Canadian Journal of Forest Research
Revue canadienne de recherche forestière

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Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2016-0147.R1
Manuscript Type:	Article
Date Submitted by the Author:	19-Jul-2016
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Keyword:	aboveground net primary productivity, litter fall, basal area, Quercus, Acer

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Variability in aboveground carbon driven by slope aspect and curvature in an eastern deciduous forest, USA.

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Abstract

In forested ecosystems, topography and tree species contribute to spatial variability in carbon (C) dynamics through differential rates of C uptake and storage; therefore, estimates of species-specific and spatial variability in C can strengthen ecosystem budgets. To produce such estimates we deconstructed watershed-scale C and component pools (e.g. wood biomass, litter) and fluxes at a fine scale using a small mixed deciduous forest catchment to determine the variation due to topographic position and species. Factors affecting fluxes included aspect, slope curvature, tree species contributions, and litter production. Annual C uptake into wood varied across the catchment from 0 to 298 kgC yr⁻¹ and was 20% greater on south aspects than north and 33% greater in swales than non-swale slopes. Out of >20 tree species found in the forest canopy of the catchment, highest C uptake in woody biomass was measured in *Q. rubra* growing in swales, followed by *Q. prinus* growing on the south aspect, with the lowest aboveground wood increment measured in *Pinus* at higher elevations on non-swale slopes. *Quercus* leaf litter moved from where it dropped into litter traps to where it settled on the forest floor, shifting the location of litter C inputs to the soil. Local variation in aboveground C rivals regional variation across regions and has the potential to introduce error when scaling C measures from points to landscapes.

Key Words: aboveground net primary productivity, basal area, litter fall, *Quercus*, *Acer*, *Carya*

1. Introduction

Carbon (C) storage is a valued ecosystem service driven largely by the composition and structure of the biotic community. Many studies have estimated carbon fluxes in forest ecosystems with measures of net primary productivity (NPP) (Waring et al. 1998, Fahey et al. 2005, Siccama et al. 2007, Richardson et al. 2009); however, few have examined how tree species-specific contributions to forest productivity differ spatially and as a function of topography (but see Yanai et al. 2012a). Defining species-specific contributions to forest productivity across topographic positions can reduce uncertainty of aboveground C budgets and identify landscape positions that play important roles in aboveground carbon uptake and storage.

Forested landscapes are often represented by single productivity values calculated from ground measurements or eddy covariance towers that provide estimated values for the non-swale surface around the tower (Stoy et al. 2013). However, spatial variability in components of productivity at a fine scale (e.g. m² to hectares) can exceed variability documented across thousands of kilometers (Houghton 2005), as well as variability measured through time (Yanai et al. 2012a). If forest productivity varies across complex topography in a non-linear fashion, then single average values may not represent cumulative productivity across a landscape and measures of C stock and fluxes at diverse positions are needed.

Spatial patterns of forest C dynamics can be influenced by topographic variability in abiotic resources such as incoming solar radiation, soil moisture, and soil nutrients. The influence of solar radiation and aspect on tree growth depends on latitude and elevation, with higher sun exposure benefiting forests that are temperature-limited and stressing species near the warm edge of their distribution (Way and Oren 2010, Sharma et al. 2011). Additional environmental variability occurs due to slope curvatures like swales, which are concave, low-

lying areas (Jin and Brantley 2011). Swales can be favorable microenvironments for vegetation due to deep soils and increased water availability, but are also disturbed by seasonal water runoff that could reduce establishment of vegetation due to surface scouring. Heterogeneity in the growing environments between swales and non-swale (planar or convex) slopes at fine-scales ($<100 \text{ m}^2$) and between aspects at slightly larger scales ($<1000 \text{ m}^2$) could drive spatial variability in forest C dynamics across a watershed ($>1000 \text{ m}^2$).

Topographic variability in C dynamics in a deciduous forest, especially resulting soil carbon, is further influenced by annual leaf litter production and redistribution. Spatial distribution of leaf litter can affect plant establishment, reduce soil temperature fluctuation, and change the biochemical composition of the soil (Facelli and Pickett 1991, Xiong and Nilsson 1999, Bartuszevige et al. 2007). Estimates of leaf production from litter traps captures the biomass dropping from the canopy of a deciduous forest, but may not capture where that leaf litter settles on the forest floor. Litter redistribution in a watershed is regulated by aspect and microtopographic depressions such as swales, understory vegetation type, and fallen logs (Orndorff and Lang 1981, Lee et al. 1999). In forested watersheds, large amounts of litter can be transported, including across slopes, by strong wind and heavy rain (Lee et al. 1999). Leaf litter moving downslope or by wind can become trapped in low-lying swales where it eventually settles and decomposes. Litter movement also depends on species composition. Litter-fall shadow, the distance leaves and litter fall to the forest floor from the tree, differs among species due to leaf shape, crown morphology, and timing of leaf fall (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). Thus, variability in leaf litter movement among species could be an important factor influencing spatial patterns in C dynamics.

Our study focused on spatial C distribution of aboveground carbon uptake and storage across a small watershed catchment that hosts a temperate deciduous forest with over 20 canopy-tree species and topographic diversity created by north and south aspects and swales and non-swale slopes. Our main objectives were to: 1) Determine tree species contributions to forest productivity in the catchment; 2) Quantify spatial patterns in aboveground C by comparing basal area and C uptake to wood between north and south aspects and on swales and non-swale slopes; and 3) Identify tree genera with the potential to influence soil C by determining spatial mismatches between leaf production and litter inputs to the forest floor. We predicted that the main contributors to forest productivity would be the dominant tree species in the study catchment, primarily oaks (*Quercus* spp.). We hypothesized that higher wood C uptake would be found on the south facing aspect compared to north due to a positive response to warmer temperatures of oaks at the north end of their distribution. We also hypothesized that aboveground C uptake on non-swales would be greater than those on swales due to higher stand basal area and density, but individual tree growth would be faster in swales due to rich soils, increased water availability, and lower competition among trees.

2. Methods

2.1 Study Site

Our study took place in the small forested watershed catchment of the Susquehanna Shale Hills Critical Zone Observatory (Shale Hills). Shale Hills is located in Huntingdon County, Pennsylvania and is an 8.53 hectare catchment on Rose Hill shale bedrock covered by a 110+ year old humid temperate forest. The mean annual temperature is 11°C and the annual

precipitation is 900 mm (Naithani et al. 2013). The catchment has north- and south-facing aspects, with an elevation change of 60 meters from the lowest point to the highest point (240-300 m above sea level) and seven large swales distributed across the catchment that are surrounded by non-swale slopes (Fig. 1). Swales were identified as low lying areas in the catchment created by seasonal runoff with convergent flow, and non-swale hill-slopes identified by areas with non-convergent flow (Andrews et al. 2011). There are 23 large-stature tree species in the catchment 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* (Lam.) 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.). Land use history of the forest over the past two centuries was homogenous across the catchment and representative for the region. Tree harvesting started in the mid-1800s, when land area may have been cleared for pasture (the catchment was never tilled), and ending by the 1930s when the last tree harvesting occurred (Wubbels 2010). Many canopy trees established between 1850-1950, as documented from age sampling with radial cores from 110 trees from eight dominant species ranging in diameter from 10-75 cm (unpublished tree core data).

2.2 Field measurements to estimate aboveground wood C

In fall 2008 each tree within the catchment with diameter-at-breast-height (DBH) over 20 cm was tagged, identified to species, DBH recorded, and GPS coordinates mapped using ESRI ArcMap Desktop 10.2 geostatistical analyst (ESRI, 2013). In fall 2012 DBHs of all living tagged trees were re-measured (Eissenstat and Kaye 2012; Kaye et al. 2015).

2.3 Field measurements to estimate leaf litter C

Leaf litter was collected in the catchment to measure annual C inputs and to identify leaf litter dynamics on the forest floor. Leaf litter was collected in 35 traps with 0.152 m² area and suspended 0.5 m off the ground (Yanai et al. 2012a). Traps were located on five elevation transects, including locations in swales and on non-swale slopes. During 2011 and 2012 leaf litter was collected once a week from September 1st to December 1st (when the deciduous trees stopped dropping leaves in the litter traps).

Leaf production by species was compared to forest floor inputs by measuring forest species composition of leaf litter in litter traps, and species composition of litter on the forest floor. Litter was collected once every two weeks in 2012 from forest floor plots located adjacent to the 35 litter traps. Forest floor plots were the same area as litter traps but not elevated from the forest floor and were marked in the corners by stakes to allow for litter movement. Litter was collected within the plot boundary off of the forest floor by hand.

All litter was dried at 57° C for a minimum of 24 hrs then sorted into species and weighed. C contributed from litter was analyzed for % foliar C using a subset of leaves from six dominant species. Samples were ground, ~3 g were massed, and analyzed for % foliar C. Percent C was used to convert litter mass to grams C. The six species analyzed were *A. rubrum*, *A. saccharum*, *F. americana*, *Q. prinus*, *Q. rubra* and *T. canadensis*; biomass of other species was assumed to have 48% C content (Bowden et al. 1992).

2.4 Data Analysis

Carbon components of the ecosystem were estimated from field measurements. Basal area (BA) (m²) per tree was calculated with the DBH data measured in 2012. The 2008 and 2012 tree DBH measurements were used to estimate woody biomass excluding foliage in grams (g) for each tree. Aboveground biomass including bark and stem and branch wood, was estimated per

tree with the following five species group allometric equations that encompass all the species in the catchment: soft maple/birch, mixed hardwood, hard maple/oak/hickory/beech, true fir/hemlock, and pine (Jenkins et al. 2003). Species group allometric equations were used rather than species-specific equations as 10% of the stems fell outside of the DBH range limits for the species-specific equations and because species-specific equations are often site specific and may not represent our study area (Jenkins et al. 2004). Carbon stored annually in aboveground wood increment (AGWI) was calculated by subtracting 2008 biomass from 2012 biomass and dividing by four years to estimate annual increment (g yr^{-1}), then converted to carbon (gC yr^{-1}) (assuming wood biomass is 48% C (Bowden et al. 1992)).

To visualize C spatial variability across the catchment, estimates of AGWI (gC yr^{-1}) were used to make a wall-to-wall interpolated map using ESRI ArcMap Desktop 10.3 geostatistical analyst (ESRI, 2015). To normalize the data, a log scale +1 was used for the AGWI interpolation. All of the trees measured were used and placed on the map with corresponding biomass (kgC) estimates calculated using species group biometric equations as described above. Ordinary kriging was found to be the best interpolation method via summary statistics of a diagnostic cross-validation comparison.

Data from the four *Carya* species (*C. glabra*, *C. tomentosa*, *C. ovata*, and *C. cordiformis*) were grouped together for analysis due to 1) possible errors in field identification of *C. glabra* and *C. tomentosa* and 2) leaf litter from *Carya ovata*, *cordiformis*, and *glabra*, could not be separated reliably by species. The majority of the 333 *Carya* trees were either *C. glabra* (~125 trees) or *C. tomentosa* (~175 trees), both of which are found on mesic to xeric slopes, upland areas, and have similar ecology and growth forms suggesting that their contribution to watershed carbon are comparable and can be grouped for analysis (Burns and Honkala 1990). However,

grouping *Carya* species together prevented species-level comparisons such as those done for all other genera.

BA and AGWI data were analyzed with three approaches. First, total density, total BA, and total AGWI were calculated on an area basis (density: stems ha⁻¹, BA: m² ha⁻¹, AGWI: gC ha⁻¹ yr⁻¹) by summing the number of stems, BA, and AGWI of all trees and dividing by the 8.53 ha area of the catchment. Similar calculations were made for the four topographic positions of south aspect, north aspect, non-swale slopes, and swale by dividing by the area of the catchment that falls within that position (3.85, 4.68, 6.64, and 1.89 ha respectively) producing total values for each topographic position. Secondly, BA and AGWI were estimated on a species basis for specific areas (north versus south aspects; swale versus non-swale slopes) and species comparisons were made with two-sample paired t-tests. Thirdly, comparisons of average BA and AGWI were calculated (m² and gC yr⁻¹) on a per tree basis and compared between north and south aspects and swale and non-swale surfaces with two-sample t-tests assuming equal variance for trees from all species together and for trees from the four dominant species. Comparisons were significant at the $\alpha=0.05$ and Bonferroni corrections were made for multiple comparisons.

Using the litter trap area and percent C content, litterfall was scaled up to landscape units (gC m⁻² yr⁻¹). A simple linear regression was performed to test the relationship between species basal area in the catchment and average annual leaf litter production. ANPP of each species in the catchment was estimated by adding AGWI (gC m⁻² yr⁻¹) and leaf litter production (gC m⁻² yr⁻¹). Spatial comparisons of ANPP were not done because of the mismatch in spatial resolution of stem growth data (inventory with 2000+ trees) with that of leaf litter data (35 traps at individual points in the catchment). We compared the litter mass estimated from litter traps with that estimated by forest floor data collections by dominant genera (*Carya*, *Acer*, *Quercus*, and *Pinus*)

instead of by species because not all species were collected in both the traps and floor plots. We tested the relationship between total leaf litter production by species ($\text{gC m}^{-1} \text{yr}^{-1}$) measured in litter traps with that measured in forest floor plots using a linear regression. R studio statistical software was used for all analyses (R Development Core Team, 2013).

2.5 Limitations

There are limitations to our estimates of aboveground C in the Shale Hills CZO catchment. Trees <20 cm DBH and trees that reached 20 cm within the four year study period were not included in the measurements, and are therefore not included in the density, BA, and AGWI estimates. This could lead to greater underestimates of carbon for late-successional species such as *Acer saccharum* that have more small stems than *Quercus* species that dominate the canopy. From additional vegetation sampling in the catchment we estimate that stems 10-20 cm DBH comprise 9% of BA and 36% of stem for all trees <10 cm DBH. ANPP is underestimated by not accounting for coarse woody debris, nutrient and C leaching, or herbivory (Pregitzer and Burton 1991, Clark et al. 2001, Goodale et al. 2002). In addition, approximately 40 trees died within the four year time period that were not included in our analysis, further underestimating ANPP and AGWI for the catchment. Understory vegetation was not included in basal area or AGWI measurements; however, other studies have found that understory vegetation contributed 1% or less to forest carbon stocks (Turner et al. 1995, Goodale et al. 2002).

2.6 Uncertainty Analysis

The amount of error surrounding ecosystem nutrient budget estimates is rarely reported but is important as the use of allometric equations introduces uncertainty into the estimates (Yanai et al. 2010, Yanai et al. 2012b). We discuss the amount of uncertainty of our aboveground C estimates following Harmon et al. 2015 guidelines that suggest reporting four

sources of uncertainty including: measurement uncertainty, sampling uncertainty, model prediction uncertainty, and model selection uncertainty. We estimated measurement uncertainty of 1% for tree DBH measurements based on values reported by Harmon et al. 2015. There is no sampling uncertainty because we measured all of the trees in the catchment, and in fact our results can provide estimates of sampling uncertainty for other studies based on spatial variability in aboveground C quantified here. Prediction uncertainty for the models requires large biomass datasets that are independent of the allometric equation parameterization, which are not available (Jenkins et al. 2003), and were therefore unable to include that source of uncertainty in our assessment. Model selection uncertainty was approximated for the biomass equations with a simple comparison of AGWI estimates based on the species group allometric equations that we used in our analysis and AGWI calculated from species-specific equations from Jenkins et al. 2004. Species-specific equations developed at sites closest to our study area were selected for the analysis. AGWI estimates varied 9% between the two types of allometric models, which can be considered a rough estimate of uncertainty in our model selection. Based on our calculations and values available from other studies, we made a conservative estimate of 10% uncertainty by summing the three sources of uncertainty because they could be additive.

3. Results

A total of 2031 trees (stems) from 23 species were measured for estimates of carbon pools and fluxes across the catchment. In the 8.53 ha catchment area, total ANPP was $443 \text{ gC m}^{-2} \text{ yr}^{-1}$, with ~66% stored in woody C increment and ~33% in leaf litter production (Table 1). *Q. rubra*, *Q. prinus*, and *Q. alba* were the top contributors to ANPP, stem density, basal area, AGWI, and leaf litter production (Table 1), with *Carya* species and *A. saccharum* also making major contributions.

Aboveground biomass and aboveground wood increment (AGWI) varied across the catchment (Fig. 2). Biomass of individual trees ranged from 18 to 2587 kg C. Areas with trees of higher biomass were located along the base of the north aspect, especially in swales (Fig. 2). Average annual AGWI ranged from 0 to 298 kgC yr⁻¹ with only 9.7% of the catchment area incorporating more than 13.4 kgC yr⁻¹ into wood. Areas of high AGWI were scattered across most of the catchment, except along the upper north aspect, where tree density and biomass were low (Fig. 2).

On an area basis, forests on south and north aspects had similar species richness, stem density, total biomass, and total basal area, but the forest on south aspects had 20% greater total AGWI (Table 2). On a species basis, most dominant species that had trees present on both the north and south slopes had higher per species total basal area and/or total AGWI on south aspect compared to north aspect (e.g. *Q. alba*, *Carya spp.*), except *Q. rubra* that had higher basal area and AGWI on the north aspect (Fig. 3). When comparing average AGWI on a tree basis, south aspect trees had on average 16% higher AGWI than north aspect trees (two-sample t-test, df = 2024, $P < 0.0001$) but BA was not different (two-sample t-test, df = 2029, $P = 0.29$) (Table 2).

Of the four dominant species in the catchment, AGWI per tree was greater on south aspects than north for *Q. prinus* (two-sample t-test, df = 550, $P < 0.001$), but not *Q. alba* (two-sample t-test, df = 274, $P = 0.829$), *Q. rubra* (two-sample t-test, df = 277, $P = 0.885$), and *A. saccharum*, (two-sample t-test, df = 127, $P = 0.311$). BA per tree was greater on south aspect than north for *Q. prinus* (two-sample t-test, df = 552, $P = 0.007$), greater on north aspects than south for *Q. rubra* (two-sample t-test, df = 278, $P = 0.008$), and not different between aspects for *A. saccharum* (two-sample t-test, df = 128, $P = 0.91$) and *Q. alba* (two-sample t-test, df = 275, $P = 0.412$).

Forests on swales had the lowest tree density and the highest biomass, BA, and AGWI compared to non-swales, as well as N and S aspects (Table 2). Comparing swales and non-swale areas, stem density was slightly lower in swales (5%), total biomass higher (10%), total basal area slightly higher in swales (4%), and total AGWI 33% higher in swales than non-swale (Table 2). Both total basal area and AGWI of dominant species (e.g. *Q. prinus*, *Q. rubra*, *Q. alba*) were higher in swales than non-swale slopes (Fig. 3).

Comparing measurements between swales and planer slopes, average BA and AGWI per tree of all species on swales were greater than on non-swale slopes. Average AGWI per tree was 41% higher in swales than on non-swale slopes (two-sample t-test, $df = 2024$, $P = <0.0001$) and average BA per tree was 9% higher in swales than on non-swale slopes (two-sample t-test, $df = 2029$, $P = 0.005$) (Table 2). For the four dominant tree species, *Q. rubra*, *Q. prinus*, *Q. alba*, and *A. saccharum*, AGWI per tree was not significantly different between non-swale slopes and swales (two-sample t-test, $df = 277$, $P = 0.291$, two-sample t-test, $df = 550$, $P = 0.212$, two-sample t-test, $df = 274$, $P = 0.588$, two-sample t-test, $df = 127$, $P = 0.251$, respectively) (Table 2). BA per tree was significantly higher in swales than non-swale slopes for *Q. rubra* and *Q. prinus* (two-sample t-test, $df = 278$, $p = 0.045$, two-sample t-test, $df = 552$, $P = 0.007$, respectively); however, it was not different for *Q. alba* and *A. saccharum* (two-sample t-test, $df = 275$, $P = 0.356$, two-sample t-test, $df = 128$, $P = 0.369$, respectively) (Table 2).

Relative species contributions of leaf litter C in the catchment reflected stem biomass and AGWI patterns. Species basal area was positively correlated with species annual leaf litter (simple linear regression, $P < 0.0001$, $R^2 = 0.852$) (Fig. 4). The three *Quercus* species (*Q. rubra*, *Q. prinus*, *Q. alba*) produced the largest amount of leaf litter, followed by *Carya* and *Acer* species (Table 1). Total litter production in litter traps and forest floor litter was significantly

correlated for *Carya* and *Acer* ($P < 0.01$, Fig. 5) but not significant for *Quercus* ($P = 0.703$) and *Pinus* ($P = 0.675$, Fig. 5). Percent carbon in leaf litter of the six species analyzed for foliar C varied from 43% in *A. rubrum* to 50% in *T. canadensis* (*A. rubrum* 43.0 ± 3.3 SE; *A. saccharum* 45.6 ± 0.1 ; *Q. rubra* 45.8 ± 0.2 ; *Q. prinus* 45.8 ± 0.3 ; *F. americana* 48.1 ± 0.6 ; *T. canadensis*, 50.2 ± 0.73).

4. Discussion

Deconstructing aboveground carbon in a small watershed catchment illustrates the heterogeneity in its components across topography and among species. Within the watershed we measured differences between annual carbon tree storage (Fig. 2) comparable to estimates across large geographic regions, and aboveground C pools and uptake were consistently highest in swales and on the south aspect. Large differences in wood C uptake in eastern deciduous forests have been measured at sites across a broad geographic area spanning the Appalachian region, with sites in Tennessee having nearly 70% greater C uptake in wood than a site in Massachusetts ($220 \text{ gC ha}^{-1} \text{ yr}^{-1}$ in TN and $130 \text{ gC ha}^{-1} \text{ yr}^{-1}$ in MA; Curtis et al. 2002). The single catchment comparison presented here points to the potential for small-scale variability in C uptake to rival large-scale ranges. Aboveground C uptake in woody biomass is a major component of forest ANPP, accounting for up to 70% of net ecosystem productivity (NEP) (Brown and Schroeder 1999, Barford et al. 2001), and a large increase in wood-carbon uptake in swales compared to non-swales likely translates to greater NEP in swales. Spatial variability in aboveground C such as those observed in this study highlights the value of examining how forest C can change across the landscape and among species to alter C pools and fluxes.

Hot and cool spots of carbon uptake were found in a mosaic across the catchment. The area with highest annual C stored (248 kgC yr^{-1}) was located at the base of a large swale on the

north aspect, where many large hemlocks and oaks could have access to deep soils and water. Areas with low annual C storage ($<2 \text{ kgC m}^{-2} \text{ yr}^{-1}$) were located on the north aspect at higher elevations on non-swale slopes. These areas had a lower density of trees and included pines and maples that were sequestering small amounts of C annually.

Differences in annual C storage in wood growth between topographic positions underscore the importance of plot-level measures occurring on variable slopes and aspects to avoid over or under-estimating C uptake for extrapolation to broader areas. Aspect-driven variability in forest productivity may have some predictability based on the forest community, and the effect of solar radiation on aspect microclimate. Warmer conditions on south aspects (30 W m^{-2} greater on average, unpublished data) in the Shale Hills catchment may drive higher productivity because the resident oak-hickory forests are at the northern end of their distribution and temperature-limited. Higher productivity in the form of more wood C uptake on the south aspect indicates that the growing environment is more suited to the oak-hickory forests than the north aspect. This relationship was supported by species-specific growth rates (discussed in detail below), because forests of species with more southern distributions were more productive on the south aspect, while those with more northern distributions (e.g. *Q. rubra*, *T. canadensis*) were more productive on the north aspect.

Spatial differences in C were also driven by slope curvature. Tree density in swales was lower, trees were larger on average, and grew faster than trees on non-swale slopes. We hypothesize that lower density of trees in swales due to seasonal disturbances from the concentration of surface water runoff in swales (Lin et al. 2006) could be responsible in part for the higher per-tree basal area and wood growth in swales because of lower competition for resources among trees. The larger size and greater growth of trees in swales are likely due to

higher resource availability from deep soils. High resource availability may lead to dominance of some trees over others, but as with aspect comparisons we did not directly measure resource availability in swales compared to non-swale slopes. However, vegetated swales have been known to trap more nutrients from surface runoff and have even been used to control contaminants (Yousef et al. 1987). A confounding factor in slope curvature comparisons is that more of the south aspect falls within swales (Fig. 1), and the south aspect had higher C uptake in wood than the north aspect. Overall, the magnitude of influence of slope curvature in aboveground C was more than that of aspect, with swales consistently having greater aboveground C stock and uptake than non-swale slopes. Furthermore, the magnitude of spatial variability in C measures exceeded the estimated uncertainty of 10% approximated for our analysis, although our conservative uncertainty analysis likely underestimated overall uncertainty.

4.1 Species contributions to aboveground C

Each of the 23 dominant tree species in Shale Hills had unique patterns of C uptake and storage across topographic positions, highlighting the functional diversity of trees in eastern deciduous forests and potential resilience to environmental change. Catchment ANPP was dominated by the genus *Quercus*, which contributed 71% of the catchment total. Among the three dominant oak species, *Q. prinus* had approximately twice as many stems in the catchment, indicating the productivity of that species was driven by many smaller stems compared to fewer larger stems of *Q. rubra* and *Q. alba*. Stems of *A. saccharum* and *A. rubrum* are forest canopy sub-dominants that generally grow at slower rates than canopy dominant trees such as the oak species in this forest; however, *A. saccharum* and *A. rubrum* contribute 14% of the total leaf litter to the catchment. The conifer species *T.canadensis* and *P. strobus* together accounted for

5% of ANPP, which is underestimated because leaf litter collection was restricted to Oct-Dec and these evergreen species can lose needles throughout the year. We attempted to evaluate this bias by estimating the annual change in foliar biomass for each species using foliage component allometric equations. The foliage component allometric equations overestimated the amount of foliage we collected annually from *T. canadensis* by approximately 20% and underestimated the amount of foliage we collected from *P. strobus* by approximately 60%. These results indicate that we may have missed 20% of the *T. canadensis* foliage during collection; but collected more than one year's foliage growth of *P. strobus* during our three months of collection.

Spatial heterogeneity in C across the catchment was associated with differential productivity among species. The greatest hotspot of C uptake in wood was driven by high productivity of *Q. rubra* trees growing on the north aspect at the base of swale, near the valley bottom (Fig. 2). Among species, the topographic position with highest C uptake varied (Fig. 6). Productivity of *Q. rubra* was greatest in swales and north aspects and *Q. prinus* was greater on the south aspect and within swales. *Q. alba* seemed minimally sensitive to slope curvature, but had greater productivity on the south aspect. Among the less dominant species, greater productivity occurred at various topographic positions, such as on the south aspect for *Q. velutina*, *Fraxinus americana*, *A. saccharum*, and *P. strobus*, while *T. canadensis* showed higher C uptake on the north aspect.

Species suitability to topographic positions is generally related to their geographic distributions. Among oak species, *Q. rubra* has a more northern distribution and reaches greater growth rates in cooler conditions, as was seen in Shale Hills. In contrast, *Q. prinus* is a more southern species tolerant of warm temperatures and lower water availability. *Tsuga canadensis* has a broad latitudinal range from Georgia to Canada, but is mostly restricted to cool valley

bottoms and ridge tops in its southern extent, and is a component of mixed northern hardwood stands. Its optimal growth on the north aspect reflects its preference to cooler climates. Our results suggest that climate-envelope models of shifting species distribution could capture and predict small-scale patterns in species suitability, as seen in Shale Hills.

4.2 Litter movement

Discrepancies between species in the litter traps and forest floor plots document horizontal movement of leaf litter as it drops. Of the four genera analyzed, *Quercus* and *Pinus* showed no correlation between litter collected in the elevated litter traps and the forest floor, indicating that litter moves laterally after dropping from the canopy. Movement, or litter redistribution, suggests that litter nutrient inputs to the forest floor may differ across the landscape, altering productivity estimates and forest floor dynamics such as moisture retention (Kreye et al. 2013). *Quercus* dominated aboveground C of this catchment and produced a majority of the leaf litter. Given that litter accounts for one third of ANPP, miscalculations of ANPP could be large when horizontal litter redistribution occurs in dominant species. Unlike *Quercus* and *Pinus*, the quantity of *Carya* and *Acer* litter in the traps and forest floor were correlated, suggesting their litter is not moving laterally. Lack of lateral movement by litter may be due to smaller leaf or leaflet surface areas, which would reduce litter movement by wind and water.

Less litter was collected from forest floor plots than litter traps for each of the four genera, which could be explained by three mechanisms: 1) decomposition, 2) mass loss due to soil fauna, and 3) litter movement. We collected forest floor litter every two weeks throughout our collection period to decrease the chance of litter decomposition. 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 (McClaugherty et al. 1985). However, when soil fauna was not excluded from the litter, 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 Shale Hills and were not excluded from this study. This may have had an effect on the total biomass collected from the forest floor plots during the collection period; however, frequent collection of litter from the forest floor plots should have decreased the chance of litter losses to macroinvertebrates. Litter movement has been quantified in other watersheds by tracing movements temporally and identifying areas of sources and sinks (Boerner and Kooser 1989, Fahnestock et al. 2000). We cannot conclude how much litter is redistributed annually from this study as we only studied litter movement for four months out of the year (Sept to Dec); however, litter has been documented redistributing throughout the entire year. One study in an Allegheny Plateau watershed found that largest quantity of litter was redistributed from January to April (Boerner and Kooser 1989). Based on frequent litter collection and information from other studies, we attribute differences in litter between traps and the forest floor to litter movement, although we did not document where litter actually settles in the watershed.

5. Summary

Aboveground carbon in the 8-ha oak-dominated watershed catchment varied based on aspect, species contributions, and litter production. While catchment values of C uptake into wood were similar to those measured in other eastern deciduous forests, within-catchment values were heterogeneous, ranging widely from 0 to 248 kgC yr⁻¹. An estimate of 10% uncertainty in our analysis indicates that the magnitude of differences observed across the watershed exceeds the magnitude of analysis uncertainty, although our approximations were conservative. Annual C uptake into woody biomass was 20% greater on south aspects than north aspects and 33%

greater in swales than non-swales. Annual carbon storage was 40% higher in trees in swales than non-swales. We recommend considering spatial heterogeneity when estimating C pools and fluxes in complex topographical watersheds, in addition to reporting uncertainty in ecosystem budgets (Yanai et al. 2010, Yanai et al. 2012b, Harmon et al. 2015). In light of projected climate change, spatial patterns of carbon uptake by species may be of interest for forest C uptake planning and accounting. Among the 20+ canopy tree species in the catchment, those in the genus *Quercus* dominated aboveground C, specifically *Q. rubra* and *Q. prinus*. The highest measured rates of carbon uptake in wood were measured in *Q. rubra* growing in swales, followed by *Q. prinus* growing on the south aspect. *Quercus* leaf litter moved laterally from the litter traps to where it settled on the forest floor, highlighting a limitation of using litter traps for spatial analysis of litter contributions to forest floor carbon. Finally, patterns of aboveground carbon in the catchment suggests a level of resilience of the forest ecosystem to environmental change due to the diversity of C cycling strategies found among tree species and topographic positions.

6. Acknowledgements

We conducted this research at the Penn State Stone Valley Forest, which is funded by the Penn State College of Agriculture Sciences, Department of Ecosystem Science and Management, and managed by the staff of the Forestlands Management Office. We would like to thank Jason Kaye, Katie Gaines, Tom Adams, Jenna Mitchell, Jared Prokopchak, Rachel Hoh, Sarah Wurzbacher, Christy Rollinson, and Julie Weitzman. Financial and logistical support and data were provided by National Science Foundation Grant EAR 07-25019 (C. Duffy), and EAR 12-39285, EAR 13-31726 (S. Brantley) for the Susquehanna Shale Hills Critical Zone Observatory and the Department of Ecosystem Science and Management.

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8. Tables

I. Aboveground net primary productivity (ANPP; $\text{gC m}^{-2} \text{yr}^{-1}$), stem counts, basal area ($\text{m}^2 \text{hectare}^{-1}$), Aboveground Woody Increment (AGWI; $\text{gC m}^{-2} \text{yr}^{-1}$), and average 2011 and 2012 leaf litter production ($\text{gC m}^{-2} \text{yr}^{-1}$) for canopy tree species found in the 8.5 ha Susquehanna Shale Hills Critical Zone Observatory watershed.

Species (species code)	ANPP $\text{gC m}^{-2} \text{yr}^{-1}$	# of stems	Basal Area $\text{m}^2 \text{ha}^{-1}$	AGWI $\text{gC m}^{-2} \text{yr}^{-1}$	Leaf Litter $\text{gC m}^{-2} \text{yr}^{-1}$
<i>Quercus rubra</i> (QURU)	120.4	280	5.4	77.5	42.9
<i>Q. prinus</i> (QUPR)	103.3	554	6.4	69.1	34.2
<i>Q. alba</i> (QUAL)	73.8	277	3.7	47.3	26.5
<i>Carya spp.*</i> (CASP)	59.1	333	3.2	35.2	23.9
<i>Acer saccharum</i> (ACSA)	30.2	130	1.1	9.3	20.9
<i>Q. velutina</i> (QUVE)	17.8	47	0.88	11.3	6.5
<i>Tsuga canadensis</i> (TSCA)	15.5	163	2.1	14.3	1.2
<i>Pinus strobus</i> (PIST)	8.80	56	0.92	6.40	2.4
<i>A. rubrum</i> (ACRU)	3.80	20	0.23	1.77	2.03
<i>Fraxinus americana</i> (FRAM)	3.46	33	0.30	2.36	1.1
<i>P. virginiana</i> (PIVI)	3.12	89	0.84	2.36	0.76
<i>Liriodendron tulipifera</i> (LITU)	1.41	13	0.19	1.33	0.08
<i>Fagus grandifolia</i> (FAGR)	0.900	7	0.06	0.740	0.16
<i>Nyssa sylvatica</i> (NYSY)	0.463	4	0.04	0.053	0.41
<i>Magnolia acuminata</i> (MAAC)	0.391	3	0.05	0.381	0.01
<i>Prunus serotina</i> (PRSE)	0.340	5	0.04	0.200	0.14
<i>Betula lenta</i> (BELE)	0.188	10	0.07	0.158	0.03
<i>Tilia americana</i> (TIAM)	0.156	3	0.02	0.036	0.12
<i>P. pungens</i> (PIPU)	0.101	2	0.03	0.101	0.0
<i>B. alleghaniensis</i> (BEAL)	0.008	2	0.01	0.008	0.0
TOTAL	443.2	2031	25.4	279.8	163.4

* Data from four *Carya* species in the catchment were grouped because of possible field identification errors and lack of distinct leaf morphology traits needed to separate leaf litter of species.

II. Forest structure and carbon dynamics in the catchment scale, and four topographic positions; south aspect, north aspect, non-swale slopes, and swales. Data from 2031 trees greater than 20-cm diameter in 2008 in the 8.5 ha watershed were included in the analyses.

	Catchment	South aspect	North aspect	Non-swale slopes	Swales
No. species	23	20	23	23	16
Area (ha)	8.53	3.85	4.68	6.64	1.89
Tree density (stems ha ⁻¹)	238.9	243.4	233.8	241.7	229.5
Total biomass (kgC m ⁻²)	9.5	9.6	9.4	9.3	10.2
Total basal area (m ² ha ⁻¹)	25.4	25.6	25.3	25.3	26.2
Total AGWI (gC m ⁻² yr ⁻¹)	279.8	307.8	256.9	261.4	348.8
Basal area per tree (cm ²) (SE)					
All spp		1050 (19.3)	1081 (20.7)	1046 (16.2)	1143 (29.9)
QURU		1464 (73.4)	1737 (65.7)	1576 (58.2)	1809 (94.0)
QUPR		1063 (36.2)	922 (25.8)	946 (24.3)	1081 (44.2)
QUAL		1110 (48.0)	1178 (69.6)	1159 (49.1)	1072 (61.5)
ACSA		725 (47.2)	733 (47.1)	715 (33.4)	796 (109.2)
AGWI per tree (kgC yr ⁻¹) (SE)					
All spp		12.6 (0.6)	10.9 (0.5)	10.8 (0.4)	15.2 (1.2)
QURU		24 (3.3)	23.4 (1.7)	22.4 (1.6)	26.8 (3.8)
QUPR		13.5 (1.2)	8.7 (0.8)	10.1 (0.7)	12.5 (1.7)
QUAL		14.7 (1.3)	14.2 (1.8)	14.1 (1.0)	15.9 (3.1)
ACSA		4.7 (0.7)	4.5 (0.7)	4.4 (0.6)	5.3 (1.0)

Note. Aboveground wood increment (AGWI) represents average annual wood C gain from 2008 to 2012. Average basal area and AGWI (per tree) with standard errors are provided for each topographic position for all species combined and for the four dominant species in the catchment. Values in bold represent significant differences between aspects (non-swale vs. swale) or slopes (south vs. north) at $\alpha = 0.05$. See Table 1 for species codes.

Figure 1. The Susquehanna Shale Hills Critical Zone Observatory with distribution of the five main tree genera. Each point represents one tree from one of the five main genera (*Acer spp.*, *Carya spp.*, *Pinus spp.*, *Quercus spp.*, and *Tsuga spp.*) or other genera. Dashed areas represent low-lying swales and stars indicate litter trap locations.

Fig. 1
279x215mm (96 x 96 DPI)

Figure 2. Tree woody biomass (kg) and average annual aboveground woody increment (AGWI) (gC yr⁻¹) at the Susquehanna Shale Hills Critical Zone Observatory in 2012. Trees > 20cm in 2008 were measured for analysis. Each point represents one tree. Point size and color indicate total woody biomass and genera, respectively. Areas of high AGWI in the watershed are colored in red and areas of low AGWI are colored in blue.

Fig. 2
279x215mm (96 x 96 DPI)

Figure 3. Basal area (BA) in m² hectare⁻¹ yr⁻¹ of 11 tree species and one genus (*Carya*) in the SSHCZO watershed by aboveground woody increment (AGWI) in gC m⁻² yr⁻¹. Top panel compares BA and AGWI for each species on south (S) and north (N) aspects and bottom panel compares values on non-swale slopes and swales. See Table 1 for species codes.

Fig. 3

103x148mm (96 x 96 DPI)

Figure 4. The relationship of basal area ($\text{m}^2 \text{ ha}^{-1}$) of 19 tree species with the total amount of leaf litter in gC m^{-2} collected in the litter traps ($n = 35$ litter traps) during 2011 and 2012. Each point represents one species, except CA sp. represents sum of four *Carya* species. Species are listed in the order of dominance (i.e. the greatest woody biomass) in the watershed. See Table 1 for species codes.

Fig. 4
167x142mm (96 x 96 DPI)

Figure 5. Comparisons of leaf litter in raised traps with that found on the forest floor of four genera (*Acer*, *Carya*, *Pinus*, *Quercus*) at Shale Hills (df = 34, N = 35 locations). Stars denote linear relationships with slopes different from zero ($P < 0.05$).

Fig. 5

161x148mm (96 x 96 DPI)

Figure 6. Comparison of species productivity on four topographic positions: south and north aspects, swales, and non-swale slopes. Size of black circles represents the species aboveground standing biomass (e.g. Q. prinus and Q. rubra have highest biomasses in the watershed, Table 1). Location of black circles calculated by the difference of species’ AGWI between south and north aspect (horizontal axis) and swales and non-swale slopes (vertical axis) (Table 3). Twelve species with the highest biomass in the watershed were included. See Table 1 for species codes.

Fig. 6
178x142mm (96 x 96 DPI)