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Variability of tree transpiration across three zones in a southeastern U.S. Piedmont watershed

Johnny L. Boggs[1] | Ge Sun[1] | Jean-Christophe Domec[2,3] | Steven G. McNulty[1]

[1]Eastern Forest Environmental Threat Assessment Center, USDA Forest Service Southern Research Station, Durham, North Carolina, USA

[2]Bordeaux Sciences Agro, INRA UMR 1391 ISPA, Gradignan, France

[3]Nicholas School of the Environment, Duke University, Durham, North Carolina, USA

Correspondence
Johnny L. Boggs, Eastern Forest Environmental Threat Assessment Center, USDA Forest Service Southern Research Station, 3041 East Cornwallis Road, Research Triangle Park, Durham, NC 27545, USA.
Email: johnny.boggs@usda.gov

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Abstract

Quantifying the spatial variability of species-specific tree transpiration across hillslopes is important for estimating watershed-scale evapotranspiration (ET) and predicting spatial drought effects on vegetation. The objectives of this study are to (1) assess sap flux density (J_s) and tree-level transpiration (T_s) across three contrasting zones a (riparian buffer, mid-hillslope and upland-hillslope, (2) determine how species-specific J_s responds to vapour pressure deficit (VPD) and (3) estimate watershed-level transpiration (T_w) using T_s derived from each zone. During 2015 and 2016, we measured J_s in eight tree species in the three topographic zones in a small 12-ha forested watershed in the Piedmont region of central North Carolina. In the dry year of 2015, loblolly pine (*Pinus taeda*), Virginia pine (*Pinus virginiana*) and sweetgum (*Liquidambar styraciflua*) J_s rates were significantly higher in the riparian buffer when compared to the other two zones. In contrast, J_s rates in tulip poplar (*Liriodendron tulipifera*) and red maple (*Acer rubrum*) were significantly lower in the buffer than in the mid-hillslope. Daily T_s varied by zone and ranged from 10 to 93 L/day in the dry year and from 9 to 122 L/day in the wet year (2016). J_s responded nonlinearly to VPD in all species and zones. Annual T_w was 447, 377 and 340 mm based on scaled-J_s data for the buffer, mid-hillslope and upland-hillslope, respectively. We conclude that large spatial variability in J_s and scaled T_w was driven by differences in soil moisture at each zone and forest composition. Consequently, spatial heterogeneity of vegetation and soil moisture must be considered when accurately quantifying watershed level ET.

KEYWORDS
forest hydrology, sap flux, soil moisture, water balance

1 | INTRODUCTION

About 50%–75% of annual precipitation that falls in southern forests in the United States returns the atmosphere through the process of evapotranspiration (ET; Sun et al., 2001), the sum of tree transpiration, canopy interception and soil evaporation (Sun et al., 2016). Natural (e.g., climate change and variability, drought) and anthropogenic stressors (e.g., land use change, urbanization), and forest management (e.g., thinning, prescribed burning) affect water quantity and water quality, and ecosystem productivity (Sun et al., 2011) by directly altering forest transpiration process, a key component of ET in forests (Domec et al., 2012; Sun et al., 2016). Water use by trees or whole stands is naturally variable due to the large differences in tree species, age, stand structure (i.e., leaf area index) and climate (Sun et al., 2011). Given the water issues with landcover change, species shift (Caldwell et al., 2016), urbanization (Boggs & Sun, 2011) and an increase in extreme events from climate change facing the Piedmont region in the southeastern United States (Wear & Greis, 2013), an improved understanding of forest ET at the species level in particular, within a forested watershed is needed. Such information is useful for developing foundational steps toward improving watershed-level estimates of forest water budgets and developing reliable ecohydrological model to predict the effects of environmental change on water and carbon resources (Li, Sun, Caldwell, et al., 2020; Li, Sun, Cohen, et al., 2020; Liu et al., 2020).

Land use change and fire regimes have produced highly variable tree species composition in the U.S. southeastern Piedmont. The region supports about 12.5 million hectares of forest land or 62% of the total land area, with 52% of forest lands covered by upland hardwoods and 34% by pines (Rummer & Hafer, 2014). The upland hardwood forest types consist of a mixture of white oak (*Quercus alba*), red oak (*Quercus rubra*), hickories (*Carya spp*.), sweetgum (*Liquidambar styraciflua*) and tulip poplar (*Liriodendron tulipifera*). The oak-pine forest type is dominated by loblolly (*Pinus taeda*), Virginia (*Pinus virginiana*) and shortleaf (*Pinus echinata*) pines, and southern red oak (*Quercus falcata*). Although many state and federal regulatory agencies require forests in the source water supply zone of a watershed be protected to slow runoff and maintain minimal discharge levels, 17% of total forest area could be lost by 2060 due to high urbanization and low timber prices with most of the losses occurring in the upland hardwood (Rummer & Hafer, 2014). Given the variability in species transpiration, the type of trees removed from the landscape will likely impact soil moisture, streamflow in headwater catchments and downstream water supply (Moore et al., 2004; Swank & Vose, 1994).

Quantifying spatial variations in species-specific sap flux density (i.e., g H_2O cm^{-2} day^{-1}) and daily tree-level transpiration (i.e., kg day^{-1} or L day^{-1}) is essential to improve stand-scaled transpiration estimates and total ET at the watershed level. In forests with closed canopies, tree transpiration is the largest component of ecosystem ET (Domec et al., 2012; Oishi et al., 2010). Sap flux density and stand level transpiration rates can vary widely by species (Boggs et al., 2015; Yi et al., 2017). For example, tree transpiration in a temperate pine-hardwood riparian buffer forest can range from 2 to 142 L day^{-1} and can increase nonlinearly with increasing tree diameter (Bosch et al., 2014). Transpiration can vary across plant species due to tree xylem structure (Ford et al., 2011), responses to vapour pressure deficit (VPD; Moore et al., 2017) and age (Brantley et al., 2019). Tulip poplar, a species with diffuse porous xylem and large amount of sapwood, can use up to threefold more water than oaks (*Quercus spp*.), a species with a narrow sapwood characterized by a ring porous structure (Ford et al., 2011).

Species level transpiration can also differ across topography or zones due to landscape level variations in microclimate and soil moisture (Emanuel et al., 2010, 2011). Hawthorne and Miniat (2016) found that transpiration per unit leaf area in hickory (*Carya spp*.) species was sensitive to the topographic position during a wet year, producing 56% less water at a cove site when compared to an upland site. However, transpiration by chestnut oak (*Quercus prinus*) decreased 41% in a dry year when compared to a wet year, but was not influenced by topographic position. Bosch et al. (2014) also found that species topographical position does not consistently influence tree transpiration rates across species.

At the stand level, linking species transpiration and soil moisture helps further refine watershed-level estimates of transpiration (Oishi et al., 2010) and improve our understanding of how forests respond to water stresses, including drought (Vose et al., 2016; Yi et al., 2017). Sap flux density and tree-level transpiration measurements refined ET predictions and have advanced dramatically during the last decade (Poyatos et al., 2020). However, questions are still being raised about how to improve watershed-level transpiration, given the variations in species composition, topography and soil moisture in a watershed. In addition, variability in tree transpiration across heterogeneous watersheds is typically not considered (or well captured) by existing models and may be one contributing factor to over or under predictions of ET and other hydrologic fluxes at local and regional scales (Sun et al., 2011). Therefore, the objectives of this study are to (1) quantify tree sap flux density and transpiration across three contrasting but adjacent zones (riparian buffer, mid-hillslope and upland-hillslope) in a wet and dry year, (2) analyse the relationships between sap flux density and VPD and (3) compare watershed-level transpiration derived from three zones.

2 | MATERIALS AND METHODS

2.1 | Study site

The forested small watershed in this study, designated as Hill Forest Watershed No. 2 (HF2), is characterized as a 38-year-old mixed pine-hardwood stand located within the Piedmont region of North Carolina (NC; Figure 1). The catchment contains a first-order stream and drains to the Flat River at North Carolina State University's Hill Demonstration Forest in Durham County, NC. HF2 is 12 ha in size, and dominated by loblolly pine (*P. taeda*), white oak (*Q. alba*), tulip poplar (*L. tulipifera*), sweetgum (*L. styraciflua*), chestnut oak (*Q. prinus*), Virginia pine (*P. virginiana*), northern red oak (*Q. rubra*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), pignut hickory (*Carya glabra*) and mockernut hickory (*Carya tomentosa*). The soils are well drained with a depth to the water table of about 2 m. They tend to function in a similar drainage capacity in the growing season (in this study May–October) and non-growing season (November–April). The NC Geological Survey (1988) reported that the soil system falls within the Carolina Slate Belt (CSB) region and varies in slope and elevation. HF2 has been used as a 'control watershed' to study the effects of tree cutting on watershed water balance since 2007 and additional soil and watershed descriptive details can be found in Boggs et al. (2013, 2015, 2016) and Dreps et al. (2014).

2.2 | Micrometeorology and soil moisture

Meteorological data have been collected at the study site since 2007 as part of a best management practice (BMP) project (Boggs et al., 2015, 2016). Precipitation was recorded in an open space with a Hobo Data-Logging Rain Gauge—RG3 (Onset Corporation, Bourne,

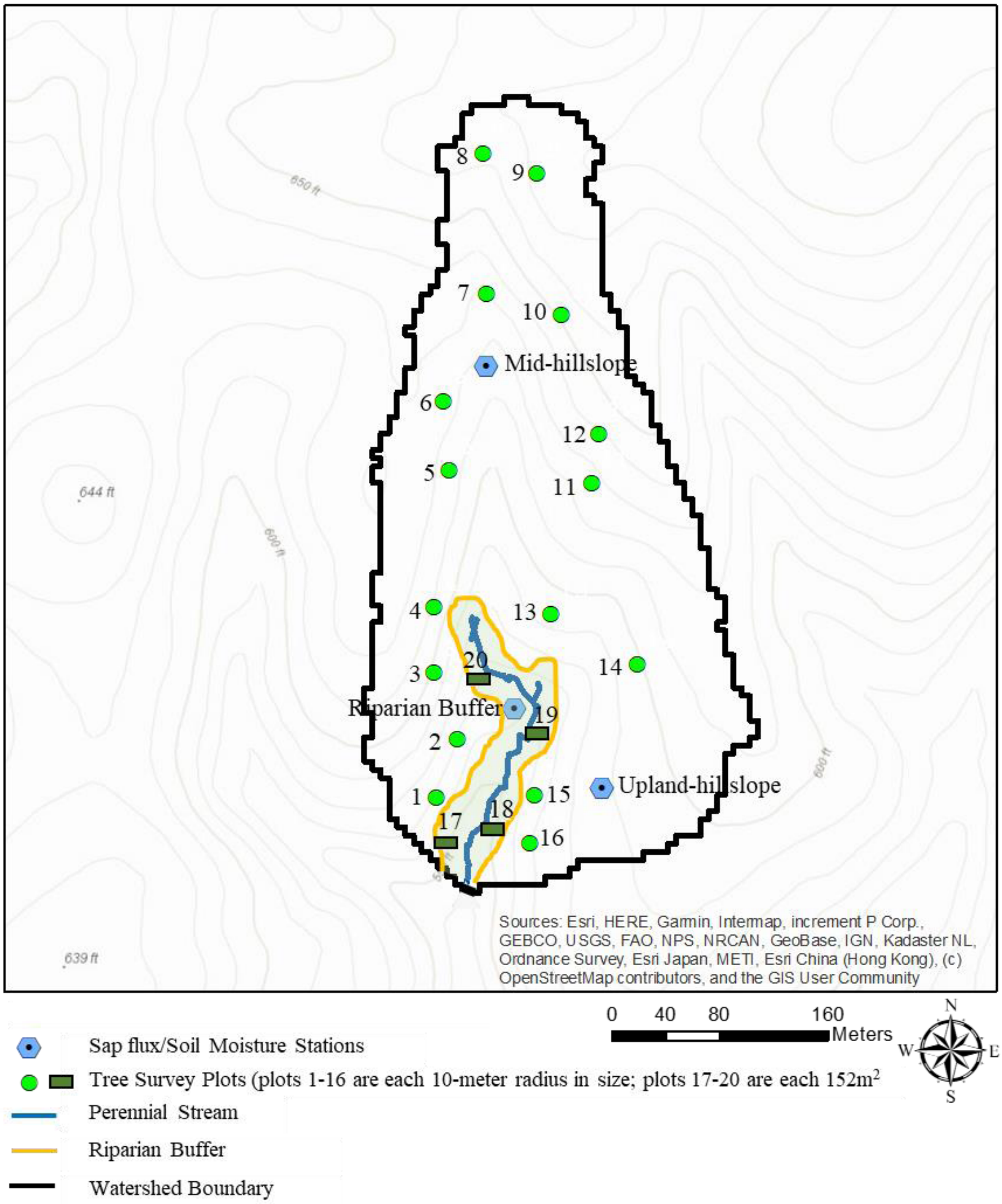

FIGURE 1 Study design in a 12-ha headwater catchment in the Piedmont of North Carolina

MA) approximately 450 m from the farthest sap flux station. Relative humidity (RH) and air temperature measurements were recorded with a Hobo Micro Station (Onset Corporation, Bourne, MA) next to the rain gauge every 10 min and averaged every hour. The hourly VPD was calculated from RH and air temperature data and reported in kilopascals (kPa) as daily averages for 24-h and daytime hours (0800–19:00).

Soil moisture and sap flux density were measured in the riparian buffer, mid-hillslope and upland-hillslope zones of the watershed from May 2015 to December 2016. The definition of the riparian buffer was based on field observations of sandy loam soils in the flat (i.e., <12% slope) stream valley bottom (Dreps et al., 2014). Mid-hillslope units correspond with the Tatum soil series and are on relatively steep (i.e., 12–50%) slopes with eroded soils that have a shallow depth to bedrock. The buffer zone has a shallow water table and upland-hillslope units have relatively flat slopes on deep soils that correspond to Cecil, Appling and Georgeville soil series (Dreps et al., 2014). Volumetric soil moisture (m^3 m^{-3} or %) readings were taken using a water content reflectometer (CS 615; Campbell Scientific, Logan, UT). Two reflectometers were installed at each zone near the sap flux monitored trees. The reflectometers were inserted parallel to the ground surface at 10 and 30 cm depths in the riparian buffer, and at 10 and 60 cm depths in the mid-hillslope and upland-hillslope. Soil moisture data were logged every 10 min using a CR1000 datalogger (Campbell Scientific, Logan, UT).

2.3 | Vegetation survey

Sixteen 10-m radius (314 m^2) vegetation survey plots were established in 2015 to quantify diameter at breast height (dbh) and stem density of trees in the mid-hillslope and upland-hillslope. Four 152 m^2 plots were used to assess trees in the riparian buffer (Boggs et al., 2016). We did not used the 10-m radius sampling design that was used in the mid-hillslope and upland-hillslope zones for the riparian buffer because it would have stretched beyond the boundary of the 15.2-m wide buffer. Therefore, rectangular-shaped plots were used to characterize the overstory vegetation in the buffer (Figure 1).

Tree diversity of the watershed in this study was composed of loblolly and Virginia pines, and several native hardwoods (Table 1). The area covered by these species varied across the watershed with loblolly pine, red maple, sweetgum and tulip poplar having higher densities in the riparian buffer than in other zones. The oak species concentrated on the upper hillslopes where chestnut oak density equalled 117 stems ha^{-1}, and white oak density equalled 85 stems ha^{-1}. Species sapwood area represented 86% of the basal area in the monitored trees in the buffer, 72% in the mid-hillslope and 74% in the upland-hillslope. Sapwood area in oak species represented the smallest percentage of the basal area when compared to the other trees, averaging 47%, while loblolly pine averaged 91%.

2.4 | Sapwood area

An increment borer was used to extract two wood cores from 18 trees in the riparian buffer zone, 19 trees in the mid-hillslope and 15 trees in the upland-hillslope. All the tree core samples were collected adjacent to, but outside of the survey plots and sap flux stations. The thickness of sapwood from each core was measured with a digital calliper and converted to sapwood area. The sapwood was clearly visible in most tree cores. If the sapwood was not obvious in the tree core, it was placed under a microscope to determine the transition point between the heartwood and sapwood. The sapwood was linked to the species stem density and dbh data to derive sapwood area in the monitored trees in the sap flux stations and sapwood area in the trees in the survey plots (Table 1). Sapwood area from the monitored trees in the sap flux stations was used to compute tree transpiration. Sapwood area and tree density from the trees in the survey plots were used to scale tree-level transpiration to the watershed-level.

2.5 | Sap flux estimates

Loblolly pine, oak tulip poplar, sweetgum, Virginia pine and red maple of various sizes were instrumented with heat dissipation sensors to measure sap flux in the riparian buffer, mid-hillslope or upland-hillslope zones (Table 2). Red maple and tulip poplar were not monitored at the upland-hillslope due to limited field resources and long distance between trees. In total, there were 69 monitored trees across the watershed; 27 in the riparian buffer, 27 in the mid-hillslope and 15 in the upland-hillslope. A 20 mm heat dissipation sensor was installed 1.4 m above the ground surface (i.e., at dbh) on the north face of the tree to avoid influence from the sun. The data from the sensors were converted from temperature difference to tree sap flux density (J_s, g cm^{-2} day^{-1}, g sap cm^{-2} sapwood area day^{-1}) for each monitored species according to Granier (1987).

American beech, hickory spp, black cherry (*Prunus serotina*), scarlet oak (*Quercus coccinea*), blackgum (*Nyssa sylvatica*), black oak (*Quercus velutina*), sourwood (*Oxydendrum arboreum*) and shortleaf pine

TABLE 1 Forest structure across the topographical gradient

	Sapwood area, sap flux stations (cm^2)			Sapwood area, survey plots (cm^2)			Tree density, survey plots (stem ha^{-1})		
Species	Buffer	Mid-slope	Upland-slope	Buffer	Mid-slope	Upland-slope	Buffer	Mid-slope	Upland-slope
Chestnut oak	–[a]	532 (90)	–[a]	–[a]	245 (67)	232 (23)	–[a]	41	117
Loblolly pine	998 (118)	703 (148)	637 (70)	507 (76)	480 (31)	588 (56)	230	223	106
Northern red oak	–[a]	–[a]	238 (48)	–[a]	145 (17)	118 (17)	–[a]	57	21
Red maple	612 (381)	228 (35)		384 (187)	234 (42)	188 (69)	49	19	16
Sweetgum	329 (68)	208 (24)	132 (0)	166 (13)	202 (27)	143 (9)	132	57	21
Tulip poplar	819 (350)	373 (58)	–[a]	327 (62)	298 (43)	428 (0)	164	61	5
Virginia pine	194 (43)	176 (43)	250 (146)	152 (0)	210 (45)	340 (50)	16	38	42
White oak	635 (233)	–[a]	845 (208)	90 (0)	141 (25)	226 (46)	16	83	85
other species							82	32	42
Total							691	612	456

Note: Sapwood area was determined from the monitored trees at the sap flux stations and from the trees in the survey plots. Sapwood area from the monitored trees in the sap flux stations was used to compute tree transpiration. Sapwood area and tree density from the survey plots was used to scale tree-level transpiration to the watershed-level. Standard errors are in parentheses. Other species (American beech, *Fagus grandifolia*; hickory spp *Carya spp.*; black cherry, *Prunus serotina*; scarlet oak, *Quercus coccinea*; blackgum, *Nyssa sylvatica*; black oak, *Quercus velutina*; sourwood, *Oxydendrum arboreum*; and shortleaf pine, *Pinus echinata*).

[a]Tree not present.

TABLE 2 Number of monitored trees in each zone and diameter at breast height (dbh) of those species

Zone	Species	Number of trees monitored	dbh (cm)
Riparian buffer	Loblolly pine	5	39.4
	Red maple	5	23.5
	Sweetgum	5	22.3
	Tulip poplar	5	29.9
	Virginia pine	3	17.4
	White oak	4	29.7
Mid-hillslope	Loblolly pine	5	31.8
	Red maple	5	18.8
	Sweetgum	5	18.2
	Tulip poplar	5	24.0
	Virginia pine	2	16.5
	Chestnut oak	5	27.0
Upland-hillslope	Loblolly pine	5	30.0
	Sweetgum	1	14.0
	Virginia pine	2	18.3
	Northern red oak	5	19.3
	White oak	2	35.2

(*P. echinata*) occupied 8% of co-dominant canopy space and were not monitored at any of the three zones for transpiration due distance and limited resources. Mean species-specific transpiration (T_s, L day^{-1}) for these non-monitored trees was determined based on a linear model developed between dbh (cm) and T_s from monitored trees:

$$\text{For 2015}, T_s = 3.1 * \text{dbh} - 34, r^2 = 0.76, p < 0.001 \quad (1)$$

$$\text{For 2016}, T_s = 3.8 * \text{dbh} - 48, r^2 = 0.70, p < 0.001 \quad (2)$$

T_s for these non-monitored trees was then converted from L day^{-1} to mm day^{-1} (equivalent to L m^{-2} day^{-1}) by dividing the total sap flow volume of the survey plot trees by plot area (78.5 m^2).

Transpiration for each zone (T_z, mm day^{-1}) was estimated from tree-scaled J_s for all monitored trees, estimates of T_s from the non-monitored trees (Equations 1 and 2), stand density (tree counts) and species composition and sapwood area. The same species sapwood area and tree counts were used for each zone to scale J_s to T_z to avoid over- or under-emphasizing watershed sapwood area for each zone. Weighted area percentages for each zone was estimated based on landscape units that included percent slope, soil type and unsaturated zone depth (Dreps et al., 2014) and field observations of species across the watershed (Boggs et al., 2015). The weighted area average (i.e., 10% buffer, 45% mid-hillslope and 45% upland-hillslope) of T_z from each zone was then used to compute the weighted average at the watershed-level, riparian buffer, mid-hillslope and upland-hillslope T_w.

Measurements of tree J_s in the buffer have been continuous since 2010 as part of other studies (Boggs et al., 2015, 2016). However, monitoring in mid-hillslope and upland-hillslope did not begin until May 2015. Despite these two zones having only 2 months (November–December 2015) of non-growing season J_s data in 2015, average daily non-growing season T_w based on J_s from this limited dataset is representative of the longer-term non-growing record for Piedmont hardwoods (~0.25 mm day^{-1}; Oishi et al., 2010). Therefore, we estimated the other 4 months (January–April 2015) of missing daily non-growing season T_w and filled other data gaps based on the average daily non-growing season T_w data.

Sap flux density varies across sapwood depth and this variability influences sap flux density calculation. To count for this variability, we used the estimates of the radial profile of sap flux density with depth for each wood type calculated from the gamma-type model in Berdanier et al. (2016). Based on this model, we developed correction factors for each species and tree anatomy/type. After the correction factor was applied to sap flux density, annual stand transpiration was computed. The trees in our study were smaller than the ones in the Berdanier et al. (2016), which means that the sap flux density corrections were likely not going to be large, and would become even smaller when corrected for the area represented by the outer 20 mm probes in relation to the other sections of the tree. Thereafter, the corrected transpiration values (sap flux density*sapwood area*correction factor) are reported in this manuscript.

2.6 | Statistical analysis

All data analyses were completed using JMP Pro 12 (JMP, 2012). Sap flux density across years and zones was determined using a paired *t*-test. The zone was defined as a riparian buffer, mid-hillslope and upland-hillslope. The *t*-test was selected, and the significance level was set to $\alpha \leq 0.05$ to determine which year or zone was statistically different from each other. The power model was used to determine the nonlinear relationship between daily VPD and sap flux density. The explanatory and response variables in the bivariate plots were log-transformed to produce the power model, $y = ax^b$. The effects test was used to determine if the VPD influenced sap flux density across the zones and if there was an interaction between VPD and the zones. VPD was log transformed to reflect the power function of the relationship between VPD and species sap flux density. P values <0.05 indicate that the independent variables and/or their interaction were significantly related to sap flux density.

3 | RESULTS

3.1 | Rainfall and VPD

Total annual precipitation was 1027 mm in 2015 and 1178 mm in 2016 (Figure 2a,b). The daily growing season (from May to October) precipitation ranged from 0.2 to 47.2 mm in 2015 (total growing season precipitation = 424 mm), and 0.2 to 119.2 mm in 2016 (total growing season precipitation = 846 mm). These data contrasted with the average (2008–2016) growing season precipitation of 636 mm, and the average

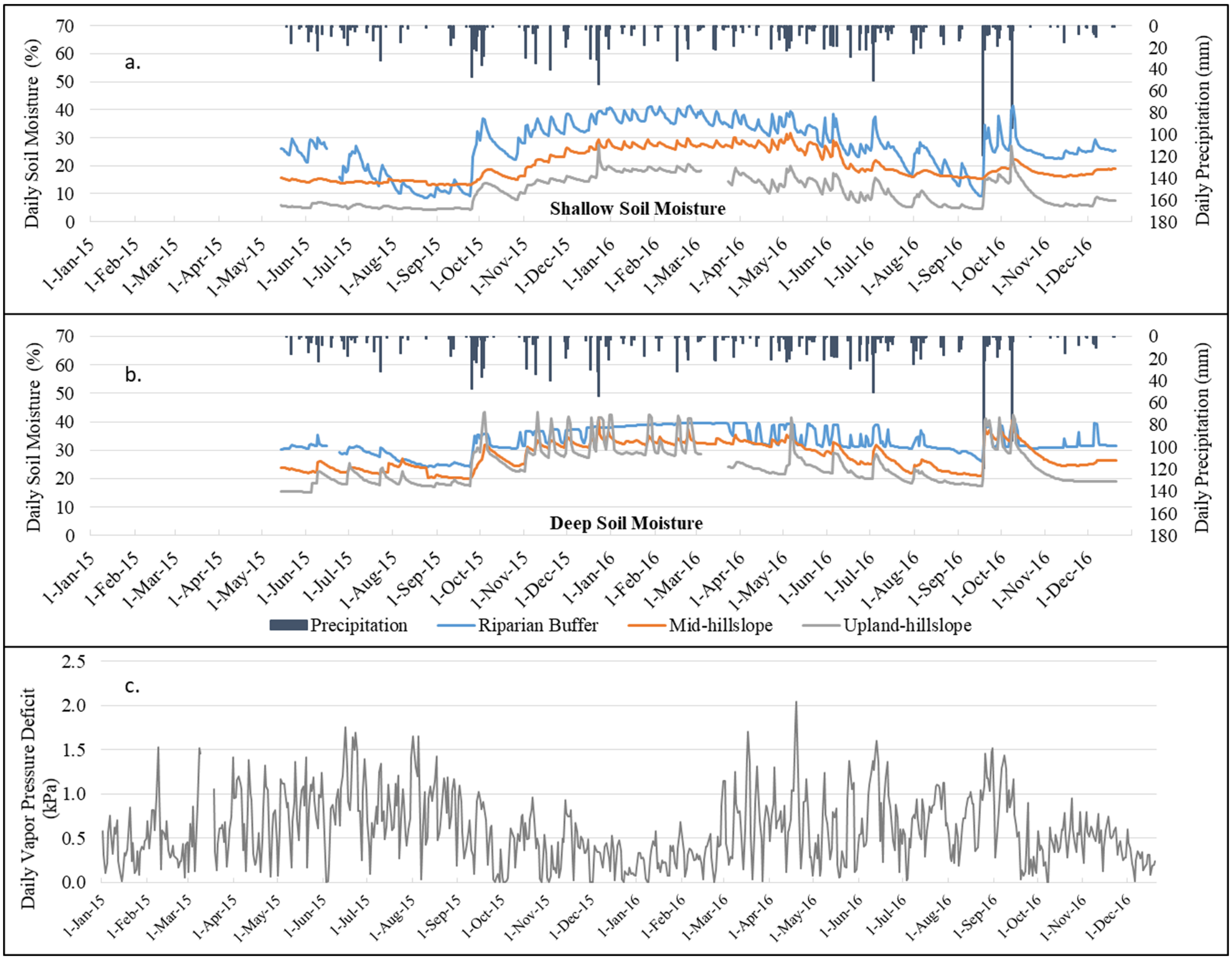

FIGURE 2 Daily (a) shallow soil moisture (10-m), (b) deep soil moisture (30-cm for riparian buffer and 60-cm for mid-hillslope and upland-hillslope) and (c) vapour pressure deficit pattern over the study period. Precipitation is shown above moisture

annual total precipitation of 1112 mm (Boggs et al., 2016). Thus, the 2015 growing season was 34% drier (dry year) than average precipitation, while the 2016 growing season was 33% wetter (wet year) than average.

Growing season VPD in the drier year of 2015 was significantly higher ($p \le 0.05$) than the growing season VPD in the wetter year of 2016 (Figure 2c). In 2015, the mean daily growing season VPD averaged 0.73 (standard error, 0.028) kPa and ranged from 0.01 to 1.7 kPa. In 2016, the mean daily growing season VPD averaged 0.65 (0.027) kPa and ranged from 0.01 to 1.5 kPa.

3.2 | Soil moisture

Although seasonal soil moisture was significantly higher in the riparian buffer than the other zones in 2015 and 2016 (Table 3), a more detailed analysis of daily soil moisture revealed that moisture varied across zones throughout the year (Figure 2a,b). For example, shallow soil moisture shifted from a wet state to a dry state halfway through the 2015 growing season in the riparian buffer. This shift is defined by a distinct change in soil moisture that falls below 15% in the riparian buffer. Shallow soil moisture in the buffer also remained in a dry state until late September (i.e., mid-hillslope moisture was higher than riparian buffer moisture from July 2015 to September 2015). The mid-hillslope and upland-hillslope did not show a strong trend of wet to dry states.

Deep soil moisture (30 cm depth) in the riparian buffer remained 20% and 38% higher, respectively than soil moisture at 60 cm deep in the mid-hillslope and upland-hillslope during the 2015 and 2016 growing seasons (Figure 2b). Soil moisture at this deeper depth in the riparian buffer also remained wet and reached a saturation point of 40% during the non-growing season. There were a few periods in the non-growing season where the deep soil moisture in the mid-hillslope and upland-hillslope was higher than the soil moisture in the riparian buffer.

3.3 | Sap flux density

Daily growing season sap flux density (J_s) varied across species, zones and years (Table 3). Comparing J_s by zone in 2015, the loblolly pine,

TABLE 3 Daily mean growing season (May–October) soil moisture and sap flux density from three sap flux stations (buffer, mid-slope and upland-slope) in 2015 and 2016, and mean growing season across those years

	Soil moisture (%)								
	Growing season, 2015			Growing season, 2016			Growing season, mean		
	Buffer	Mid-slope	Upland-slope	Buffer	Mid-slope	Upland-slope	Buffer	Mid-slope	Upland-slope
	20 (0.5)aA	15 (0.1)bA	6 (0.2)cA	26 (0.4)aB	20 (0.3)bB	11 (0.3)cB	23 (0.5)a	17 (0.2)b	9 (0.2)c
	Sap flux density (J_s, *g cm*$^{-2}$ *day*$^{-1}$)								
Species									
Chestnut oak	–[a]	67 (2)A	–[a]	–[a]	84 (3)B	–[a]	–[a]	76 (9)	–[a]
Loblolly pine	124 (4)Aa	109 (4)Ab	75 (3)Ac	122 (4)Aa	99 (3)Ab	91 (3)Ab	123 (1)a	104 (5)b	83 (8)c
Northern red oak	–[a]	–[a]	42 (1)A	–[a]	–[a]	47 (1)B	–[a]	–[a]	45 (3)
Red maple	83 (3)Aa	108 (4)Ab	–[a]	101 (3)Ba	99 (3)Aa	–[a]	92 (9)a	104 (4)b	–[a]
Sweetgum	109 (4)Aa	87 (3)Ab	75 (3)Ac	92 (3)Ba	108 (3)Bb	65 (2)Bc	101 (8)a	97 (10)a	70 (5)b
Tulip poplar	106 (3)Aa	115 (5)Ab	–[a]	104 (4)Aa	115 (4)Ab	–[a]	103 (1)a	115 (0.2)b	–[a]
Virginia pine	137 (5)Aa	–[a]	75 (3)Ab	79 (2)Bb	101 (4)a	110 (4)Ba	108 (29) a	105 (4)a	92 (17)b
White oak	98 (4)Aa	–[a]	87 (3)Ab	96 (3)Aa	–[a]	101 (3)Ba	97 (1)a	–[a]	94 (7)a

Note: Standard error is in parenthesis. Daily means with the same letters are not significantly different at $p < 0.05$. Uppercase letters define the year versus year within the same zone, and lowercase letters define zone versus zone within year.
[a]Species was not present at that area in the watershed or not in close enough proximity to the sap flux station to be monitored. Soil moisture at the 10 cm depth.

sweetgum, Virginia pine and white oak J_s in the riparian buffer were significantly higher than J_s in those same species in the mid-hillslope and upland-hillslope (Table 3). In contrast, the tulip poplar and red maple J_s in the riparian buffer were significantly lower than tulip poplar and red maple J_s in the mid-hillslope.

In 2016, the loblolly pine was the only species where J_s in the riparian buffer was significantly higher than J_s in the mid- and upland-hillslopes (Table 3). The red maple and white oak J_s were not significantly different across zones. The tulip poplar and Virginia pine had significantly higher J_s on the mid-hillslope than did the same species in the riparian buffer. The mid-hillslope J_s in sweetgum trees were significantly higher than sweetgums located in the riparian buffer and upland-hillslope.

By year, the loblolly pine, tulip poplar and white oak were the only species where J_s did not change significantly. J_s is all other species increased or decreased from 2015 to 2016.

Growing season means showed that white oak J_s trees were not significantly different across zones (Table 3). The J_s in loblolly pine, sweetgum and Virginia pine decreased significantly across zones (riparian buffer > mid-hillslope > upland-hillslope) and decreased with decreasing soil moisture content (Table 3). J_s in tulip poplar and red maple increased significantly across zones (riparian buffer < mid-hillslope) and increased with decreasing soil moisture content.

3.4 | Relationship between VPD, sap flux density and zones

A power function model was used to determine the relationship between the daily growing season (May–October) VPD and J_s from the monitored tree species in 2015 and 2016. Daily J_s in all species were significantly related to VPD across all zones in both years with the highest r^2 values occurring in 2015 when compared to 2016 (Table 4). The nonlinear relationship generally led to increased deviations at higher VPD values.

In 2015 and 2016, we found the interaction of VPD and zone was significantly correlated to J_s in loblolly pine, sweetgum and Virginia pine but not related in red maple, tulip poplar and white oak ($p < 0.05$; Table 5). The effects of VPD and zone on J_s also varied depending on the data series (24-h vs. daytime hours) that was used to compute J_s and VPD. In 2015, for white oak, the interaction between VPD and zone was not significantly related ($p = 0.14$) to J_s with the 24-h data but the interaction was significantly related ($p = 0.01$) to J_s with the daytime data. In 2016, for white oak, the interaction between VPD and zone was slightly significant ($p = 0.09$) to J_s with the 24-h data but the interaction was significantly related ($p = 0.04$) to J_s with the daytime data. In 2016, for tulip poplar, the interaction between VPD and zone was not significantly related ($p = 0.3$) to J_s with the 24-h data but the interaction was significantly related ($p = 0.003$) to J_s with the daytime data.

3.5 | Relationship between zones, sapwood area, dbh and tree-level transpiration

Mean daily transpiration in the monitored trees ranged from 10 to 93 L day^{-1} in 2015 and 9 to 122 L day^{-1} in 2016 (Figure 3). Mean dbh ranged from 14 to 40 cm, sapwood area ranged from 132 to 1000 cm^2, and both were linearly related to transpiration in all

TABLE 4 Results of the power function model for average 24-h daily vapour pressure deficit (VPD) and sap flux density (J_s, g cm^{-2} day^{-1}) during the growing season (May–October) from the monitored tree species in each zone in 2015 and 2016

	2015				2016			
Species	*a*	*b*	r^2	*P*	*a*	*b*	r^2	*P*
Loblolly pine								
Riparian buffer	141	0.57	0.64	<0.0001	135	0.81	0.53	<0.0001
Mid-hillslope	133	0.56	0.82	<0.0001	100	0.72	0.53	<0.0001
Upland-hillslope	83	0.46	0.58	<0.0001	90	0.55	0.27	<0.0001
All zones	116	0.53	0.66	<0.0001	109	0.70	0.42	<0.0001
Red Maple								
Riparian buffer	90	0.37	0.52	<0.0001	106	0.49	0.56	<0.0001
Mid-hillslope	125	0.47	0.73	<0.0001	99	0.65	0.54	<0.0001
All zones	107	0.43	0.64	<0.0001	102	0.57	0.53	<0.0001
Sweetgum								
Riparian buffer	123	0.48	0.74	<0.0001	100	0.45	0.54	<0.0001
Mid-hillslope	92	0.30	0.44	<0.0001	109	0.60	0.49	<0.0001
Upland-hillslope	75	0.21	0.24	<0.0001	63	0.45	0.28	<0.0001
All zones	94	0.29	0.39	<0.0001	86	0.52	0.34	<0.0001
Tulip poplar								
Riparian buffer	117	0.48	0.75	<0.0001	116	0.54	0.55	<0.0001
Mid-hillslope	122	0.35	0.43	<0.0001	106	0.45	0.25	<0.0001
All zones	118	0.37	0.48	<0.0001	111	0.49	0.36	<0.0001
Virginia pine								
Riparian buffer	156	0.59	0.59	<0.0001	84	0.43	0.58	<0.0001
Mid-hillslope	133	0.56	0.82	<0.0001	103	0.82	0.61	<0.0001
Upland-hillslope	83	0.46	0.58	<0.0001	106	0.52	0.25	<0.0001
All zones	117	0.53	0.65	<0.0001	99	0.57	0.39	<0.0001
White oak								
Riparian buffer	99	0.23	0.19	<0.0001	90	0.33	0.29	<0.0001
Upland-hillslope	91	0.18	0.28	<0.0001	93	0.13	0.04	0.02
All zones	94	0.19	0.25	<0.0001	93	0.22	0.11	<0.0001

Note: The power function equation is shown ($y = ax^b$); y = sap flux density and x = VPD. $P < 0.05$ means the relationship between VPD and sap flux is significant.

zones in 2015 and 2016. The slope coefficients between zones were not significantly different (Figure 3). When dbh and sapwood area were small (<20 and <400 cm^2, respectively), daily transpiration ranged from 9 to 45 L day^{-1}. For trees with larger sapwood area (800 to 1000 cm^2), daily transpiration ranged from 72 to 122 L day^{-1}.

3.6 | Watershed-level transpiration

Growing season weighted watershed-level transpiration (T_w) was similar in 2015 (i.e., 284 mm) and 2016 (i.e., 285 mm; Table 6). In contrast, the growing season watershed-level transpiration (by zone, T_z) in the riparian buffer ranged from 334 to 363 mm while growing season T_z in the mid-hillslope ranged from 306 to 313 mm. The growing season T_z on the upland-hillslope produced the lowest transpiration, 245 mm in 2015, and 246 mm in 2016. The daily growing season T_z in the riparian buffer in 2015 and 2016 averaged 1.7 (0.06) mm day^{-1} and 1.4 (0.06) mm day^{-1}, respectively and reached a maximum of 2.6 and 2.7 mm day^{-1}. The daily growing season T_z in the mid-hillslope in 2015 and 2016 averaged 1.2 (0.05) mm day^{-1} and 1.0 (0.05) mm day^{-1}, respectively and reached a maximum of 2.4 and 2.5 mm day^{-1}. The daily growing season T_z in the upland-hillslope in 2015 and 2016 averaged 1.0 (0.03) mm day^{-1} and 0.9 (0.03) mm day^{-1}, and reached a maximum of 2.0 mm day^{-1}. There was also a strong seasonal component to T_w in 2015 and 2016, where 80% (i.e., 284 mm) and 79% (i.e., 285 mm) of the stand transpiration occurred in the growing season. Regardless of which zone was used to derive T_w, the non-growing season T_w was always statistically lower than the growing season T_w (Table 6).

The annual total T_w was 361 mm in 2015, and 370 mm in 2016. In 2015 and 2016, loblolly pine accounted for 40%–50%, white oak 13%–14%, tulip poplar 11%–14%, sweetgum 6%–7%, Virginia pine 4%–8% and red maple 4% of growing season T_w and T_z.

TABLE 5 Effects test of the relationship between species sap flux density and average vapour pressure deficit (VPD), zone (buffer, mid-slope, upland-slope) and the interaction between VPD and zone in 2015 and 2016

Sap flux density versus	24-h data				Daytime (0800–19:00) data			
	2015		2016		2015		2016	
	F ratio	Prob > F	F ratio	Prob > F	F ratio	Prob > F	F ratio	Prob > F
Loblolly pine								
VPD	360	<0.0001	203	<0.0001	472	<0.0001	717	<0.0001
Zone	88	<0.0001	45	<0.0001	108	<0.0001	80	<0.0001
VPD*Zone	18	<0.0002	9	0.0001	30	<0.0001	14	<0.0001
Red maple								
VPD	177	<0.0001	148	<0.0001	204	<0.0001	413	<0.0001
Zone	79	<0.0001	1.5	0.2	107	<0.0001	0.9	0.3
VPD*Zone	2.2	0.12	0.3	0.6	0.6	0.4	0.9	1.0
Sweetgum								
VPD	219	<0.0001	164	<0.0001	332	<0.0001	553	<0.0001
Zone	44	<0.0001	78	<0.0001	113	<0.0001	176	<0.0001
VPD*Zone	19	<0.0001	6	0.003	42	<0.0001	16	<0.0001
Tulip poplar								
VPD	129	<0.0001	78	<0.0001	165	<0.0001	257	<0.0001
Zone	17	<0.0001	0.9	0.3	11	<0.0001	0.4	0.6
VPD*Zone	0.1	0.71	1.1	0.3	1	0.31	8.9	0.0031
Virginia pine								
VPD	268	<0.0001	134	<0.0001	161	<0.0001	376	<0.0001
Zone	102	<0.0001	13	<0.0001	74	<0.0001	63	<0.0001
VPD*Zone	27	<0.0001	4	0.02	57	<0.0001	10	<0.0001
White oak								
VPD	31	<0.0001	19	0.007	51	<0.0001	74	<0.0001
Zone	5	0.03	0.5	0.48	5	0.02	0.2	0.64
VPD*Zone	2	0.14	2.8	0.09	6	0.01	4	0.04

Note: Relationships from 24-h and daytime (0800–19:00) observations of sap flux density and VPD are shown. F ratio and probability statistics are shown. *P* value <0.05 indicate that the independent variable or their interaction was significantly related to sap flux density.

4 | DISCUSSION

The heat dissipation method was used to determine water loss from trees in a small watershed: species-specific sap flux density, tree-level transpiration and watershed-level transpiration. Results from each spatial scale were compared across species, zones and years. Even though in both years the different tree species accounted for the same proportion of watershed-level transpiration (i.e., around 45% for loblolly pine, 14% for white oak, 12% for tulip poplar and the other species representing less than 30%), we found a large variability of sap flux over time, and among trees and spatial zones within the watershed. Such variabilities are essential for understanding environmental controls on tree transpiration, plant resilience to drought and scaling up transpiration measurements from the tree level to stand and landscape scales. In addition, this work defines the range of variability in species water use in a small headwater and provide baseline or foundational data for complementary studies.

4.1 | J_s across species and zones

In the dry year, water use rates by most tree species were sensitive to the topography, and their J_s values increased with increasing soil water availability in the zones (Table 3). For example, growing season J_s in loblolly pines in the riparian buffer was 14% higher than J_s in loblolly on the mid-hillslope and 65% higher than J_s in loblolly on the upland-hillslope. In addition, growing season J_s in white oak in the riparian buffer was 12% higher than J_s in white oak on the upland-hillslope. By contrast, growing season J_s in tulip poplar and red maple in the riparian buffer was 12%–13% lower than J_s in poplar and maple on the mid-hillslope. This suggests that tulip poplar and red maple may have utilized shallow soil water in the riparian buffer early in the growing season with no relative increase in transpiration rates when compared to the mid-hillslope zone, and may have been water-stressed later in the season as there was a sharp decline and wide fluctuations in soil moisture in the buffer when

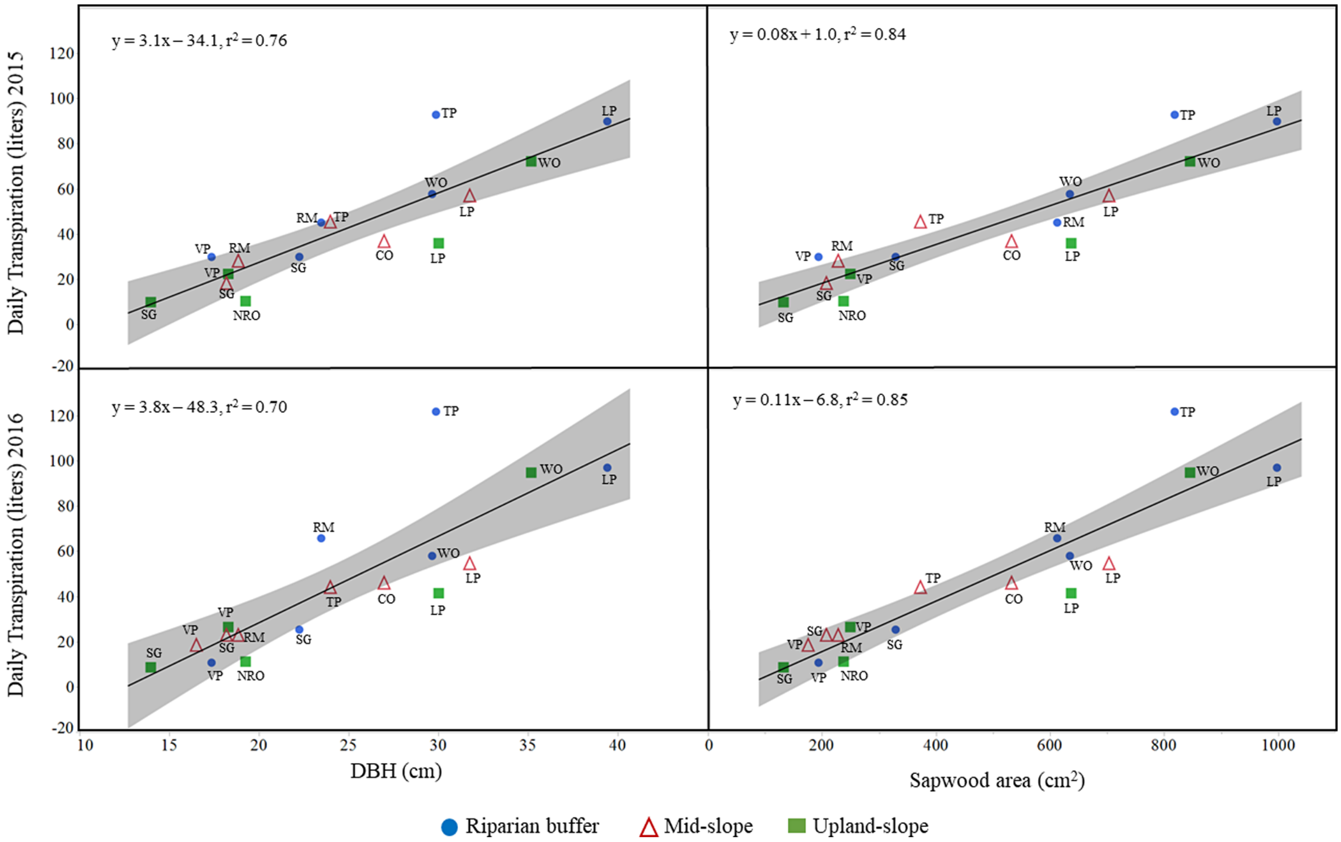

FIGURE 3 Relationship between diameter at breast (dbh) and sapwood area, and daily species transpiration across all zones for the monitored trees in the growing season (May–October) of 2015 and 2016. The regression line represents the relationship for all zones (the regression line for each zone are not shown, however the regression coefficients of those line are not significantly different). The shaded area depicts 95% confidence interval for the trend. CO, chestnut oak; LP, loblolly pine; NRO, northern red oak; RM, red maple; SG, sweetgum; TP, tulip poplar; VP, Virginia pine; WO, white oak

compared to the mid-hillslope (Hawthorne & Miniat, 2016). In addition, there was likely enough energy and soil water in the soil profile for poplar and maple to maintain water use rates on the mid-hillslope during a period when mid-hillslope soil moisture was higher than the riparian buffer.

We observed a soil moisture shift from a wet state to a dry state (soil moisture content <15%) halfway through the 2015 growing season in the riparian buffer, and soil moisture remained in a dry state until late September (i.e., mid-hillslope moisture was higher than riparian buffer moisture from July 2015 to September 2015). This depletion of soil water in the buffer zone likely reduced J_s in maple and poplar trees. This switch between wet and dry states in the buffer was not as pronounced in 2016, likely because it was a wet year. Thus, riparian buffer and mid-hillslope red maple J_s were not significantly different and not influenced by the topography in the wet year. In addition, J_s in white oak was statistically the same in the buffer and upland zones in the wet year, 96 versus 101 g cm^{-2} day^{-1}, indicating no sensitivity to zones. Hawthorne and Miniat (2016) also found variations in species-based transpiration responses to climatic variation and topographic position, and they suggest that variability in species responses to drought may lead to complex shifts in species composition.

4.2 | J_s response to VPD

Although J_s rates in all species were related to VPD (Table 4), it is worth noting that the relationships between growing season VPD and J_s in 2015 in the riparian buffer were stronger than in 2016 (i.e., higher r^2 values), likely because the soils in the watershed were drier and the evaporative potential was significantly higher in 2015 than in 2016 (Domec et al., 2009). Growing season VPD in 2015 was significantly higher (by 5%) than the VPD average for the watershed, and growing season VPD in 2016 was significantly lower (by 10%) than the average (Boggs et al., 2016). The variation suggests that VPD likely compensated for any potential drought-induced reduction in J_s in 2015 for some species in this study, as would be supported by Oishi et al. (2010). Emanuel et al. (2010) also reported that soil water stress conditions could decouple species J_s from VPD and become increasingly more dependent on soil moisture.

The effects test indicated that species, zone and year influenced J_s in the monitored trees (Table 5). In 2015, zone and VPD were significantly related to J_s in all species and the interaction between VPD and zone was significantly related to J_s in all species except white oak. Oak trees have been shown to have consistent deep-water access that can influence water use (Lanning et al., 2020). Oren and Pataki (2001) also

TABLE 6 Comparison of zone watershed-level transpiration (T_z) based on scaled sap flux density data from the buffer, mid-slope and upland-slope against watershed-level transpiration (T_w) based on weighted T_z from all three stations

Year	Precipitation	Buffer T_z			Mid-slope T_z			Upland-slope T_z			Zone weighted buffer, mid-slope and upland-slope T_w		
		Nongrowing	Growing	Annual	Nongrowing	Growing	Annual	Non-growing	Growing	Annual	Non-growing	Growing	Annual
	mm												
2015	1027	84	363	447	61	306	367	91	245	336	77	284	361
2016	1178	113	334	447	65	313	378	98	246	344	85	285	370
Mean	1103	99	349	447	63	310	373	95	246	340	81	285	365

Note: The weighted area average to compute T_w from each zone was 10% for the riparian buffer, 45% for the mid-slope and 45% for the upland-slope.

found that species-specific transpiration respond differently to soil moisture and climate—for instance transpiration in red maple indicated a greater response to soil moisture depletion when compared to white oak. In 2016, the effects test results were more mixed where growing season VPD, zone and their interaction were significantly related to J_s in loblolly pine, sweet gum and Virginia pine but not significantly related to J_s in red maple, tulip poplar and white oak. Species-specific transpiration responds differently to soil moisture depletion for several reasons including deep-water access even when shallow soil water is available (Lanning et al., 2020; Oren & Pataki, 2001).

For tulip poplar and white oak, daytime values of VPD improved the interactive relationship of VPD and zone with J_s (i.e., p values improved from 0.3 to 0.003 for tulip poplar in 2016; Table 5). This likely occurred because trees are more stressed during the day than at night and rely on greater amounts of soil moisture. This improvement was limited to poplar and white oak, which further suggest the need for more work to understand the challenges that may influence species-specific transpiration. VPD can be easily calculated from RH and air temperature, two variables that are commonly measured both regionally and locally. By further developing the relationship between species sap flux density and VPD, we can help expand the application of these results.

4.3 | Tree- and watershed-level estimates of transpiration

Sapwood area explained nearly 85% of the variability in daily tree-level transpiration (T_s; in the monitored trees) across all zones, with tulip poplar generating higher than predicted transpiration for its diameter and sapwood area in the riparian buffer and mid-hillslope (Figure 3). In contrast, loblolly pine had lower than predicted transpiration for its sapwood area in the mid-slope and upland-slope. Unlike species J_s that was related to zone, an effect test revealed that T_s rates were significantly correlated to sapwood area and species but not to zone (sapwood—F ratio 122.8, $P = <0.0001$; species—F ratio 9.2, $P = 0.0076$; zone—F ratio 2.1, $P = 0.20$). This is not surprising as T_s is closely linked to and driven largely by sapwood area (Wullschleger & Norby, 2001).

Annualized zone weighted watershed-level transpiration (T_w) was very similar from a dry year to a wet year (361 mm vs. 370 mm; Table 6) in part because J_s was not significantly different for loblolly pine, white oak and tulip poplar between years. These three species occupied 50% of the sapwood area and were responsible for almost 75% of the water loss in both years (i.e., 73% in 2015) and (i.e., 76% in 2016). Oishi et al. (2010) also found similarities or small variations in transpiration across wet and dry years, 329–349 mm over 4 years. Hawthorne and Miniat (2016) also found that species composition may explain the similarity between T_w between wet and dry years.

There were differences in scaled T_w, depending on which T_z was used to represent tree water use (Table 6). We compared T_z based on scaled J_s data from the buffer, mid-slope and upland-slope against T_w based on weighted T_z from all three stations to determine their relative differences. Riparian buffer zone estimates of annual water loss were 24% higher in 2015 and 21% higher in 2016 than T_w based on weighted T_z from all three stations. Annual water loss from the mid-hillslope was only 2% higher in 2015 and 2016 than T_w based on weighted T_z from all three stations while water loss from upland-hillslope was 7% lower in both years than T_w. The riparian buffer and upland-hillslope produced larger percent differences than mid-hillslope likely because they did not fully capture the spatial changes in species J_s response to VPD as well as the range of watershed soil moisture conditions and stand structure across the watershed (Mitchell et al., 2012). In addition, the hydrologic controls on tree J_s in these two zones likely shifted from climatic factors to soil moisture as VPD increased, and soil moisture rapidly decreased (Emanuel et al., 2010). The riparian buffer and upland-hillslope zones also had larger amplitudes for drainage and soil moisture compared to the mid-hillslope. The coefficient of variation in soil moisture was 24% in the mid-hillslope, 32% in the riparian buffer and 48% in the upland-hillslope. If we assume weighted T_z across the three zones offered the best estimate of T_w, then it appears T_z from the mid-hillslope was within a reasonable range to determine annual T_w. J_s-scaled T_w from the buffer and upland-hillslope resulted in broader estimates of T_w than mid-hillslope and should probably not be used as standalone zones to determine T_w.

5 | CONCLUSIONS

Results from this study fill a knowledge gap regarding species water use across contrasting zones in a watershed in the Piedmont region. We found that the response in species water use to decreasing soil water content across zones was dependent on the species, year and VPD. Water use response to VPD in the dry year varied by species, which suggests the need for additional studies to understand the controls on species-specific transpiration. Mid-hillslope sap flux density provided the best estimates for watershed-level transpiration because this zone captured the range of watershed soil moisture conditions and stand structure across the watershed.

Water use by trees could intensify soil hydrological drought (i.e., lack of soil moisture) during short-term dry periods of low precipitation. Under normal climatic conditions, red maples and tulip poplars will likely create more soil water storage and benefit storm water abatement when compared to other common trees in the region. However, the advantages of these species might be less critical during increasing or prolonged droughts.

This study improves our broader understanding of the relationship between species-specific transpiration and soil moisture. Linking soil moisture, tree water use and climatic variability at the watershed level is rarely done, but is critical to refining transpiration estimates, managing the effects of drought and understanding hydrological processes in unmanaged and managed watersheds across various regions. New plantations with fast growing tree species (e.g., loblolly pine) are being planned across the southern United States to meet the rising demand for wood production. Findings from this project could help public and private landowners decide which trees might be better to maximize the benefits and costs related to water in tree planting across the Piedmont.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Johnny L. Boggs https://orcid.org/0000-0003-4826-1843

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