# Interspecific Ecological and Meteorological Controls on Forest Canopy-derived Hydrology and Biogeochemistry in the Southeastern United States

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During storm events, as precipitation moves through the forest canopy it is transformed in both quantity and quality, thus delivering highly enriched water to the forest floor. Throughfall is spatially distributed beneath the forest canopy while stemflow is localized to the roots and soils in the immediate vicinity of individual tree trunks. Previous research has demonstrated that storm characteristics (e.g., intensity, duration, and magnitude), canopy structural parameters, and species composition have a significant control on canopy-derived nutrient fluxes. However, in the southeastern United States, contributions of the forest canopy to nutrient cycling have largely been overlooked, although the magnitude of tree biodiversity in the region separates these forests from their more-studied counterparts. Therefore, a field study was established in an oak-hickory forest in Mississippi to categorize the interspecific control on canopy-mediated nutrient cycling during precipitation events. Throughfall collectors and stemflow collars were located underneath the canopies of four oak (Shumard, Southern Red, Post, and White) and two hickory species (Shagbark and Pignut), with three replicates for each species. Hydrologic flux and nutrient samples were collected following individual precipitation events beginning in Fall 2014 and continue to present. Meteorological characteristics and precipitation chemistry were collected at a nearby open site.

Preliminary results indicate that stemflow volumetric flux was significantly different between species ($p<0.001$) but throughfall volumetric flux was not ($p=0.624$). Among the oak species, Shumard oak partitioned an average of 73.6% of incident precipitation into throughfall and 1.6% into stemflow, the largest among all species, with the remaining 24.8% partitioned into canopy interception. Mean concentrations of total nitrogen (TN) in throughfall were greatest in Shumard oak (1.44 mg/L) and post oak (1.39 mg/L) while stemflow concentrations were greatest in shagbark hickory (1.81 mg/L) and white oak (1.20 mg/L) and intermediate in Shumard oak (0.96 mg/L). Dissolved organic carbon (DOC) concentrations in throughfall were significantly different than precipitation ($p=0.038$) but not between species ($p=0.342$), while DOC concentrations in stemflow were significantly different than precipitation ($p<0.001$) and between species ($p<0.001$). Results suggest that Shumard oak canopies facilitate the largest hydrologic fluxes in oak-hickory forests that correspond to intermediate biogeochemical fluxes of nitrogen, enabling this species to directly modify the substrata and its growing conditions. Improved understanding of species-specific roles in nutrient cycles in highly diverse southern forests is critical to developing effective management strategies to mitigate shifts in species composition and ecosystem functions as regional climates change.

## introduction

Deciduous forests represent a significant land cover classification in much of the temperate US and contribute meaningful ecosystem services such as carbon sequestration, water and air purification, storm water management, recreational retreats, in addition to providing valuable timber products. These services are constrained by forest health, which can be measured via several parameters including net primary production and biomass accumulation, evapotranspiration, resiliency to disturbance, and forest nutrient balances (Long et al., 2009; Pan et al., 2009; Wear and Huggett, 2011; Woodall et al., 2013). These services are ultimately constrained by the external climate from which forests derive water and nutrients.

Within the forest canopy, there are distinct pathways in which precipitation and nutrients reach the forest floor and move throughout a watershed (Figure 1). Throughfall is water that passes through the forest canopy and is deposited to the forest floor. Throughfall is a spatially and temporally variable hydrologic flux that is influenced by a host of variables including: physiological and morphological traits related to forest composition; seasonality and the presence of foliage; precipitation characteristics; and meteorological conditions. Variability in canopy density may arise from several inherent physiological traits such as crown density, crown cover percentage, and leaf area index (LAI), which contribute to throughfall variability, especially in tropical forests where species diversity is high (Park and Cameron, 2008). In temperate forests, species with denser canopies like Acer rubrum (red maple) have significantly smaller throughfall fluxes than shallower canopies like Quercus prinus (chestnut oak) (Alexander and Arthur, 2010). The presence of foliage increases throughfall variability by providing additional surfaces for drip points and decreases overall throughfall flux by providing additional surfaces for interception (Helvey and Patric, 1966; Peterson and Rolfe, 1982).

Precipitation characteristics including magnitude, intensity, and duration are considered abiotic factors that influence throughfall partitioning. The strong correlation between throughfall and precipitation magnitude has been documented in forest types around the world such as Amazonian rainforests (Marin et al., 2000), coniferous arid forests (Shachnovich et al., 2008), semi-arid oak forests (Carlyle-Moses et al., 2004), and temperate rainforests (Link et al., 2004; Oyarzún et al., 2011). Precipitation intensity is positively correlated with throughfall partitioning, whereby the mechanism of more and faster falling raindrops disturb foliar surfaces and reduce canopy retention capabilities (Ponette-González et al., 2010; Staelens et al., 2008). Longer duration storm events reduce the spatial variability of throughfall (Loescher et al., 2014) in addition, longer duration events are typically associated with lower vapor pressure deficits, which inhibit intra-storm evaporation from the canopy and contribute to throughfall (Llorens et al., 1997).

Stemflow is rainfall that has been captured by the forest canopy and funneled down woody surfaces to be deposited at the base of the trunk. Stemflow has much longer residence times and therefore is an important pathway in nutrient cycling. Physiological and morphological traits of a species are much more important for stemflow generation because the residence time of stemflow on forest surfaces is much greater and persists for a longer period of time. Levia et al. (2010) monitored stemflow flux at 5-min intervals within storm events and found that stemflow yield was more similar within trees of the same species than within trees of the same basal area. It was also observed, that within a species, stemflow yield was correlated to tree size (Levia et al. 2010) and that smaller trees were more efficient at generating stemflow (Siegert and Levia, 2014). Carlyle-Moses and Price (2006) found a similar relationship between rough and smooth bark species during smaller precipitation events, but during larger events, once the bark storage capacity of the rough bark species was reached, stemflow generation exceeded all other dominant canopy trees regardless of bark thickness. Seasonality also plays a key role in stemflow production not only by changing the canopy composition in terms of foliage presence but also through meteorological influences. The presence of foliage interferes with stemflow production in much the same manner as it does for throughfall production—by providing additional canopy surfaces for interception.

Only a few studies have documented the effects of rainfall intensity on stemflow production. When rainfall intensity exceeds the flowpath capacity of branches and trunks, the pathways overflow and contribute to throughfall, thus reducing total stemflow production (Herwitz, 1987). During high intensity storms, obstructions on woody surfaces by rough morphology can slow down pathways and also create drip points, reducing stemflow production (Carlyle-Moses and Price, 2006; Herwitz, 1986). Wind speed and direction also influence stemflow production. Van Stan et al. (2011) found that smaller trees gained more access to incident rainfall when it was inclined due to increased wind speeds and were thereby able to generate more stemflow than under conditions of vertical rainfall. In tropical forests where canopy roughness is much greater and a emergent trees are common, inclined rainfall plays a significant role at wetting tree trunks along vertical gradients and generating stemflow (Herwitz and Slye, 1995).

Throughfall and stemflow pathways may become enriched with nutrients and other solutes via washoff of dry deposition during antecent dry periods or canopy leaching. Dry deposition, in either gaseous or particulate form, accumulates in the forest canopy between rainfall events. The mechanism by which the forest canopy intercepts dry deposited materials are controlled by canopy architecture and leaf surface area and is highly specific to the material and the associated deposition velocity (Katul et al., 2011). Canopy leaching comes from internal forest structures and is controlled by phenoseasons (Levia et al., 2011; Van Stan et al., 2012; Zhang et al., 2006), canopy structure (Beier et al., 1993), forest composition (Pryor and Barthelmie, 2005), and canopy-dwelling flora and fauna (Levia, 2002). These movements are influenced by a suite of internal and external forcings that ultimately control the amount of solutes deposited to the forest floor. Internal forest characteristics that have been shown to influence enrichment of nutrients along subcanopy hydrologic pathways include bark microrelief (Levia et al., 2011), canopy geometry (Levia and Herwitz, 2005), stand age (Buttle and Farnsworth, 2012), and canopy hydrophobicity (Holder, 2007). External forest characteristics include precipitation characteristics (Hofhansl et al., 2012), precipitation phase (Levia, 2003), seasonality (Van Stan et al., 2012), and proximity to pollution sources (Avila and Alarcon, 1999). Changes in precipitation characteristics such as magnitude, duration, and intensity or in overall storm tracks have the potential to alter the movement of water and nutrients in forests.

Across the eastern portion of the United States, the vast majority of forest types are dominated by oak species. As such, oaks are a crucial component of forest hydrology and biogeochemical cycling, influencing both the temporal and spatial distribution of water and nutrients in forests. However, the biogeography of oak species in forests across the United States is changing due to anthropogenic management of fire regimes (Brose et al., 2001; Nowacki and Abrams, 2008), accelerated mammalian browsing (Abrams, 2003; Cote et al., 2004), insects (Stephen et al., 2001), disease (Bruhn et al., 2000), and climatic disturbances leading to a broad decline of oaks (Clinton et al., 1993; McEwan et al., 2011; Voelker et al., 2008). In order to predict and manage oak decline, it is first necessary to understand and quantify the role of oaks to forest nutrient cycling. Therefore, the objectives of this study are to quantify the importance of oaks versus co-dominant hickories in their role in regulating water and nutrient cycles in a southeastern deciduous forest.

## Study Site

This research was conducted at a field site located at Sessums Natural Area in Oktibbeha County, MS (33°25'27.8"N 88°45'36.6"W) in a 15 hectare catchment (Figure 2). Dominant canopy trees at the site include white oak (*Q. alba*), post oak (*Q. stellata*), cherrybark oak (*Q. pagoda*), Shumard oak (*Q. shumardii*), shagbark hickory (*Carya ovata*) and pignut hickory (*C. glabra*). Leaf area index (LAI) of the stand is 5.77 $m^2$ $m^{-2}$. The site is located at the contact point between the Demopolis chalk formation to the northeast and the Ripley formation to the southwest. Soils at the site are silty clay loams ranging from somewhat poorly drained (Kipling) to well drained (Sumter) depending on landscape position (NRCS 2013). Annual summer temperatures (JJA) range from 23.5℃ to 27.7℃ with an average monthly precipitation of 11.0 cm. Annual winter temperatures (DJF) range from 6.6 ℃ to 14.4 ˚C with an average monthly precipitation of 13.9 cm (20 year average) (SRCC 2014).

## Methods

Four oak species and two hickory species (see Table 1) were selected for the study. Three trees from each species were selected for monitoring throughfall and stemflow fluxes. Underneath the discrete canopy of each tree, a 1L high density polyethylene bottle fitted with a 20.3 cm diameter funnel was deployed to capture throughfall. Each tree was also outfitted with stemflow collars by longitudinally cutting high density polypropylene (HDPE) tubing, which was sealed to the trees with silicone caulk and drained into large collection bins. Volumes were measured following discrete rainfall events greater than 5 mm, and grab were collected for nutrient analysis. Open precipitation was monitored at the nearby Mississippi State University Dairy Farm. Precipitation amount, duration, and intensity were measured with a tipping bucket rain gauge (Onset HOBO RG3-M, Dallas TX) and grab samples for chemical analysis were collected from a 1L HDPE collector, of the same design as throughfall collectors.

To convert volumetric measurements of precipitation and

**Table 1. Summary of tree species characteristics including diameter at breast height (DBH), basal area, canopy area, specific leaf area, and bark thickness of the 18 trees selected for monitoring in this study.**

| Tree Species | DBH (cm) | Basal Area ($m^2$) | Canopy Area ($m^2$) | Specific Leaf Area ($cm^2/g$) | Bark Thickness (mm) |
|---|---|---|---|---|---|
| **Southern Red Oak** | 61.5 | 0.3 | 60.7 | 122.9 | 0.92 |
| | 65.5 | 0.3 | 170.5 | | |
| | 78.7 | 0.5 | 306.1 | | |
| **Shumard Oak** | 48.5 | 0.2 | 24.1 | 263.3 | 1 |
| | 70.9 | 0.4 | 65.7 | | |
| | 76.7 | 0.5 | 53.1 | | |
| **White Oak** | 49.5 | 0.2 | 77.1 | 85.7 | 1.22 |
| | 61.5 | 0.3 | 122.5 | | |
| | 88.9 | 0.6 | 198.1 | | |
| **Post Oak** | 49.3 | 0.2 | 151.3 | 115.1 | 1.19 |
| | 58.7 | 0.3 | 126.7 | | |
| | 69.3 | 0.4 | 164.3 | | |
| **Pignut Hickory** | 18.0 | 0.0 | 23.3 | 285.6 | 0.85 |
| | 36.3 | 0.1 | 11.8 | | |
| | 77.5 | 0.5 | 194.6 | | |
| **Shagbark Hickory** | 25.9 | 0.1 | 15.0 | - | 0.42 |
| | 31.5 | 0.1 | 56.9 | | |
| | 49.8 | 0.2 | 74.8 | | |

throughfall into comparable depth equivalents, the following equation was used:

$$D = \frac{V}{A} \qquad (1)$$

where D is the depth of throughfall or precipitation (cm), V is the measured volume of water collected during an event ($cm^3$), and A is the area of the 20.3 cm diameter funnel (324.3 $cm^2$). Stemflow volumes were converted to depth equivalents based on the canopy area of each collecting tree. Depth equivalents were then compared to rainfall amounts to determine each tree's stemflow partitioning. Funneling Ratios (FR) (Herwitz, 1986) were determined by

$$FR = \frac{SF}{P_g \times BA} \qquad (2)$$

where *SF* is stemflow volume (mL), *Pg* is precipitation (cm), and *BA* is the basal area of each tree ($cm^2$).

Samples were returned to the laboratory, filtered to remove particulates greater than 0.45µm, and stored at 4°C within 24 hours. Total organic carbon (TOC) concentrations were determined using spectrometry methods with a HACH Low Range Total Organic Carbon Test kit and processed on a HACH DR5000 Spectrophotometer (Loveland, CO). Inorganic nitrogen components, $NO_{3-}$ and $NH_{4+}$ were determined using colorimetry methods on a Bran+Luebbe Autoanalyzer 3 (Mequon, WI).

## Results and Discussion

The distribution of incident rainfall by the forest canopy was highly variable and dependent on tree species. In all tree species, throughfall comprised the majority of canopy partitioning, where pignut hickory and post oak partitioned the largest amount of incident rainfall into throughfall (85.3% and 84.3%, respectively) while Shumard oak and white oak partitioned the least (71.6% and 72.3%, respectively) (Figure 3, Table 2). Throughfall volumetric flux was strongly correlated with rainfall amount, with the strongest correla-

**Table 2. Summary of throughfall (TF), interception (I), and stemflow (SF) partitioning as a percent of incident rainfall, stemflow funneling ratio (FR), dissolved organic carbon (DOC) concentrations, and dissolved inorganic nitrogen concentrations ($\text{DIN}=\text{NO}_{3-} + \text{NH}_{4+}$) in throughfall and stemflow for each of the six tree species of this study. [Note that the percent partitioning values for TF, I, and SF are averages across all storms and do not sum to 100%.]**

| Species | %TF | %I | %SF | FR | TF DOC (mg/L) | SF DOC (mg/L) | TF DIN (mg/L) | SF DIN (mg/L) |
|---|---|---|---|---|---|---|---|---|
| Southern Red Oak | 82.3 | 13.1 | 0.3 | 0.27 | 15.62 | 41.01 | 0.96 | 0.93 |
| Shumard Oak | 71.6 | 25.1 | 1.0 | 0.29 | 13.21 | 34.26 | 1.69 | 0.88 |
| White Oak | 72.3 | 18.3 | 0.2 | 0.12 | 21.71 | 77.33 | 0.67 | 1.29 |
| Post Oak | 84.3 | 6.9 | 0.2 | 0.31 | 25.32 | 73.89 | 0.65 | 0.75 |
| Pignut Hickory | 85.3 | 12.1 | 1.0 | 0.62 | 17.23 | 37.51 | 0.56 | 1.22 |
| Shagbark Hickory | 74.9 | 17.3 | 3.6 | 0.44 | 20.74 | 35.10 | 0.60 | 1.12 |
| Rain | | | | | 6.16 | | 3.18 | |

tions observed for southern red oak ($r^2$=0.92) and pignut hickory ($r^2$=0.88) and slightly weaker correlations observed for white oak ($r^2$=0.78) and post oak ($r^2$=0.79) (Figure 4). The latter two species had the largest average canopy areas (Table 1) but were characterized by large canopy gaps and a high degree of spatial heterogeneity, which has been shown to be more difficult to model (André et al., 2011).

Stemflow partitioning represented a very small portion of canopy partitioning, where southern red oak, white oak, and post oak diverted the smallest portion to partitioning (0.3%, 0.2%, and 0.2%, respectively) while shagbark hickory overwhelmingly diverted the largest (3.6%) (Figure 5, Table 2). While shagbark hickory bark tends to flake outwards and provide drip points (Herwitz, 1986), the capacity of this species to generate stemflow may be compensated by the thinner bark (Table 2) and therefore lower bark water storage capacity (Van Stan et al., 2016). Stemflow volumetric flux was much more variable than throughfall flux, as it is influenced by an array of tree traits and rainfall conditions, therefore the relationship between stemflow volume and rainfall amount was considerably weaker. However, stemflow volume was most well correlated with rainfall amount for Shumard oak ($r^2$=0.81) and to a lesser degree for all other tree species, with the weakest correlation for white oak ($r^2$=0.28) (Figure 5). To a degree, stemflow generation in smoother-barked species is more strongly correlated to rainfall amount than generation in species with rougher bark, such as the distinction between Shumard oak and pignut hickory on one end of the spectrum and white oak on the other (Table 1). In species with very smooth bark, such as American beech, the ease of generating stemflow can actually lead to higher inter-storm variability and less predictive models (Siegert and Levia, 2014). Pignut and shagbark hickory were most efficient at generating stemflow, with funneling ratio values of 0.62 and 0.44, respectively (Table 2). Although oak species had smaller average funneling ratios, the variability and range were similar to those observed in hickory species, with the exception of white oak (FR=0.12) (Figure 6).

Dissolved organic carbon fluxes in throughfall and stemflow can be derived from both atmospheric deposition and canopy exchange (Arisci et al., 2012; Moreno et al., 2001). In throughfall, DOC concentrations were all greater than DOC concentrations observed in rainfall, but only marginally so (Figure 7). White oak and post oak DOC concentrations were significantly higher in throughfall than rainfall but no other significant differences between species were observed (Table 3). In stemflow, DOC concentrations were much greater than those observed in throughfall or rainfall, as is commonly observed in the literature (Arisci et al., 2012; Guo et al., 2005; Inamdar et al., 2013). However, given the difference in volume between throughfall and stemflow, total flux of DOC is typically greater in throughfall (Neu et al., 2016). In addition to significantly larger DOC concentrations in stemflow relative to rainfall, many interspecific stemflow concentrations were also significantly different (Table 3). Stemflow DOC concentrations in species from the white oak subsection (white oak and post oak) were significantly greater different than those in the red oak subsection (southern red oak and Shumard oak) as well as

**Table 3. Comparison of Total organic carbon (TOC) concentrations in rainfall compared to throughfall and stemflow using pairwise t-test. P-values are given in the table below and bolded values are significant ($\alpha$=0.05). SRO=Southern red oak, SO=Shumard oak, WO=White oak, PO=Post oak, PH=Pignut hickory, SH=Shagbark hickory.**

| | Rain | SRO | SO | WO | PO | PH |
|---|---|---|---|---|---|---|
| **Throughfall** | | | | | | |
| SRP | 1.000 | - | - | - | - | - |
| SO | 1.000 | 1.000 | - | - | - | - |
| WO | 0.088 | 1.000 | 1.000 | - | - | - |
| PO | 0.012 | 1.000 | 0.464 | 1.000 | - | - |
| PH | 0.863 | 1.000 | 1.000 | 1.000 | 1.000 | - |
| SH | 0.181 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| **Stemflow** | | | | | | |
| SRP | 0.003 | - | - | - | - | - |
| SO | 0.025 | 1.000 | - | - | - | - |
| WO | <0.001 | 0.002 | <0.001 | - | - | - |
| PO | <0.001 | 0.005 | <0.001 | 1.000 | - | - |
| PH | 0.013 | 1.000 | 1.000 | <0.001 | 0.002 | - |
| SH | 0.019 | 1.000 | 1.000 | <0.001 | <0.001 | 1.000 |

the hickories (pignut and shagbark), but no significant difference was observed between the red oaks and hickories (Table 3). The rougher bark characteristics of white oak and post oak leads impedes stemflow drainage and increases the residence time of stemflow, which allows for additional canopy exchange/leaching (Levia et al., 2010).

For inorganic nitrogen species, NO$_{3-}$ and NH$_{4+}$, no significant differences were observed between rainfall, throughfall, and stemflow (Figures 7 and 8). In all instances, inorganic nitrogen was less in throughfall and stemflow compared to rainfall (Table 3), which could be attributed to canopy uptake (Lovett and Lindberg, 1986).

## Conclusion

Vegetative canopies transform incident rainfall in both quantity and quality, redistributing water and nutrients to the forest floor. In forest ecosystems where many species are present such as oak-hickory forests, the impact of specific tree species on this redistribution process is evident. All tree canopies reduced incident rainfall by partitioning water into throughfall, stemflow, and interception. Throughfall partitioning was similar across study species both in terms of quantity (71.6% to 85.3%) and quality (DOC: 13.21 mg/L to 25.32 mg/L; DIN: 0.56 mg/L to 1.69 mg/L) while stemflow partitioning displayed significant interspecific differences. In this study, species with thin bark such as shagbark hickory and species with smooth bark such as Shumard oak produced the largest volumetric fluxes of stemflow. In contrast, species with rough bark such as white oak and post oak were associated with the highest concentrations of DOC in stemflow, due to longer residence time and canopy exchange. These traits enable trees to directly modify the substrata and the surrounding growing space. Improved understanding of species-specific roles in water and nutrient cycles in highly diversity southern forests will play a critical role in developing effective management strategies to mitigate shifts in species composition and ecosystem functions as regional climates change.

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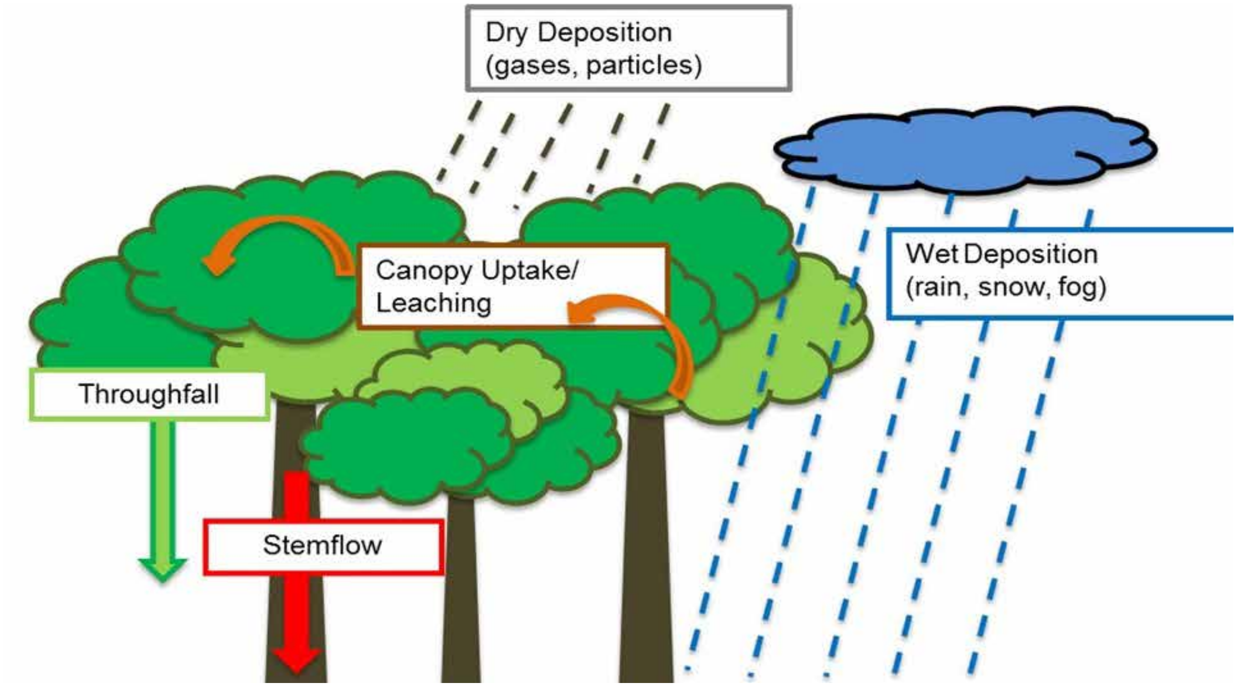

*Figure 1. Schematic of hydrologic and biogeochemical flowpaths in forest ecosystems.*

*Figure 2. Location of experimental study plot in eastern Mississippi.*

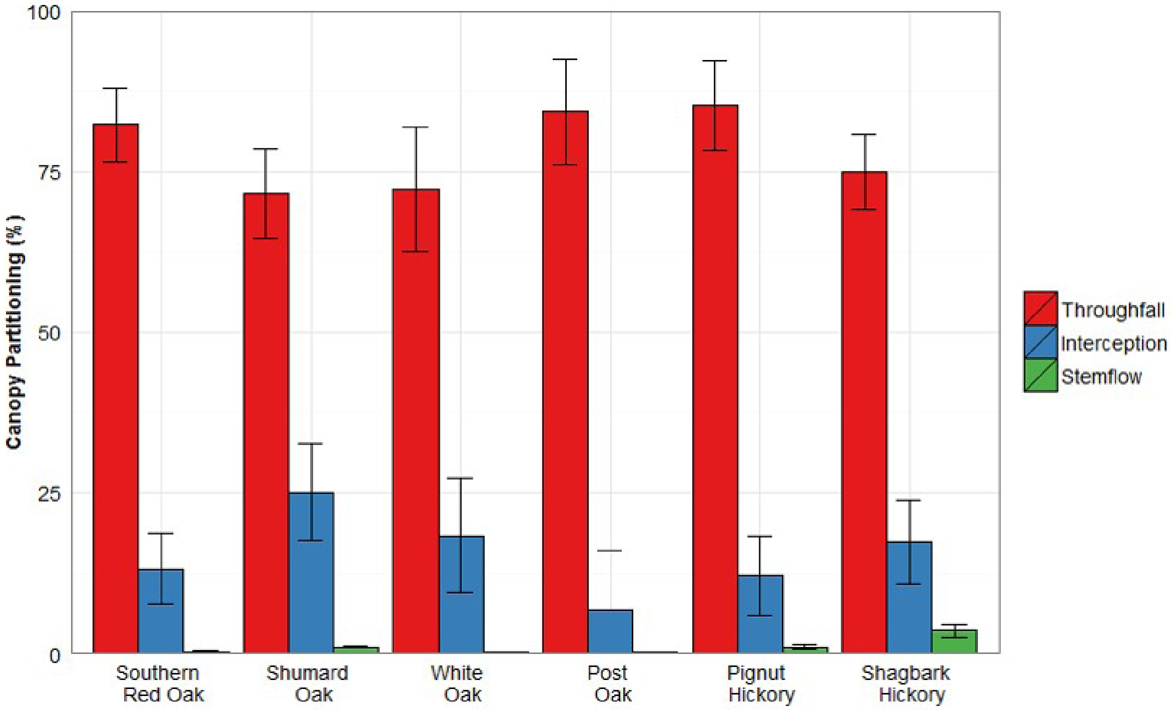

*Figure 3. Average partitioning of rainfall into throughfall, interception, and stemflow with standard error bars for each of the 6 tree species in this study.*

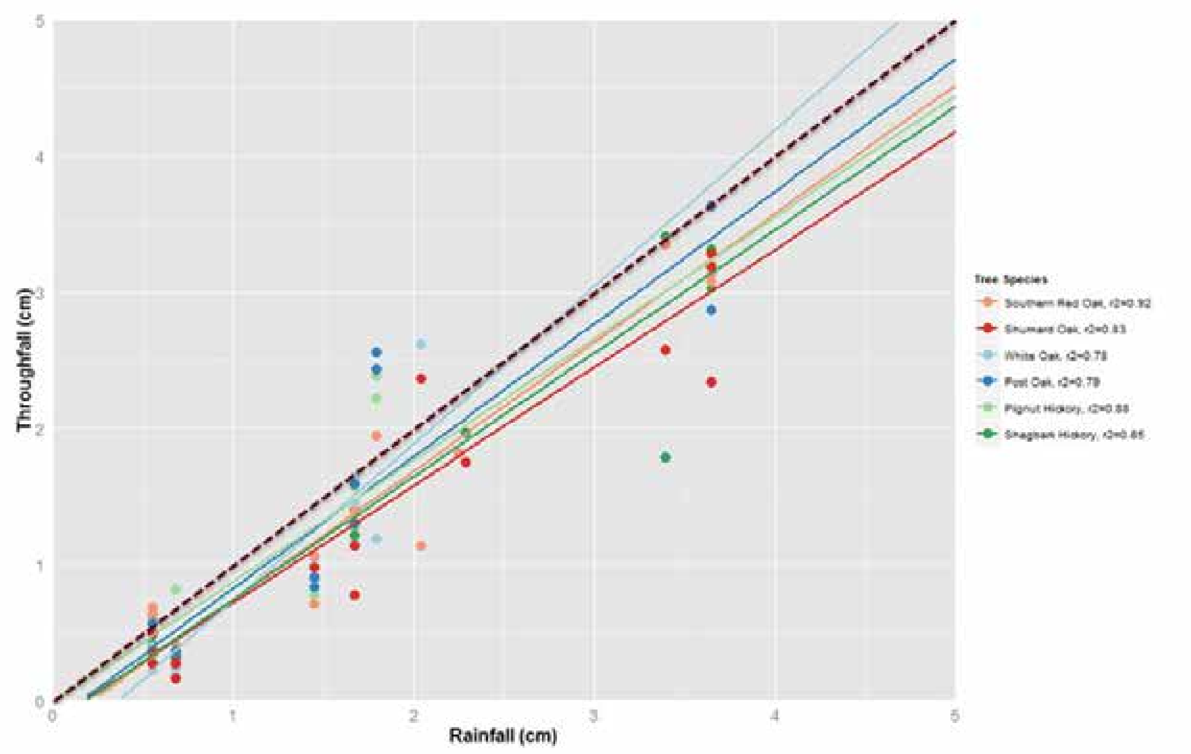

*Figure 4. Throughfall volumetric flux in relation to rainfall amount for each of the 6 tree species in this study. The dotted black line represents the 1:1 line, such that points plotted below the line indicate that throughfall was less than rainfall.*

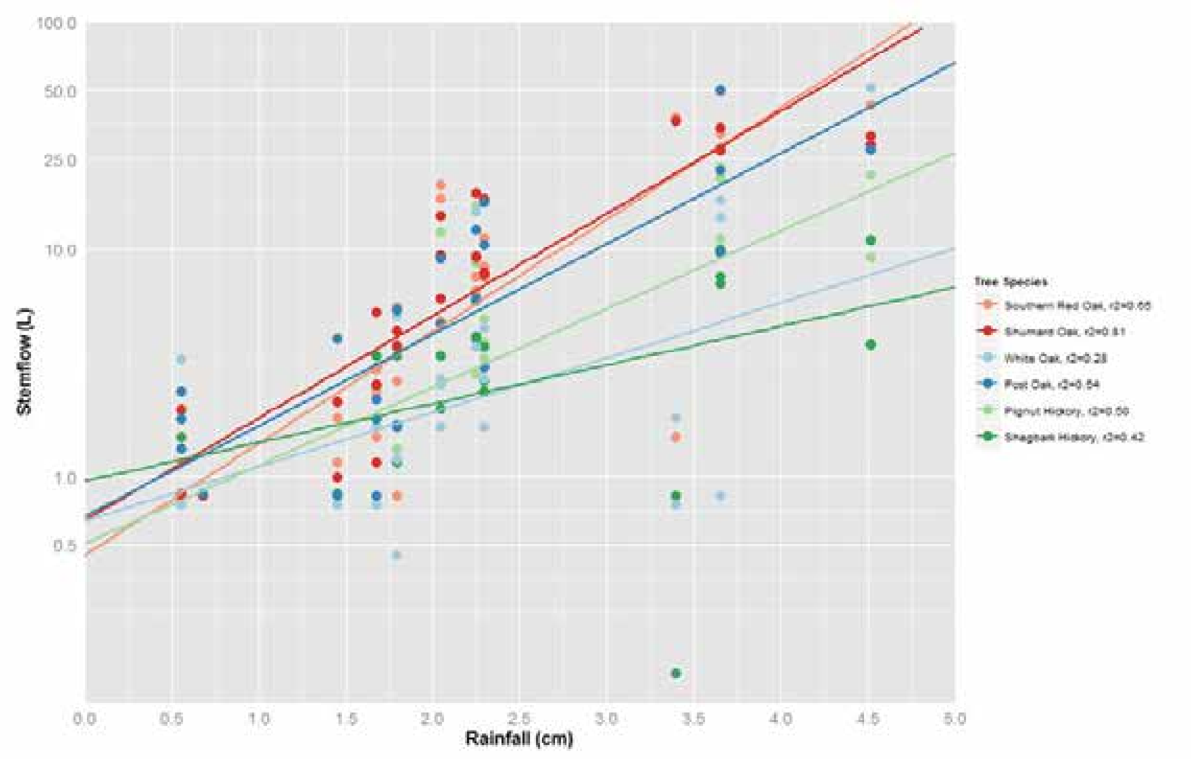

*Figure 5. Stemflow volumetric flux in relation to rainfall amount for each of the 6 tree species in this study.*

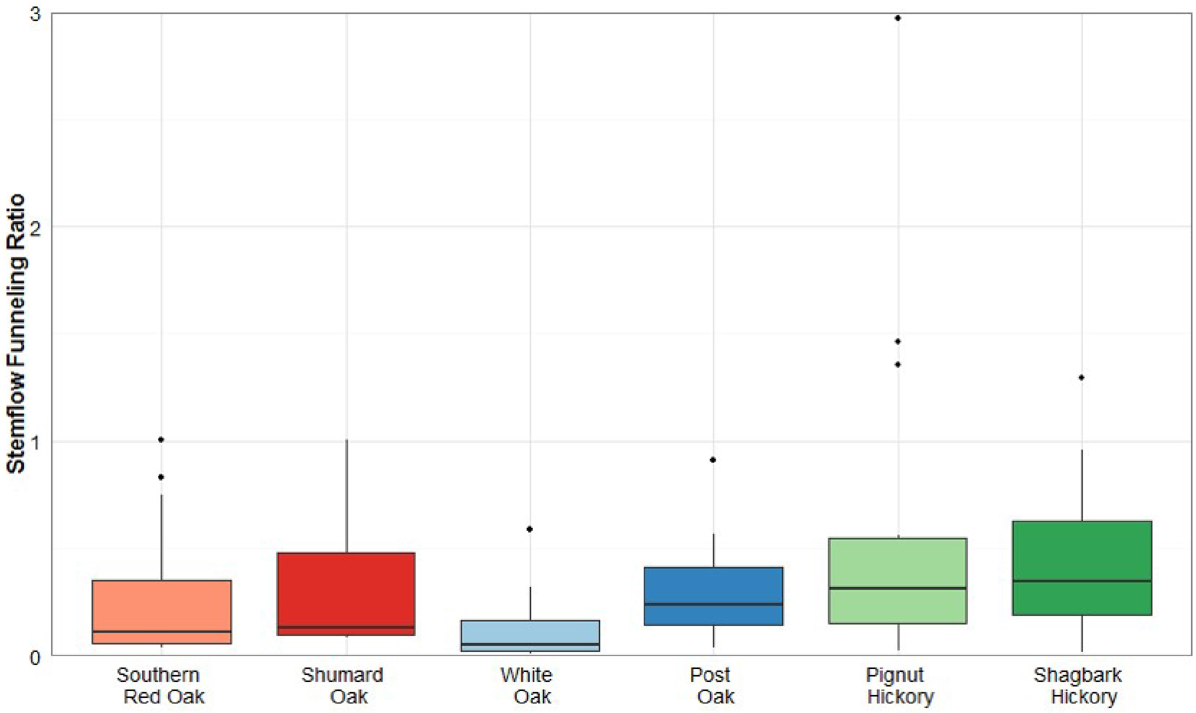

*Figure 6. Stemflow funneling ratio for each of the 6 tree species in this study. Boxplots illustrate the distribution of TOC concentrations with the horizontal black bar representing median concentrations, the box representing the first and third quartiles, the whiskers representing 1.5 times the interquartile range, and the circles representing outliers.*

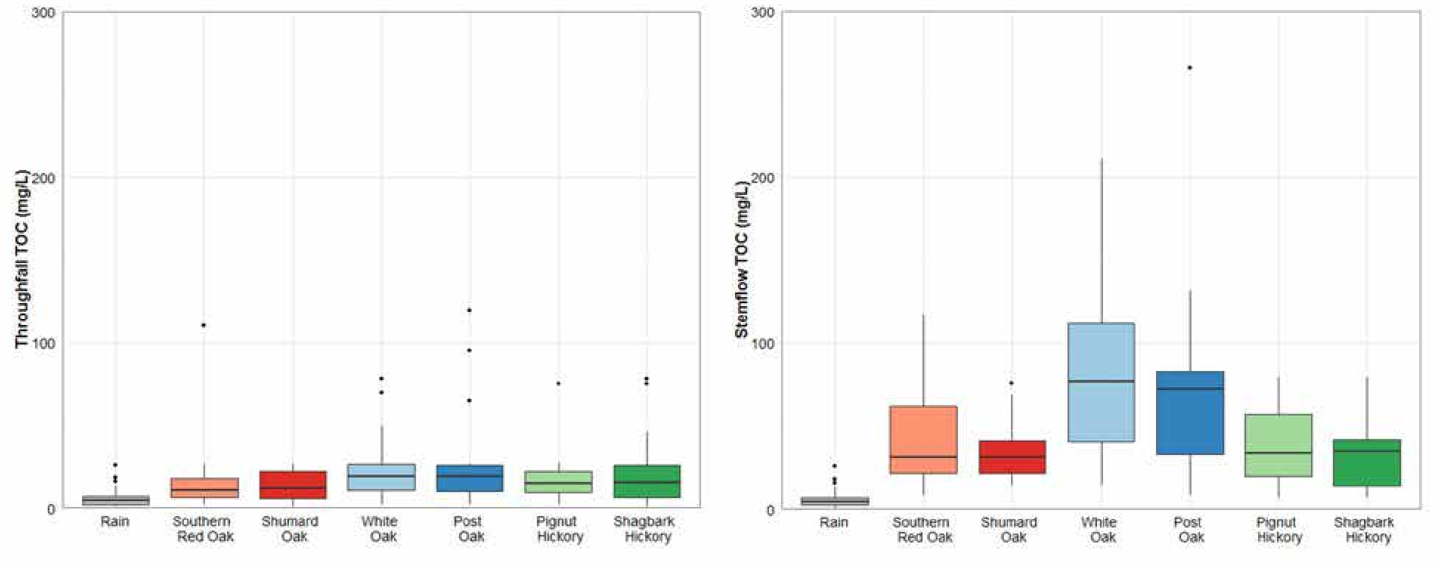

*Figure 7. Total organic carbon (TOC) concentrations of rainfall compared to throughfall (left) and stemflow (right) for each of the 6 tree species in this study. Boxplots illustrate the distribution of TOC concentrations with the horizontal black bar representing median concentrations, the box representing the first and third quartiles, the whiskers representing 1.5 times the interquartile range, and the circles representing outliers.*

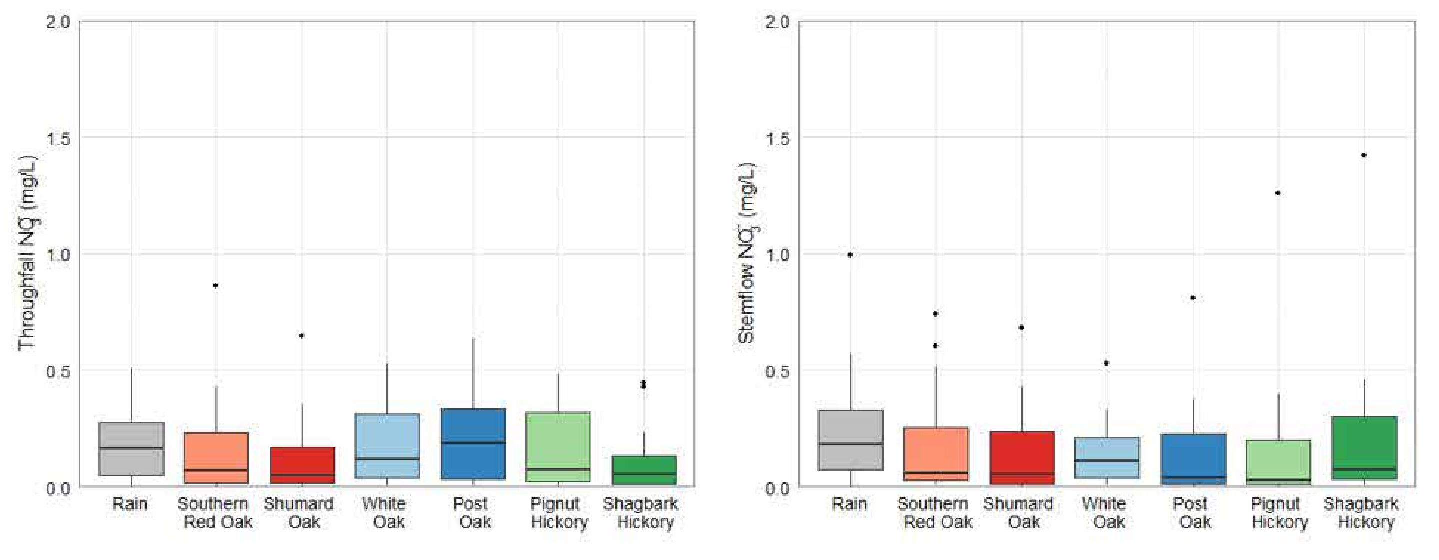

*Figure 8. Nitrate ($NO_{3-}$) concentrations of rainfall compared to throughfall (left) and stemflow (right) for each of the 6 tree species in this study. Boxplots illustrate the distribution of $NO_{3-}$ concentrations with the horizontal black bar representing median concentrations, the box representing the first and third quartiles, the whiskers representing 1.5 times the interquartile range, and the circles representing outliers.*

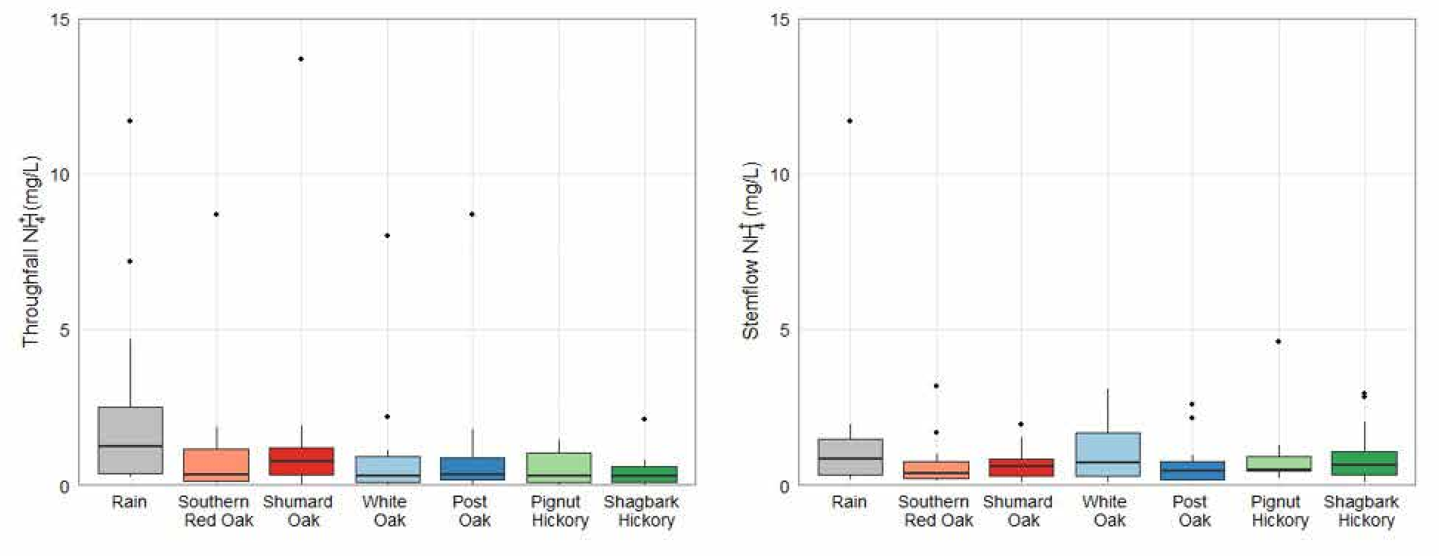

*Figure 9. Ammonium ($NH_{4+}$) concentrations of rainfall compared to throughfall (left) and stemflow (right) for each of the 6 tree species in this study. Boxplots illustrate the distribution of $NH_{4+}$ concentrations with the horizontal black bar representing median concentrations, the box representing the first and third quartiles, the whiskers representing 1.5 times the interquartile range, and the circles representing outliers.*