻² yr⁻¹ collected in 2012 than 2011 (Fig. A.A.2). Year to year variability in C donated through leaf litter may affect the annual C budget at the SSHCZO and in addition affect other ecosystem processes such as soil formation.

The total leaf litter C flux and the total C stored annually in trees was not equal across the genera. The SSHCZO is dominated by oaks and the oaks donated on average 52% of the total leaf litter C flux and stored 33% of the total C annually in wood. Hemlock, oak and pine had a lower leaf litter C flux than C stored annually, while hickory and maple had a higher leaf litter C

flux than C stored annually in wood (Fig. 1.17). Tree genera did not grow and store C at the same rates at the SSHCZO (Fig. 1.18). Oak grew the fastest over the four year period (2008 to 2012) followed by hickory, hemlock, maple, and pine. During the 2012 growing season, hickory grew the fastest in the trees with dendrobands, followed by oak, hemlock, pine then maple (Figure 1.19). In addition, trees from the tree survey differed in growth rates based on dbh (Figure 1.20). Trees with a larger dbh generally had faster growth rates. Individual trees that were fitted with dendobands had year-to-year variation in growth rates from 2008 to 2012 (Figure A.A.3). In 2012 the growth rate measurement was more sensitive to change in growth due to the dendrobands. Future studies interested in growth rates should measure trees with.dendrobands, in addition to a total change in dbh, to determine how species-specific growth rates affect ANPP throughout the year.



Figure 1.17. Total leaf litter C flux and total C stored annually in trees in gC m⁻² yr⁻¹ by common genera (hickory (*Carya* spp.), hemlock (*Tsuga* spp.), maple (*Acer* spp.), oak (*Quercus* spp.), pine (*Pinus* spp.)) at SSHCZO.



Figure 1.18. Average gC stored annually by species genera from the tree survey. There is a difference in the storage rates (growth) between genera. One way ANOVA df 1950, oak (*Quercus* spp.) n = 1158 trees, hickory (*Carya* spp.) n = 333 trees, hemlock (*Tsuga* spp.) n = 163 trees, maple (*Acer* spp.) n = 150 trees, pine (*Pinus* spp.) n = 147 trees, p = 0.000. A post hoc Tukey test showed that oak storage rates differed significantly from all other genera; pine, maple, hemlock, and hickory storage rates did not differ significantly from each other, except for pine and hickory, p < 0.05.



Figure 1.19. Average change in dbh (cm) of dendrobands over time in two week intervals with standard error bars. Dendrobands were fastened and measured on five genera (hemlock (n = 13), hickory (n = 28), maple (n = 13), oak (n = 41), and pine (n = 15)).



Figure 1.20. Growth rates of all trees (in gC yr⁻¹ stem⁻¹) in the tree survey (n = 2078) at the watershed by diameter-at-breast-height (dbh) in cm. Each point represents an individual tree from five different genera (hemlock, hickory, maple, oak, pine). As the dbh increases, growth generally increases.

The biomass plots, including all stems with dbh greater than 3cm, stored 344,491.5 gC m⁻² in the wood. The trees from the tree survey, located in the biomass plots, stored 283,383.8 gC m⁻² in wood. From this estimate, the tree survey accounts for 82% of the total C stored in the watershed, the understory and subdominant trees account for 18% of the total C stored in the watershed.

Discussion:

Forest ecosystems play a large role in the C budget, with C dynamics responding directly to changes in the climate and atmospheric concentrations that may have major economic implications and impact global biodiversity (Clark et al 2001). While many ground measurements of aboveground C and ANPP extend back decades (Goodale et al 2002, Houghton 2005), very little is documented of aboveground C distribution across watersheds. While average annual values for C stored, C flux, and ANPP are valuable in comparing productivity to other watersheds, they do not provide a good representation of the spatial variability found within the watershed. My objective was to create a spatially explicit C budget for the SSHCZO and I hypothesized that C distribution in the watershed was affected by topographic features. However, very few trends of C stored and leaf litter C flux were seen in the data, I believe this is because of the high spatial variability across the watershed.

It is easy to see from the interpolated maps that there is a large amount of variability in productivity across the SSHCZO including an ANPP range from 200 to 1300 gC m⁻² yr⁻¹; however, it is more difficult to explain the cause of variation. At the SSHCZO C stored in the trees is more variable than leaf litter C flux. The variable spatial distribution of C stored across the watershed seems to be driven by individual trees that are growing at different rates. Hotspots of C stored in the trees on the interpolated map are driven by small groups of oaks or hemlocks that are growing at rapid rates. It was hypothesized that less C would be stored in biomass at higher elevations due to decreased water availability and because slow-growing pines occupy high, dry, elevations at the watershed (Gower et al 1997); however, there was no trend seen in C stored in the biomass plots by elevation. It was also predicted that there would be more C stored on planar surfaces than in swales because the swales act as a water throughway creating a
difficult environment for vegetation to establish. The biomass plots did show a significant difference in C stored in swale verses planar surfaces. It was hypothesized that less C would be stored on steep slope angles because it was expected that seeds from the seed bank would move downhill with gravity, water, and wind, making it more difficult for seeds to settle and establish on steep slopes; however, there was no evidence of lack of vegetation on steep slopes. Most temperate seeds are not easily moved long distances and can settle in small depressions on the landscape, so it is not surprising that this hypothesis was not supported.

There was one hotspot of leaf litter C flux at the watershed on the southeast aspect, driven by a single litter trap that accumulated on average more litter over the year compared to the other traps (383 gC m⁻² yr⁻¹ compared to 220 gC m⁻² yr⁻¹, respectively). The particular litter trap had a large amount of understory vegetation immediately around the trap that could have caused the increase in biomass compared to the other traps.

I predicted higher leaf litter C flux at lower elevations due to leaves moving downhill with gravity; however, there was no relationship with elevation. Less C was expected to be collected on steeper slope angles because the litter would move downhill on a steeper slope compared to a flatter slope but no relationship between C donated and slope angle was found. More C was predicted to be collected in swales because the swales would collect the litter compared to the planar slopes; however, there was no difference between leaf litter C flux in swales or planar surfaces. The lack of leaf litter C flux relationships between elevation, slope angle, and swale presences could be explained by three mechanisms, 1) litter traps cannot convey litter movement downslope, 2) litter did not have enough time to move during the study, and 3) litter trap placement under variable productive trees influenced the total amount of C donated to each trap. I believe that these results can be explained by a combination of all three mechanisms. While litter traps are excellent to predict the amount of litterfall a site donates annually, the litter traps used in this study were elevated, making it less likely that they caught litter moving downslope. To look more closely at litter redistribution once the litter has dropped to the forest floor, floor traps, in addition to elevated traps, should be utilized to catch the moving litter throughout the year. Trap placement and species composition could have influenced the lack of topographical trends because each tree species differs in litter production and traps that are located under highly productive trees, especially oaks that produce leaves with large biomass will have more total leaf litter C collected.

Northern aspects in the Northern Hemisphere have been documented with higher productivity than their counterparts (Sharma et al 2011). In this study, there was a significant difference in the average amount of C stored annually in the trees by aspect with more C stored on the south aspect instead of the north aspect. This is contrary to the hypothesis that more C would be stored on the north aspect because it is moister and colder. On the south aspect there are fewer trees; however, the trees occupying the south aspect, especially the oaks and hickories, are growing at a faster rate, storing more carbon annually. Other studies have found that trees contribute unevenly to C sequestration based on species that are slow or fast growing (Kirby and Potvin 2007, Brown et al 1997). Pines and hemlocks that occupy the north aspect are growing much slower than the oaks and hickories on the south aspect. While there was a significant difference between the C stored in the trees on the north and south aspect, no difference was seen in the leaf litter C flux or the C stored in the biomass plots. This is surprising because one would assume that if the trees on the south aspect are more productive, they would produce more litter. However, as previously mentioned, if productive trees were located over the litter traps then it could affect the total amount of litter. In the biomass plots, the south aspect had less trees but

more understory vegetation, while the north aspect had more trees but little to no understory vegetation, possibly evening out the C stored in the biomass plots.

For this study, the average leaf litter C flux was predicted by two years of data collection. In a temperate watershed litterfall can have large year to year variation. The second year of collection was a mast year for Chestnut Oaks adding a large amount of mass to the total litterfall. However, excluding fruit, woody debris, and unidentifiable leaves, there was still a significant difference between the amounts of litter collected during the two years. A possible explanation for the difference is that the understory grew significantly from 2011 to 2012, especially Service Berry (*Amelanchier* spp.), contributing more litter to the total amount of litterfall. When comparing the amount of litter collected by *Amelanchier* spp. in 2011 and 2012 (0.14 gC m⁻² yr⁻¹ and 4.3 gC m⁻² yr⁻¹, respectively), more was collected in 2012; however, 4.3 gC m⁻² yr⁻¹ is only 1% of the total litter collected in 2012; not enough to explain the difference between years. This indicates that there is more likely to be annual differences between the dominant genera in the watershed.

There are several possible errors that could affect the productivity prediction in this study. ANPP was defined as the change in amount of organic matter that was produced in the trees and lost in leaf litter during a given time interval. While this definition is beneficial because C stored annually by the trees and leaf litter C flux can be added to estimate ANPP; the definition has some drawbacks. ANPP may be underestimated by not taking course woody debris, plant respiration, nutrient leaching, or herbivory into account (Pregitzer and Burton 1991, Clark et al 2001, Goodale et al 2002). Understory vegetation was not included in the making of a C distribution map of C stored annually, underestimating the C stored annually; however, results of other studies that have found that when predicting how topography affects C storage,

understory vegetation contributed 1% or less to forest carbon stocks (Turner et al 1995, Goodale et al 2002). I wanted to account for the all standing biomass including the understory vegetation, but measuring the change in dbh of all understory vegetation in a watershed is difficult, so instead the standing biomass of vegetation with dbh of at least 3 cm was used in 35 plots. If only trees with dbh 20 cm or greater were used from the tree survey the standing biomass would have been underestimated by 18 percent. Current estimates of standing biomass and C stored in woody biomass in this study may be overestimated because general allometric equations were used instead of species-specific equations (Jenkins et al 2004). General allometric equations were used to predict C stored in woody biomass without foliage because foliage was accounted for from the litter traps.

Another possible error with this study is that the leaf litter C flux was not on the same scale as C stored annually in trees because only 35 traps were used compared to every tree in the watershed with dbh over 20 cm. The interpolated maps differ by resolution (the C stored having a better resolution than leaf litter C flux) and interpolations make educated guesses as to what values are between points. The farther points are away from each other, the greater the amount of error. While having more leaf litter traps would have been desirable, they would have been timely and expensive to collect from. If a more conventional approach was used and only a few restricted number of traps were used and not distributed across the entire watershed, ANPP estimates of the watershed could have changed drastically. If traps were placed in an area that was highly productive, the estimate of C donated through leaf litter would have been overestimated. Contrary, if traps were placed in areas with less productivity, the estimate of leaf litter C flux would be underestimated. While it is desirable to have many litter traps, it is more

important to have the traps located evenly throughout the entire watershed, to account for variability in ANPP.

A useful addition to this study would be a mixed or a spatial model that could predict C stored annually and leaf litter C flux based on topography and species. In previous mixed models aspect, slope, and elevation have been useful for spatial and temporal distribution of species composition and productivity (Stage and Sala 2007 and Naithani et al 2013). If a mixed model could predict C storage and flux then long-term ground-based measurements and cost could be minimized. This would be ideal when researching C distribution across a watershed affects other belowground ecosystem process.

The lack of topographic trends between C stored annually leaf litter C flux show how incredibly variable productivity can be in a small watershed. C distribution is not as simple and many variable interact to determine distribution. One watershed value of ANPP does not convey the variation in productivity across a landscape and adding spatial distribution will provide useful data for current C budgets. Spatially explicit C budgets can provide useful insight into other spatially studied ecosystem processes and future research that studies interactions between components of the critical zone should look to include spatial C distribution.

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Chapter 2: Litter Movement through a Temperate Watershed Introduction:

Many studies have collected litterfall to study ecosystem functions in temperate forests (Andrews and Schlesinger 2001, Savage and Davidson 2001, Davidson et al 2002, Ehman et al 2002), however, little is known about the magnitude of error that is associated with collecting litterfall from litter traps and how this error could affect the study of linkages to other ecosystem processes. It is commonly accepted that litter collected from traps represents the litter that will be incorporated into the soil, however, this is not necessarily the case. Litter moves due to topography and climatic factors such as rain and wind (Orndorff and Lang 1981). When considering spatial variation in litter donated to the soil it is essential to consider litter movement after it falls to the forest floor. While elevated litter traps are ideal to measure total annual litterfall production, predicting litter movement and where it will be incorporated into the soil is more difficult. Thus it is important to measure litter in ground traps in addition to elevated traps because elevated traps cannot trap moving litter (Tsukamoto 1991).

Spatial distribution of leaf litter can affect plant establishment, reduce soil thermal amplitude, and change the biochemical composition of the soil (Facelli and Picket 1991, Xiong and Nilsson 1999, Bartuszevige et al 2007). Litter redistribution in a watershed is regulated by aspect, microtopographic depressions, understory type, and fallen logs (Orndorff and Lang 1981, Lee et al 1999). Spatial dynamics should be considered in nutrient budget estimation, especially in small forested watersheds, because large amounts of litter can be transported long distances, including slope to slope by strong wind and heavy rain (Lee et al 1999). Downslope movement of litter is the greatest in lower elevations on slopes and least on ridge tops and valley bottoms, where inclination is less (Boerner and Kooser 1989). Litter movement also depends on species composition. The leaf litter-fall shadow, how far leaves can fall to the forest floor from the tree's crown, differs between species due to leaf shape, crown morphology, and timing of leaf fall (Ferrari and Sugita 1996). In general, evergreen species have a narrower litter-fall shadow compared to hardwood species (Ferrari and Sugita 1996). In a study focusing on leaf litter redistribution in an Allegheny Plateau watershed, *Quercus* spp. leaves were more likely to move after they hit the ground than non-*Quercus* spp., mainly due to their large leaf surface area (Boerner and Kooser 1989). When working in an oak dominated watershed, not being able to predict oak movement can present a large issue when predicting spatial distribution of aboveground net primary production (ANPP).

For my study, which provides spatial distribution of leaf litter C flux to a watershed, it is important to know if litter collected in elevated traps can provide accurate prediction of spatial distribution. If litter collected in elevated traps cannot provide accurate spatial predictions, then providing watershed scale predictions of ANPP distribution, that is calculated by adding distributions of leaf litter C flux and C stored annually in woody biomass will be inaccurate. I hypothesized that biomass of litter collected in elevated litter traps from five tree genera (hemlock, hickory, maple, oak, and pine) could not predict what was collected in forest floor plots and in addition, canopy composition could not predict what biomass was collected from the elevated traps and floor plots below due to leaf litter movement. The objective of this study was to determine how much litter movement affected carbon distribution in a small temperate forested watershed. If leaf litter C flux and distribution differs significantly between litter collected in the elevated traps and forest floor plots then current methods using elevated litter traps to predict litter contribution to the soil should be reconsidered.

Materials and Methods:

Data Collection:

At 35 litter was collected from elevated litter traps, forest floor plots, and canopy composition was recorded to compare biomass of litter collected and species present in the canopy. The traps were distributed on six transects that covered both the north and south facing slopes, spanned an elevation gradient of 60 meters and alternated between planar slopes and swales across the Susquehanna Shale Hills Critical Zone Observatory (SSHCZO). The SSHCZO is a small temperate forested watershed that is oriented west to east with a north and south aspect. The watershed is about 8 hectares in size and 400 meters long. The litter traps were made with a plastic bin (0.1518 m², 33 cm width x 46 cm length x 12 cm depth), plastic legs to balance and hold the litter trap about .5 meters off of the ground. Litter was collected on a weekly basis from September 4th to November 12th, 2012. Litter was dried in a Binder Oven at 57 degrees Celsius for a minimum of 24 hours, separated by species, and mass determined. Floor plots were set up next to each litter trap, perpendicular to the slope aspect (Fig. 2.1).



Figure 2.1. Forest floor plots adjacent to the litter traps. Three plots the size of the litter traps (33 cm wide x 46 cm long) were placed on either side of the trap. Litter was collected from one plot in succession (west to east) every two weeks.

Six plots the same size as the litter traps (33 cm wide x 46 cm long) were made using transect flags and flagging tape. Litter was collected by hand from one of the six plots every two weeks from September 9th to December 2nd, 2012 in succession (west to east). All leaves that had been

dropped on the ground in 2012 were collected. Leaves from 2011 that were decomposing were not collected. Litter was transported back to the lab, dried for at least 24 hours at 57°C in a Binder Drying Oven, separated by species and mass determined. The last collection date (December 2nd) was used for the final annual biomass value for each trap, as the collection was cumulative throughout the season (Figure A.A.5).

Raw data of biomass collected in gC m⁻² yr⁻¹ and percent canopy composition were converted to relative importance values so that litter collected and the canopy composition could be compared. Relative importance values for each species were calculated for the litter traps and floor plots based on the percent of the total biomass collected. At each trap the percent of the total biomass collected of each species was calculated for the species relative importance value. To get a total relative importance value for each species, the species relative importance value at each of the 35 locations were added for both traps and floor plots. To calculate a total watershed value of litter collected in the elevated litter traps and litter collected in the floor plots, the total amount of litter collected at all traps or floor plots was added and divided by the total surface area of the traps (5.3 m^2). To convert biomass into grams of carbon, 48% carbon content was used (Bowden et al 1992).

To quantify the relative importance of species in the forest canopy, a canopy survey was conducted to measure canopy composition. The canopy species were surveyed around each of the 35 litter traps at seventeen points at 45 degree intervals at a 3 meter and 6 meter radius by looking up at each point and identifying the species directly overhead (Fig 2.2).



Figure 2.2. Canopy survey sampling points around each trap. At 45 degree intervals, species immediately above the litter trap, 3 meter, and 6 meter marks were recorded (the 17 points diagrammed).

For each species in the six meter canopy plot above the litter traps, a relative importance value was calculated by determining the percent of total composition for each species in the plot. For example, if *Acer saccharum* was present in one out of the seventeen survey points at a trap then it would have an importance value of .058 ($1 \div 17$). Species relative importance values at each of the 35 survey locations were summed to get a total watershed relative importance value.

Statistical Analysis:

Regressions with alpha = 0.5 were used in Minitab (Minitab Statistical Software 2010) to compare the biomass collected in the litter traps and floor plots and relative importance values of the canopy, litter traps, and floor litter plots. Litter biomass (gC m⁻² yr⁻¹) and relative importance values of five genera (hemlock, hickory, maple, oak, pine) were used in the regressions. For a

total genera importance value, species importance values were added together. Hemlock included only *Tsuga canadensis* (L.) Carr.; hickory included *Carya tomentosa* (L.) Nutt., *C. glabra* (P. Mill.) Sweet, *C. ovata* (P. Mill.) K. Koch, and *C. cordiformis* (Wangenh.) K. Koch; maple included *Acer saccharum* Marsh., and *A. rubrum* L.; oak included *Quercus prinus* L. syn., *Q. rubra* L., *Q. alba* L., and *Q. velutina* Lam.; and pine included *Pinus virginiana* P. Mill., and *P. strobus* L..

Spatial Modeling:

To visually compare the distribution of litter donated from the litter traps and floor plots (in gC m⁻² yr⁻¹) at the SSHCZO, two interpolated maps using ArcGIS were made (ESRI 2012) using the biomass collected in the 35 elevated traps and floor plots. Using geostatistical analysis, both the elevated trap and floor plot maps were interpolated. Ordinary kriging was found to be the best interpolation method by using a cross validation. To normalize the data, data was first log transformed.

Results:

The total watershed value of litter collected in the elevated litter traps was 220 gC m⁻² yr⁻¹. The total watershed value of litter collected at the watershed from the forest floor plots was 120 gC m⁻² yr⁻¹. For each of the five genera (hemlock, hickory, maple, oak, pine) there was more litter collected from the elevated litter traps than the forest floor plots (Fig. 2.3).



Figure 2.3. The total amount of gC m^{-2} yr⁻¹ collected from the litter traps and floor plots from the five genera hemlock, hickory, maple, oak, and pine.

Relative importance values at the watershed scale were compared for species in the floor plots, litter traps, and canopy composition. For *A. rubra* (ACRU), *A saccharum* (ACSA), *Amelanchier* spp. (AM SP), *Fraxinus americana* (FRAM), *P. strobus* (PIST), and *T. canadensis* (TSCA) the species had higher relative importance in canopy cover than in the litter traps or floor litter. For *Carya* spp. (CA SP), *P. virginiana* (PIVI), *Q. alba* (QUAL), *Q. prinus* (QUPR), *Q. rubra* (QURU), and *Q. velutina* (QUVE) the species had higher relative importance in the litter trap and floor litter than in the canopy (Fig. 2.4).



Figure 2.4. Relative importance values of floor litter, litter traps, and canopy cover for twelve different species at the SSHCZO. Relative importance values for litter traps and floor litter were calculated by adding the percent of the total biomass collected at 35 traps. Relative importance for the canopy was calculated by totaling the canopy cover importance values at the 35 traps. Species included are ACRU (*Acer rubrum*), ACSA (*A. saccharum*), AM SP (*Amelanchier* spp.), (CA SP *Carya* spp.), FRAM (*Fraxinus americana*), PIST (*Pinus strobus*), PIVI (*P. virginiana*), QUAL (*Quercus alba*), QUPR (*Q. prinus*), QURU (*Q. rubra*), QUVE (*Q. velutina*), TSCA (*Tsuga canadensis*).

Regressions for the five genera showed that there were some correlations between the litter traps, floor litter, and canopy composition (Fig. 2.5). Correlation indicates that the canopy cover is correlated with the mass collected in the litter traps and forest floor plots and the mass collected in the litter traps are correlated with the mass collected in the forest floor plots. No hemlock was collected in the floor plots; however, there was a correlation between the canopy importance values and the litter trap importance values. There was a correlation between both the biomass of hickory and maple collected in the litter traps and the forest floor plots and between the canopy composition importance values and the litter traps and the litter traps and floor plots importance values. There was no correlation for the oaks between the biomass collected in the litter traps and the forest floor plots and between the forest floor plots and no correlation between the canopy composition in the litter traps and the forest floor plots and between the forest floor plots and no correlation between the canopy composition in the litter traps and the forest floor plots in the litter traps and the forest floor plots and no correlation between the canopy composition

importance values and the litter trap and forest floor importance values. There was no correlation between the biomass collected in the traps and the forest floor plots for the pines, however, there was a relationship between the canopy composition importance values and the litter traps and forest floor plots.



Figure 2.5. Regressions for species genera (hemlock, hickory, maple, oak, pine) at the SSHCZO, df = 34, N = 35 locations. The first row regresses actual values (gC m⁻²) of litter collected in the litter traps to actual values (gC m⁻²) of litter collected in the forest floor plots. The second row regresses canopy importance values (IV) to litter trap importance values of the genera collected in the litter traps. The third row regresses canopy importance values of the genera collected in the forest floor plots. Stars denote regressions where a linear relationship occurs (p < 0.05), litter traps are correlated to the floor plots or the canopy is correlated to the litter trap or forest floor plots.

For the spatial analysis, the elevated litter traps cross validation confirmed that ordinary kriging was the best interpolation method for the data, as the model had the best unbiased predictions (mean = 0.00152), accurate standard error values (root-mean-square standardized = 1.100), small root-mean-square and average standard error values (0.112 and 0.10104, respectively), and the predictions did not deviate for the measured values (Fig. 2.6). For C collected in floor plots a cross-validation comparison was used and ordinary kriging, was found to be the best interpolation method for the data, as the model had the best unbiased predictions (mean = 0.011), accurate standard error values (0.190 and 0.196, respectively), and the predictions did not deviate from the measured values (Fig. 2.7). Litter collected in the litter traps ranged from 151 to 527 gC m⁻² yr⁻¹ (Fig 2.6) and litter collected from the forest floor plots ranged from 17 to 211 gC m⁻² yr⁻¹ (Fig 2.7). Litter collected in floor plots ranged standard errors to be collected in floor plots ranged the south aspect.



Figure 2.6. An interpolated map of the C collected from elevated litter traps at the SSHCZO in 2012. Each data point represents a litter trap and the average gC m^{-2} yr⁻¹ collected at the trap each year. Areas of high C collection (orange) correspond with litter traps that had higher amounts of C collected annually.



Figure 2.7. An interpolated map of the C in forest floor leaf litter collected at the SSHCZO. Each data point represents a floor litter plot and the total gC m^{-2} yr⁻¹ collected at the plot each year.

Areas of high C collection (orange) correspond with floor plots that had higher amounts of C collected annually.

Discussion:

Over the past few decades many studies have collected leaf litter from litter traps to predict what is being incorporated into the soil. However, very little is known about the magnitude of error that is involved with using litter traps as a proxy to predict the litter contributed to the soil because litter moves after it falls to the forest floor. Elevated litter traps are ideal to use to predict the total litter contributed to a watershed but do not convey where the litter settles (Tsukamoto 1991). Floor traps can catch litter that is moving on the forest floor and can determine where and how much litter is moving. When calculating an accurate spatially explicit carbon budget in a small watershed, litter movement needs to be included in the measurements (Lee et al 1999).

This study found that if elevated litter traps were used instead of forest floor plots, the litter predicted to be incorporated into the soil at the trap location could be overestimated by 40 percent. Each genera had less litter collected from the forest floor plots. Less litter in the forest floor plots could be explained by three mechanisms: 1) litter movement, 2) decomposition, and 3) mass loss due to soil fauna, all of which are likely. Litter does not only move in the fall when litter is being dropped, it moves throughout the entire year. One study in an Allegheny Plateau watershed found that most litter was redistributed in January to April (Boerner and Kooser 1989). This research only studied litter movement from September to December. If measurements were taken all year, a larger biomass of forest floor litter may have been found in the lower elevation plots as litter from upslope had more time to move downslope. A small amount of decomposition could have taken place during the study. Previous studies have found that maples and oaks lose 55 and 40% of their mass, respectively, throughout the year in litter bags, excluding soil fauna such as earth worms (McClaugherty et al 1985). However, when

earth worms were not excluded from the litter, the maples and oaks lost 92-97% and 63-70% of their mass in one year, respectively (Holdsworth et al 2012). Earth worms are present at the SSHCZO and may have had an effect on the total biomass collected from the forest floor plots during the collection period.

Interpolated maps display more variability of litter donated from the litter traps than the floor plots. This may be because there was a wider range of litter donated in gC m⁻² yr⁻¹ to the traps than in the floor plots. The litter collected in the litter traps had a hotspot on the southeast aspect driven by one litter trap. Less total litter was collected in the floor plots, however, the south aspect collected more litter than the north aspect. A possible explanation for this trend is that there is more understory vegetation on the south aspect that is donating litter to the forest floor plots and this trend is not seen in the elevated litter traps because the vegetation is not tall enough to be captured in the elevated litter traps. The difference in litter collected in the forest floor plots compared to the elevated litter traps displays that litter must be collected from forest floor plots when looking at where and how much litter is donated to the soil.

This study only observed litter that was collected in the forest floor plots, it did not conclude where in the watershed the litter is moving. However, this study demonstrates that litter is moving in the watershed and that there are discrepancies between what species are found in the canopy, litter traps, and floor plots. A few genera did not have correlations between the canopy, litter traps, and floor plots. Oak and pine showed no correlation between litter collected in the elevated litter traps and the forest floor. Because oak dominates this watershed, inaccurately predicting oak litter distribution could present a large issue when looking at overall spatial distribution. The lack of relationship between what was found in the traps and plots could be explained by the litter moving from the plot once it hits the forest floor or decomposition.

Unlike the oaks and pines, hickory and maple litter collected in the traps were correlated with what was collected in the forest floor plots. Hemlock was not collected in any of the floor plots most likely because litter was collected by hand and the needles were too small to pick up. Because what was collected in the litter traps was correlated with the collection in the forest floor plots, maples and hickories may not be moving out of the forest floor plots or decomposing as quickly as the oaks and pines. However, this is not probable, as previous research has found that maples decompose quicker than oaks because of higher quality litter (Melillo et al 1982, McClaugherty et al 1985, Holdsworth et al 2012). Maples and hickories have a smaller leaf surface area, which may make them less mobile and less likely to be blown far distances on the ground.

The canopy cover of oak was not correlated with the litter collected in the trap or floor plot. Oak was more present in the litter collection than in the canopy. This trend may have been seen because while oaks still had a high presence in the canopy cover, oak crowns are not as dense as maples, and make up a smaller percentage of the canopy cover but are very dominant in the leaf litter and donate the majority of the biomass due to their large leaves. The canopy cover of hemlocks was not correlated with the litter found in the litter traps. Hemlock had a high canopy presence but relatively low importance in the litter traps. This trend is most likely due to the relatively small biomass hemlocks donate in litter due to their small needles. Maples and hickories did have correlations between the canopy, litter collected in the traps, and floor plots. Both maple and hickory had high presence in the canopy, and in the litter traps and plots, so it is not surprising that there is a correlation, especially if the leaves are not being blown away due to their small surface area.

Determining which genera move farther once they hit the forest floor is important especially when mapping the spatial distribution of leaf litter C flux. If some genera do not move as far, litter traps could be used as proxy to collect litter that will be donated to the soil, however, if genera that contribute a lot of total biomass (such as oaks) are readily moving long distances on the forest floor, floor plots should be used.

Studies that focus on carbon budgets in small watersheds should consider collecting litter not only from traps but also floor plots to reduce the amount of error that is connected with only using litter traps. Litter traps are useful to predict the total amount of litter donated to a watershed but cannot predict the amount of litter donated to the soil at the litter trap site because litter is constantly moving and decomposing. Only using litter traps in areas where litter is moving from overestimate the amount of litter by up to 40 percent. Litter dynamics and redistribution should also be taken into account when observing the spatial distribution of litter donated to a site, as the spatial distribution could change drastically between the litter traps and floor plots.

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Conclusion

Before this study very few C dynamic studies provided a spatially explicit aboveground C budget that showed C distribution over a small, temperate, forested watershed. Spatially explicit C budgets can be beneficial in helping understand how different ecosystem processes and topography affect productivity and can display the pure variability of productivity across a watershed. Litter is constantly moving due to topography, wind, and rain. When studying C distribution across a landscape a key component to predict litter movement is determining where C the litter will settle. This study predicted the potential error associated with assuming litter from elevated traps would settle at the trap location. Large errors associated with certain genera should make future researchers reconsider current litterfall collection methods.

Productivity varied across the landscape with ANPP of 223 to 3410 gC m⁻² yr⁻¹, with an average value of 550 gC m⁻² yr⁻¹. Species and topography seemed to drive this variable productivity and C distribution. The C stored in the trees was greater on the south aspect compared to the north and the C stored in the biomass plots were greater in planar plots that plots located in swales. It was difficult to test for relationships based on topography for leaf litter C flux, as there was so much variability across the landscape. The oaks stored and contributed the most C compared to hickories, hemlocks, maples, and pines. Oaks also grew the faster, storing more C annually than the other genera. If only the trees in the watershed were used to predict annual C storage than it is possible that the C storage would be underestimated by about eighteen percent. In future studies, researchers should try to include the understory and coarse woody debris in estimates of productivity to minimize error. This study also found more total litter in 2012 than in 2011. Due to the possible variation in the total yearly litterfall, it is a good idea to

make C distribution studies multiyear projects to provide a more accurate estimate of leaf litter C flux.

All species donated more leaf litter to the elevated litter traps than to the floor plots. This difference in the total amount of litter collected can only be explained by litter moving out of the plots or decomposition. If only elevated litter traps are used to predict the amount of C that will be incorporated into the soil (in areas litter is moving from), the amount of C could be overestimated by about 40 percent, or if plots are placed in areas that the litter is moving to the C could be underestimated. The oak canopy cover was not correlated with the biomass collected from elevated litter traps or floor plots, and the litter traps were not correlated with the biomass collected from the floor plots. Oaks donate the most litter to the watershed (52%) and if their litter is moving large distances, it is important to capture the movement in spatial studies. In this study it is likely that the litter only moved a small distance during the collection period because an increase in litter was not found in the lower elevation plots.

There was a difference in spatial distribution of the litter collected in the elevated traps and floor plots. The hotspot in the southeast aspect of the elevated litter traps is driven by a trap that received a large amount of leaf litter throughout the year due to the dense understory of maples surrounding it. The forest floor plots on the south aspect donated more litter than the north. The south aspect has a denser understory and more microdepressions that may be catching more litter. Due to a lack of a dense understory the litter on the north aspect may be more exposed to wind that is blowing through the watershed, blowing leaves out of the floor plots before collection. In future C distribution studies, it is essential that floor plots be used in addition to elevated litter traps to decrease the amount of error that is associated with litter movement.

A spatially explicit C budget is more useful when studying the interactions between different ecosystem processes, topography, and productivity than a single average watershed value of ANPP. Future studies should incorporate a spatial aspect into their research and also deeply consider the best methods to convey C distribution. In addition to using trees and elevated litter traps to predict C stored annually and leaf litter C flux, the forest understory and forest floor plots should be used to decrease the amount of error in estimating these C pools and fluxes. Collaborations should be made across multiple scientific fields to study how the different ecosystem processes interact and affect spatial distribution of productivity.

Appendix A: Additional Figures



Figure A.A.1. The percent area of the watershed (8.5 hectares²) of ANPP in gC m⁻² at the SSHCZO ranging from 200 to 3413 gC m⁻² yr⁻¹. The average ANPP at the SSHCZO was 450 gC m⁻² yr⁻¹. Only 1.2% of the annual C stored was greater than 500 gC m⁻² yr⁻¹, this small percent fell between 886 to 3413 gC m⁻² yr⁻¹.



Figure A.A.2. Average gC m⁻² yr⁻¹ donated through litter fall in 2011 (n = 35) and 2012 (n = 35). The mean average for 2011 was 159 gC m⁻² yr⁻¹ and the mean average for 2012 was 182 gC m⁻² yr⁻¹. One sample t-test df 68, p = 0.006.



Figure A.A.3. A comparison of yearly growth rates on tree genera with dendrobands (hemlock, hickory, maple, oak, and pine). Each point represents an individual tree (n = 110 trees). Growth in cm yr⁻¹ is the total change in growth in 2012 from the dendroband measurements. Average cm yr⁻¹ is the average annual growth over a four year period, estimated by an initial dbh measurement in 2008 and a final dbh measurement in 2012. A 1:1 ratio line represents where total change in growth should equal average annual growth. A difference between growth rates indicates that annual growth for an individual tree has year-to-year variation.



Figure A.A.4. Comparative growth rates of five tree genera (hemlock, hickory, maple, oak, and pine) with dendrometers and without dendrometers.



Figure A.A.5. Forest floor litter collection over time for five tree genera: hemlock, hickory, maple, oak, and pine.



Figure A.A.6. Watershed relative importance values (IV) of canopy cover, 2011 litter, 2012 litter, forest floor litter, for all species collected at the SSHCZO.



Figure A.A.7. Distribution of deciduous and evergreen trees at the SSHCZO.

Appendix B: Shale Hills Data

All data collected at the SSHCZO is made available to the public on the Susquehanna Shale Hills Critical Zone Observatory website at http://criticalzone.org/shale-hills. Tree survey data, raw data of litter collected from the elevated traps (in grams), and dendrometer measurements over time can be found under time series data in the data catalog. Litter collected from the elevated traps and from the floor plots has been archived in 317 Forest Resources Building at the Pennsylvania State University, State College, PA.

Updates to the tree survey data were made in 2012. Over 200 trees did not have gps coordinates and to calculate the coordinates I used triangulation. For each unknown tree, three trees with known coordinates were used. The distance to the known tree and the azimuth was measured. New x coordinates were calculated by adding the original x coordinate of the known tree to the distance*sin(azimuth). New y coordinates were calculated by adding the original y coordinate of the known tree to the distance*cos(azimuth). Averaging the three "new" x and y coordinates determined the gps coordinates for each unknown tree.

Appendix C: Species Code Key

Species Code	Species Name	Common Name
ACRU	Acer rubrum	Red Maple
ACSA	Acer saccharum	Sugar Maple
AM SP	Amelanchier spp.	Service Berry
BELE	Betula lenta	Black Birch
CAGL	Carya glabra	Pignut Hickory
CA SP	<i>Carya</i> spp.	Hickory species
FAGR	Fagus grandifolia	American Beech
FRAM	Fraxinus americana	White Ash
HA SP	Hamamelis spp.	Witch Hazel
LITU	Liriodendron tulipifera	Tulip Tree
MAAC	Magnolia acuminata	Cucumber Magnolia
NYSY	Nyssa sylvatica	Sour Gum
PIST	Pinus strobus	Eastern White Pine
PIVI	Pinus virginiana	Virginia Pine
PRSE	Prunus serotina	Black Cherry
QUAL	Quercus alba	White Oak
QUPR	Quercus prinus	Chestnut Oak
QURU	Quercus rubra	Northern Red Oak
QUVE	Quercus velutina	Black Oak
TIAM	Tilia americana	American Linden
TSCA	Tsuga canadensis	Eastern Hemlock
		All unidentifiable
OTHER	Other category	leaves, fruits, and small
		woody debris