

RESEARCH ARTICLE

Water use of co-occurring loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*) in a loblolly pine plantation in the Piedmont

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Abstract

Measuring water use in co-occurring loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) enhances our understanding of their competitive water use and aids in refining watershed water budget model parameters. This study was conducted in a 12-ha forested headwater catchment in the Piedmont of North Carolina, southeastern U.S., from 2018 to 2019 (pre-thinning) to 2020 (post-thinning). Sap flux density (J_s), species-level transpiration (T_s), and watershed-level transpiration (T_w) were quantified. Water use efficiency (WUE) in loblolly and shortleaf pines was compared, alongside an investigation into how both species' J_s and T_s responded to atmospheric vapor pressure deficit (VPD). Loblolly pine had 19%–36% higher J_s than shortleaf pine. Daily T_s for loblolly pine ranged from 15.0 to 29.0 L/day while T_s in shortleaf pine ranged from 3.0 to 6.8 L/day. The T_s was significantly higher in loblolly pine when compared to shortleaf pine likely due to higher canopy position and higher growth rates of the former. WUE, defined by annual tree biomass growth per tree water use, was not significantly different between the two. Daily J_s and T_s in both species responded non-linearly to VPD, with loblolly pine being more sensitive and variable. Species-specific water use should be considered when quantifying T_w and developing reliable models to predict the effects of forest management practices on water resources.

KEYWORDS

transpiration, loblolly pine, shortleaf pine, sap flux density

1 | INTRODUCTION

Forest management has important implications for surface water yield and groundwater recharge by altering tree water use in the humid southeastern U.S. (Pisarello et al., 2022; Sun et al., 2010). For example, streamflow in a watershed covered by native mature deciduous hardwoods was reduced by 200 mm a year or 20% when the cover was converted to white pine (*Pinus strobus* L.) forest plantations (Swank & Douglass, 1974). Younger et al. (2023) reported that watersheds dominated by longleaf pine (*Pinus palustris* Mill.) generally had higher water yield compared to those dominated by loblolly pine (*Pinus taeda*) with higher leaf area. It is common that some streams dry up completely in productive plantations due to their high transpiration rates in the southern eastern U.S. coastal plains (Sun et al., 2002, 2010). In addition, the conversion of natural forests to forest plantations can potentially decrease tree resistance to drought (Domec et al., 2015). Climate change is likely to cause forest tree species change and shifts in the water balances under a changing climate and management objectives (Caldwell et al., 2016; Sun & Vose, 2016). Increasing our understanding of species-specific water use and water use efficiency (WUE) from co-existing species can be used in forest management and planting strategies to help maintain an adequate water supply for downstream lakes and

Research Impact Statement

Species-specific water use should be considered when quantifying tree transpiration and developing reliable models to predict the effects of forest management practices on water resources.

reservoirs (Ford et al., 2011). Existing forest hydrological models cannot describe hydrological responses to forest management (i.e., species conversion) due to the absence of water use information at species levels (Sun et al., 2023).

In the 1950s, there were almost no loblolly pine plantations in the southern United States. However, loblolly pine has been widely planted to meet rising wood demand. Now there are over 16 million hectares of planted pine with most of that expansion occurring over a 25-year period (1985–2010) (Langner et al., 2020; Wear & Greis, 2013). Loblolly pine serves as a source of revenue for millions of people (PINEMAP, 2021) and is the leading timber-producing species in the U.S. Loblolly pine is considered a fast-growing tree that is adapted to wetter soils due to a shallow root system (Brewer, 1975). In addition, loblolly pine may have a higher rate of transpiration and water use than some other species in the south, which can enable it to grow more rapidly. The loblolly–shortleaf pine forest community is the dominant forest type in the southeastern U.S. and its area is forecasted to remain roughly level through 2060 due to continued investment in plantations and active forest management (Wear & Greis, 2013). Without active planning, loblolly–shortleaf pine forest communities might transition to mixed hardwood in the future (Matusick et al., 2020).

In the 1930s, shortleaf (*Pinus echinata*) pine was more abundant than loblolly pine and provided wood for furniture, pulp material, pallets, and other products for decades (Sutter, 2019). Overharvesting of shortleaf pine forests, fire suppression, and efforts of the southern pine tree improvement program fostering genetically modified loblolly and slash pines resulted in a dramatic reduction in the presence of shortleaf across the landscape (Guldin, 2019). Forestland dominated by shortleaf represents currently around 2.4 million hectares across 22 states and many of these hectares of shortleaf pine co-occur with loblolly pine. This is a decline of 53% since 1980 and 91% since 1896 (Oswalt, 2013). In North Carolina, three-fourths of the remaining shortleaf stands are found in the region of this study—Piedmont (NC Forest Resources Assessment, 2010). Shortleaf pine is a slower-growing species than loblolly that is adapted to drier soils and has a deeper root system that may allow it to access water from deeper soil layers (Carlson & Harrington, 1987). Hypothetically, shortleaf pine may have a lower rate of transpiration and higher WUE (i.e., the amount of biomass produced for a certain amount of water a tree uses), which could help it to survive in prolonged dry conditions.

The Shortleaf Pine Initiative seeks to restore a portion of the woodlands where shortleaf pine was once the dominant or co-dominant species (Guldin & Black, 2018). For example, the Ouachita National Forest has acquired loblolly pine stands from land purchases with timber companies. Once these woodlands reach maturity, the loblolly pine will be cut, and the stands will be reforested with shortleaf pine to maintain the native shortleaf pine ecosystem. As these restoration efforts expand, and loblolly pine plantations continue to increase in the southeastern U.S., species-specific water use studies need to be explored to ensure that the land management goals of loblolly–shortleaf pine forests are met without compromising water resources and the benefits they provide (Sun & Vose, 2016).

To our knowledge, no data exist that compare water use and WUE between co-occurring shortleaf pine and loblolly pine, two historically dominant and ecologically important southern pines. Understanding species-specific (e.g., shortleaf) water use and WUE, and WUE responses to forest management will likely be some of the main targets in the management of rural and urban forests and water resources in the future as climate patterns continue to vary across the region (Hoffman et al., 2023; Zhang et al., 2023). Understanding the nuances of species-specific and co-occurring water use can contribute to a more comprehensive approach to refining the ecological roles that tree species have in managed pine forests. This study contributes to the knowledge about the water use of specific pines, which can add to our capacity to address broader challenges in the context of climate change and ecosystem resilience. Therefore, the objectives of this study were to: (1) quantify sap flux density (J_s) and species-level transpiration (T_s) in shortleaf pine and loblolly pine, and watershed-level transpiration (T_w) in the Piedmont region of North Carolina, (2) compare WUE of these species, and (3) determine the effect of soil moisture and vapor pressure deficit (VPD) on J_s and T_s before and after a thinning.

2 | MATERIALS AND METHODS

2.1 | Study site

The watershed in this study, designated as Hill Forest One (HF1) is characterized as an eight-year-old planted loblolly pine stand located within the Piedmont region of North Carolina (NC) (Figure 1). The catchment drains the first-order streams into the Flat River watershed at North Carolina State University's Hill Demonstration Forest in northern Durham County, NC. The ecoregion is classified as Carolina Slate Belt (CSB)

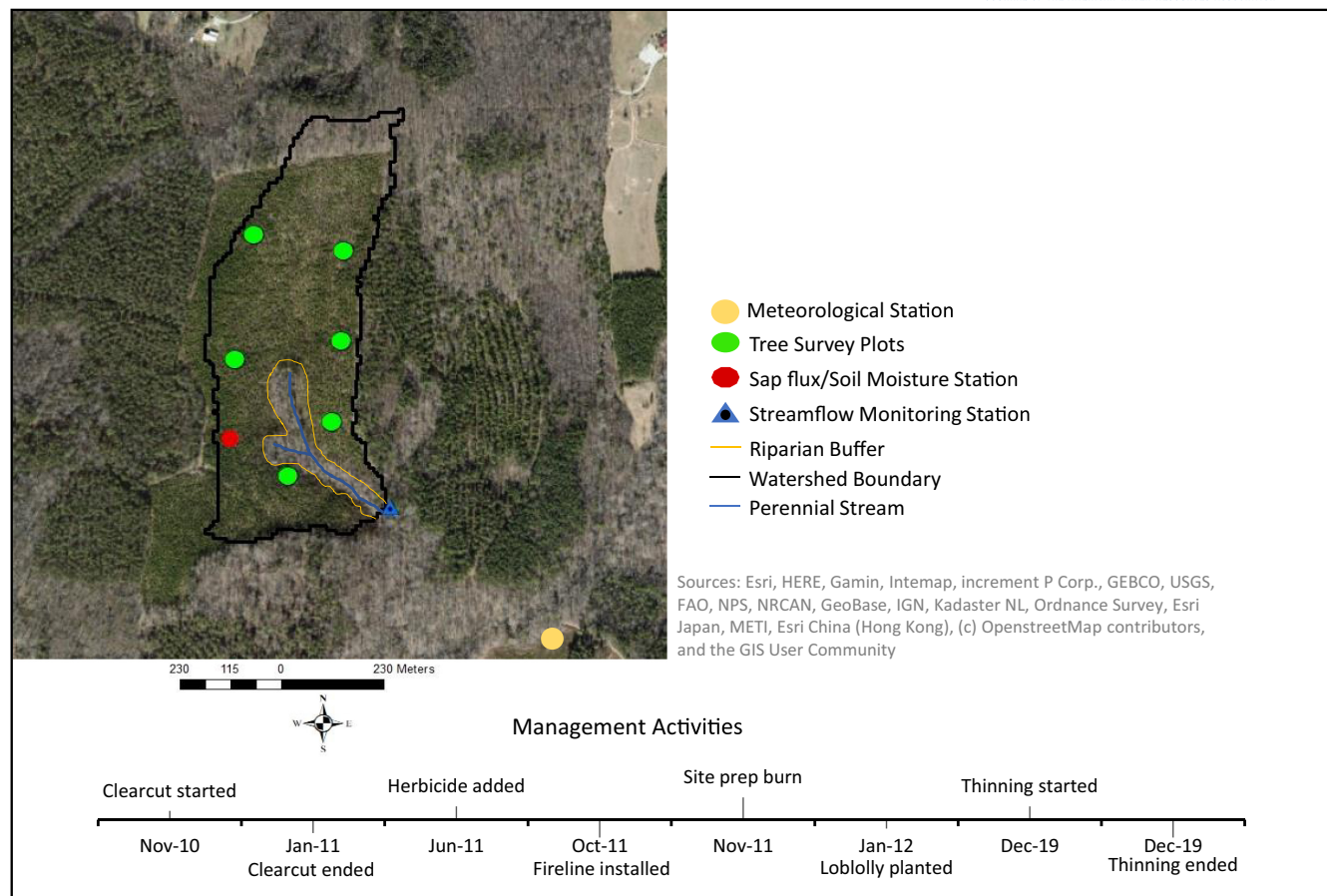


FIGURE 1 Study design and management activities in a 12-ha headwater catchment in the Piedmont of North Carolina.

and the soils on the upland slopes are defined as well-drained with a depth to water table greater than 2 m. The total land surface in the CSB covers 9% of NC and extends into the surrounding states of Virginia and South Carolina (Cleland et al., 2007). The soil series is mainly comprised of silt loam, gravelly silty clay loam to sandy loam soils. Additional details about the study watershed can be found in Boggs et al. (2016).

2.2 | Tree planting and precommercial thinning

Before the catchment was clear-cut in 2010, it was a 40-year-old mixed pine-hardwood forest with 536 trees per hectare (280 hardwoods and 256 pines per hectare). The study design and management activities for planting the loblolly pines after the harvest are shown in Figure 1. In 2012, improved loblolly pine seedlings of Piedmont origin were planted at 1075 trees per hectare (3.05 m × 3.05 m spacing). In addition to the planted loblolly pines, naturally regenerated loblolly and shortleaf pines were present throughout the stand. The natural pines grew from the seed crop of the mature pines that were in the watershed before the clear-cut. Thus, by 2019 the tree spacing for loblolly and shortleaf trees in the watershed had reached 4268 trees per hectare (3943 loblolly and 325 shortleaf). In December 2019, a precommercial thinning was performed in the watershed to remove the overcrowded trees (thinned from 4268 trees per hectare to 1191 trees per hectare), allowing the remaining trees to grow faster and enhance the overall health and quality of the stand and to improve the timber production. The trees were hand-fallen and left on the ground to decompose. Hand-felling the trees was the most cost-effective method and the felled trees left on the ground aid in moisture retention and provide shelter for various wildlife species in the forested watershed.

2.3 | Micrometeorology

Meteorological data have been monitored in this watershed since 2007 as part of a Best Management Practice (BMP) project (Boggs et al., 2016). Precipitation was measured in an open area with a Hobo Data-Logging Rain Gauge—RG3 (Onset Corporation, Bourne, MA, USA) approximately 500 m from the sap flux station. Relative humidity (RH), solar radiation, and air temperature (T_a) measurements were also

recorded with a Hobo Micro Station (Onset Corporation, Bourne, MA) next to the rain gauge every 10 min and averaged for every hour. The hourly VPD was calculated from RH and T_a data and reported in kilopascal (kPa). Mean daily VPD was computed when solar radiation was greater than 0.6 W/m^2 to represent daytime values. Daily VPD was used in the analysis in this study to provide a broad perspective on species water use across atmospheric moisture conditions. Both daily and hourly VPD values contribute to our understanding of how the species respond to atmospheric moisture, with daily VPD indicating a prolonged response and hourly VPD a more immediate response.

2.4 | Tree characteristics

The diameter at breast height (1.4 m above-ground level, dbh) was measured from five loblolly pine and four shortleaf pine trees each year from 2018 to 2020. Since this was a plantation or monoculture stand, the assumption was that three to five trees of each species at the mid-hillslope in the watershed could be used to characterize water use in the stand. Boggs et al. (2021) found that sap flow data measured from three to five trees in a mixed-pine hardwood stand on the mid-hillslope provided the best estimates for watershed level transpiration (when compared to the riparian buffer and upland-hillslope locations) because this zone captured the range of watershed soil moisture conditions and stand structure across the watershed. In 2020, the monitored trees were cored with a 5.2-mm increment borer to extract two wood samples. This study started several years after the improved loblolly pine were planted; therefore, we could not determine if the monitored loblolly pine trees were the improved planted trees or from the seed origin. The monitored shortleaf trees were from seed origin. Harrington et al. (1989) found that differences in root system structure between planted and seeded loblolly and shortleaf pines were similar for the two species. The thickness of sapwood from each core was measured with a digital caliper. The tree cores were then mounted and sanded to determine the annual basal area growth rate. After the cores were scanned, annual growth was measured with ImageJ (U.S. National Institutes of Health, Bethesda, MD, USA), an image processing and analysis software program. The 2020 dbh and annual growth data were used to determine the sapwood area for each tree. Annual above-ground biomass was estimated from an allometric equation by Jenkins et al. (2003) for both loblolly pine and shortleaf pine. Annual tree counts and basal area were determined from six 5-m radius permanent tree survey plots in the watershed (Figure 1).

2.5 | Sap flux, species- and watershed-level transpiration, WUE and soil moisture

Sap flux density (J_s , $\text{g/cm}^2/\text{day}$, i.e., mass of tree sap per sapwood area per day) in the pines and moisture in the soil were measured on the mid-hillslope of the watershed from January 2018 to December 2020. The sensors were replaced once, in 2019. The trees were cored after year three and sap flux density was adjusted based on changes in annual growth. The mid-hillslope zone of the watershed corresponds with the Tatum soil series and is on a relatively steep (i.e., 12%–50%) slope with eroded soils that have a shallow-to-deep water table (Dreps et al., 2014). Five loblolly pines and four shortleaf pines, that were within a 15-m radius of the plot center, were instrumented with heat dissipation probes to measure sap flux (Granier, 1987). A 20 mm sap flux sensor was installed 1.4 m above the ground surface (i.e., at dbh) on the north face of each tree to avoid direct sun influence. The sensors were covered with an aluminum shield to minimize any influence from direct solar warming. Sensor signals were converted from temperature difference to tree sap flux density for the pines according to the computation method outlined in Granier (1987). Our thermal dissipation method did not deviate from Granier's original design. Studies have shown decreases in the accuracy of the Granier equation if the thermal dissipation method deviates from the original design (Fuchs et al., 2017). In addition, the coefficients of this empirical function have already been verified for different pine species (including loblolly pine) growing under different climates using local mass balance or eddy covariance-based approaches (Domec et al., 2010; Oren et al., 1998; Tor-Ngern et al., 2017; Ward et al., 2018). The raw temperature difference data were collected every 30 s and logged every 10 min with the CR1000 data logger (Campbell Scientific, Logan, UT, USA). The data were then processed using the Baseline program to ensure consistent editing of the sap flux data (Oishi et al., 2016). Errors in the water use data due to sensor and power failures were removed from the dataset and gap-filled based on a linear model developed between tree biomass and water use from trees in this study with no obvious errors in the data. The gap-filling equations were as follows: Loblolly pine water use (kg/day) = $-4.1 + 0.50 \times \text{Biomass (kg/tree)}$, $r^2 = 0.91$, $p < 0.001$ across years; and shortleaf pine water use (kg/day) = $-3.7 + 0.63 \times \text{Biomass}$, $r^2 = 0.73$, $p < 0.001$ across years (Figure 2). In Figure 2, there are 12 data points (four trees and 3 years, 2018, 2019, 2020) for shortleaf and 15 data points (five trees and 3 years, 2018, 2019, 2020) for loblolly.

J_s can vary across sapwood depth and this variability can influence the J_s calculation. To account for this variability, we used the estimates of the radial profile of J_s with depth for loblolly and shortleaf pine that were calculated from the gamma-type model in Berdanier et al. (2016). Based on this model, we developed a correction factor for each species and applied it to the transpiration data (correction factor = 0.93 for loblolly pine and 0.98 for shortleaf pine). The correction factor was relatively minimal for these small pine trees. Nadezhkina et al. (2002) found that errors in estimating whole-tree sap flow from single-point measurements were less for smaller trees than for larger trees due to a more homogeneous distribution of velocity in the sapwood of smaller trees when compared to larger trees. The corrected values for J_s and species-level transpiration (T_s) are reported and discussed in this manuscript. The sapwood area from the monitored trees was multiplied by J_s

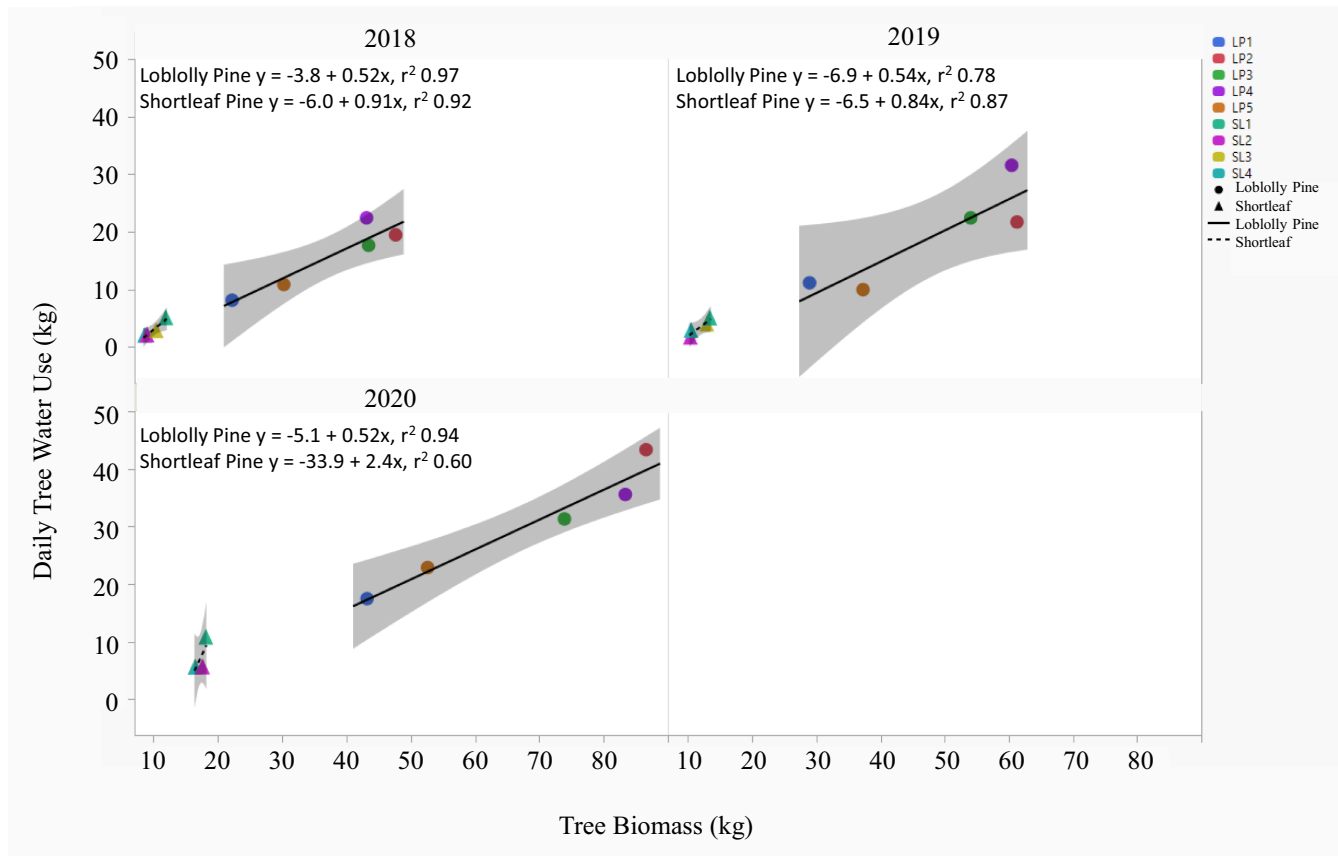


FIGURE 2 Relationship between tree biomass and daily tree water use for LP and SL in 2018, 2019, and 2020. LP, loblolly pine; SL, shortleaf pine. The shaded area depicts 95% confidence interval for the trend.

to compute T_s (reported in L/day and m^3 /year). Watershed-level transpiration (T_w , mm/year and mm/day) was calculated based on T_s (m^3 /day) multiplied by the number of trees in the watershed divided by the watershed size (m^2).

All-tree WUE ($kg\ biomass/m^3\ H_2O$) was determined from the aboveground tree biomass ($kg/tree$) from the current year minus tree biomass from the previous year divided by tree water use from the current year ($m^3\ H_2O/year$). All volumetric soil moisture (m^3/m^3) readings were taken using a water content reflectometer (CS 615; Campbell Scientific, Logan, UT, USA). The reflectometer was installed at the sap flux station near the monitored trees and inserted parallel to the ground surface at 10 cm. Volumetric soil moisture data were logged every 10 min using a CR1000 data logger (Campbell Scientific, Logan, UT, USA).

All data analyses were completed using JMP Pro 13 (JMP, 2013). The differences in tree growth data, climate variables, J_s , and transpiration across years and species were determined using a two-sample t test where the t test was used to compare the means between the two groups ($p < 0.05$). Akaike information criterion (AIC) was used to compare which model (bi-exponential, quadratic, or linear) best fits the VPD, sap flux density, and tree transpiration data. The bi-exponential 4P model had the best fit (i.e., lowest AIC) as the data exhibited a decay and threshold pattern. The prediction model is expressed as $y(t) = A_1 \times e^{-k_1 \times VPD} + A_2 \times e^{-k_2 \times VPD} + C$, where A_1 and A_2 are the amplitudes of the two exponential components, k_1 and k_2 are the decay constants of the respective exponential terms, and C is a constant term.

3 | RESULTS

3.1 | Climate and soil moisture

Annual precipitation was 1686 mm in 2018, 1141 mm in 2019, and 1535 mm in 2020. The mean daily volumetric soil moisture content was significantly lower in 2019 than in 2018 and 2020. The mean daily VPD was significantly higher in 2019 than in 2018 and 2020. Mean daily solar radiation was statistically similar across the years. Precipitation in the months of 2019 aligned with the monthly 30-year precipitation averages from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) while monthly precipitation in 2018 and 2020 was above the 30-year normal.

3.2 | Sapwood area, annual growth, and biomass

Tree sapwood area, height, dbh, and biomass values were significantly larger in the loblolly pines than in the shortleaf pines (Table 1). Tree biomass in the loblolly pines ranged from 37.3 ± 4.8 kg/tree in 2018 to 67.9 ± 8.6 kg/tree in 2020 while tree biomass in the shortleaf pines ranged from 10.0 ± 0.8 kg/tree in 2018 to 17.1 ± 0.4 kg/tree in 2020. The results revealed a positive relationship between tree biomass and daily water use for both loblolly (slope=0.50) and shortleaf pine (slope=0.62). Similar slope values suggest comparable patterns of biomass influence on water utilization for shortleaf and loblolly pines. The annual basal area tree growth was higher in the loblolly pines when compared to the shortleaf pines (Figure 3a). Growth varied during the study period with 2016 indicating the highest growth year in both species, 3.5 ± 0.28 cm²/year/tree for loblolly and 2.2 ± 0.33 cm²/year/tree for shortleaf. The annual basal area growth increased 300% in 2020 in the loblolly pines and 1100% in the shortleaf pines following the thinning in 2019. Cumulative per tree biomass between loblolly pine and shortleaf pine began to diverge during the 2016 growth season with the largest difference occurring in 2020 (170 kg vs. 45 kg, respectively, Figure 3b).

At the stand level, loblolly pine dominated the pine plantation forest (mean basal area = 18.7 ± 2.6 (m²/ha)), with shortleaf pine representing about 4% of the total pine basal area (0.7 ± 0.2 (m²/ha)) (Table 2). Stand level basal area decreased by 30% (23.2 ± 3.3 m²/ha to 16.2 ± 1.7 m²/ha) from 2019 to 2020 for loblolly pine and 24% (0.76 ± 0.3 m²/ha to 0.58 ± 0.2 m²/ha) from 2019 to 2020 for shortleaf pine (Table 2). Seventy-three percent of the loblolly pines and 67% of the shortleaf pines were removed during the thinning (3943 ± 892 trees/ha in 2019 to 1083 ± 124 trees/ha in 2020 and 325 ± 137 trees/ha in 2019 to 108 ± 40 trees/ha in 2020, respectively, Table 2).

3.3 | Tree-level sap flux density (J_s), species- (T_s), and watershed-level (T_w) transpiration

Daily J_s was 36% higher in loblolly pine than in shortleaf in 2018 (128 ± 2.9 vs. 82 ± 2.2 g/cm²/day), 35% higher in 2019 (104 ± 2.3 vs. 68 ± 1.7 g/cm²/day), and 19% higher in 2020 (152 ± 2.7 vs. 123 ± 2.6 g/cm²/day) (Figure 4A). Daily T_s for loblolly pine ranged from 15.0 ± 2.5 to 29.0 ± 4.2 L/day while T_s in shortleaf pine ranged from 3.0 ± 0.7 to 6.8 ± 1.3 L/day with the highest water use occurring after the thinning (Figure 4B). The relationship between shortleaf J_s and loblolly J_s was similar across soil moisture conditions (Figure 5a). The slopes between shortleaf T_s and loblolly T_s were the same at 0.24—for every unit of water used by loblolly, 0.24 units were used by shortleaf (Figure 5b). J_s and T_s in both loblolly and shortleaf pine responded nonlinearly to VPD during the pre-and post-thinning periods with loblolly pine T_s appearing to be more sensitive and variable to VPD than shortleaf pine (Figure 6a,b).

Annual T_s increased in loblolly pine from 2018 to 2019 (5.5 ± 0.9 to 6.8 ± 1.4 m³/year) while T_s in shortleaf pine was similar during this period (1.1 ± 0.3 to 1.2 ± 0.3 m³/year) (Table 1). After the thinning, T_s increased in both species, 56% in loblolly pine (i.e., 6.8 ± 1.4 to 10.6 ± 1.5 m³/year) and 108% (1.2 ± 0.3 to 2.5 ± 0.5 m³/year) in shortleaf pine. Although annual T_s was significantly higher in loblolly pine when compared to shortleaf pine, WUE in shortleaf pine was not significantly different than loblolly pine in 2018, 2019, or 2020 (Table 1).

TABLE 1 Comparison of LP and shortleaf pine characteristics, transpiration, and WUE from 2018 to 2019 (pre-thinning) and in 2020 (post-thinning).

		2018	2019	2020
Sap flux monitored trees				
LP	Sapwood area (cm ²)	117.6 (12.8)a	146.1 (16.7)a	194.1 (20.7)a
SL		39.8 (2.7)b	45.9 (2.8)b	62.8 (1.5)b
LP	Height (m)	7.6 (0.2)a	8.0 (0.2)a	8.7 (0.3)a
SL		6.1 (0.07)b	6.3 (0.06)b	6.7 (0.03)b
LP	DBH (cm)	12.4 (0.7)a	13.8 (0.8)a	15.9 (0.9)a
SL		7.3 (0.2)b	7.8 (0.2)b	9.1 (0.1)b
LP	Biomass (kg/tree)	37.3 (4.8)a	48.4 (6.5)a	67.9 (8.6)a
SL		10.0 (0.8)b	11.8 (0.8)b	17.1 (0.4)b
LP	Tree transpiration (m ³ H ₂ O/year)	5.5 (0.9)a	6.8 (1.4)a	10.6 (1.5)a
SL		1.1 (0.3)b	1.2 (0.3)b	2.5 (0.5)b
LP	WUE (kg/m ³)	2.5 (0.2)a	1.7 (0.1)a	1.9 (0.1)a
SL		2.7 (0.5)a	1.7 (0.3)a	2.4 (0.6)a

Note: WUE (kg/m³) = tree biomass (kg/tree) from the current year minus tree biomass from the previous year divided by tree water use from the current year (m³ H₂O/year). Comparison of means was done within years, across species—means with the same letters are not significantly different ($p < 0.05$). Standard errors are in parentheses.

Abbreviations: DBH, diameter at breast height; SL, shortleaf pine; WUE, water use efficiency.

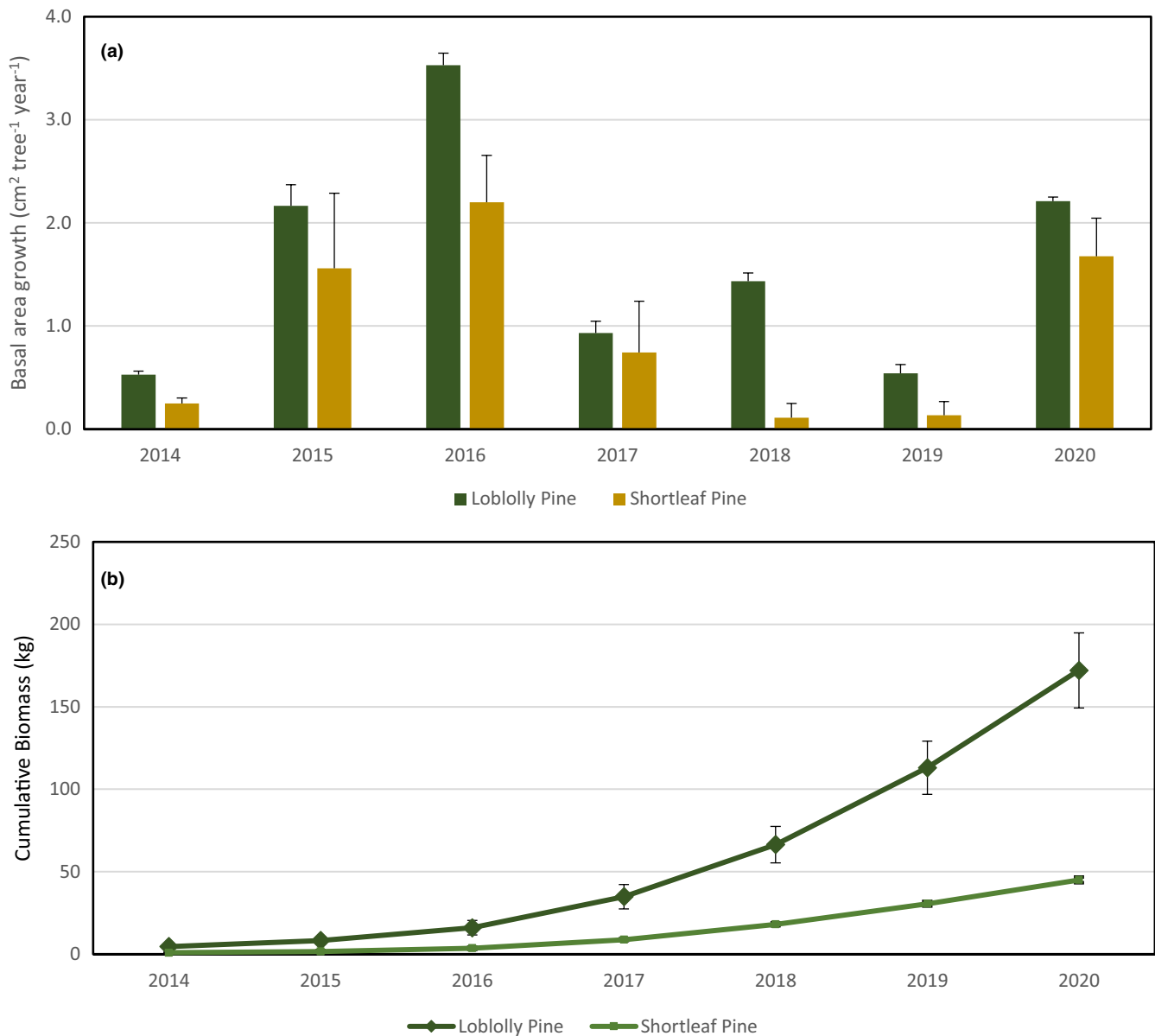


FIGURE 3 Annual (a) basal area growth and (b) cumulative biomass before (2014–2019) and after (2020) the thinning for LP and shortleaf pine.

Loblolly pines represented 95% of the basal area in the watershed and contributed around 98.6% to T_w pre-thinning, whereas shortleaf pines were 5% and contributed 1.4% to T_w (Table 2). During post-thinning, the loblolly pines were 96% of the basal area in the watershed and contributed around 97% to T_w and shortleaf pines were 4% and contributed 3% (Table 2).

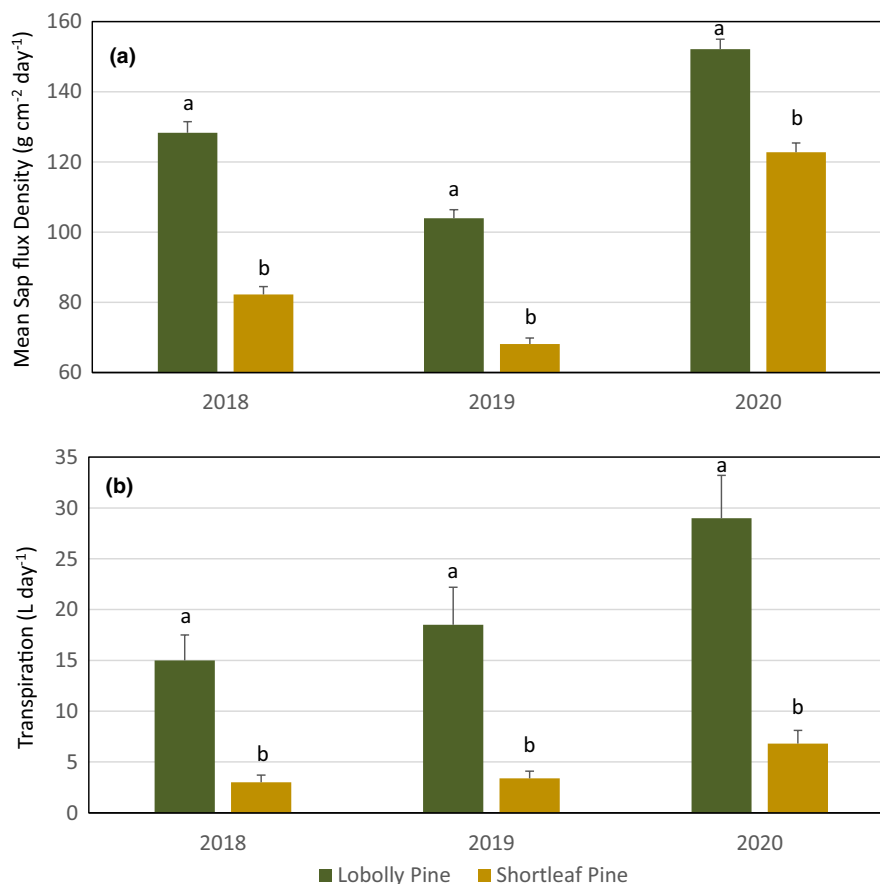
4 | DISCUSSION

This study quantified the relative differences in water use among loblolly pine and shortleaf pine in an experimental watershed to further refine our understanding of species-specific transpiration and the role it might play in the water budget of forested watersheds in the Piedmont region (Boggs et al., 2015, 2021). Forest water use information is important for understanding the full hydrological cycle in watersheds which are increasingly complex due to urbanization and climate change (Boggs & Sun, 2011). The goal of this study was to compare J_s , T_s , T_w , and WUE in loblolly pine and shortleaf pine and determine how J_s and T_s in each species respond to soil moisture and VPD before and after a thinning.

TABLE 2 Basal area, number of trees, and stand transpiration from loblolly and shortleaf pine before (2018–2019) and after (2020) the thinning.

Year	Basal area		Number of trees		Stand transpiration		
	Loblolly	Shortleaf	Loblolly	Shortleaf	Loblolly	Shortleaf	Total
	m ² /ha		ha ⁻¹		mm/year		
2018	16.7 (2.7)a	0.75 (0.2)b	3835 (923)a	238 (113)b	191	2.5	194
2019	23.2 (3.3)a	0.76 (0.3)b	3943 (892)a	325 (137)b	236	3.3	240
2020	16.2 (1.7)a	0.58 (0.2)b	1083 (124)a	108 (40)b	100	2.7	103

Note: Means with the same letters are not significantly different ($p < 0.05$).

**FIGURE 4** Comparison of (A) mean daily sap flux density and (B) daily transpiration in LP and shortleaf pine before (2018 and 2019) and after (2020) the thinning. Means with the same letter are not significantly different ($p < 0.05$). Standard error bars are shown.

4.1 | Sap flux density and species-level transpiration

The effect of species on water movement depends on various factors including how it is expressed (J_s vs. T_s). J_s considers the sapwood area to be normalized while T_s accounts for the large sapwood area. Adelman et al. (2008) found that J_s did not vary across the species in their study in a subalpine—spruce (*Picea Engelmannii*), fir (*Abies lasiocarpa*), pine (*Pinus contorta*), and aspen (*Populus tremuloides*) species. Conversely, they also found that T_s varied among those same species by a factor of four, with *P. tremuloides* having the lowest transpiration rate and *P. engelmannii* the highest. Understanding both specific J_s and T_s allows for further examination and discussion of factors that influence water use including species, structural drivers, and the links between canopy exposure/position and sapwood area. In this study, we found a similar result to Adelman et al. (2008) where the effect of species on transpiration was more dramatic in T_s than in J_s , particularly after the thinning (Figure 4). Loblolly pine and shortleaf pine are typically dominant and co-dominant in their canopy position, respectively. Research has shown that species physiology and structural drivers such as height and hierarchical position in a stand will drive differences in water use among species (Aranda et al., 2012; Oishi et al., 2010; Pataki & Oren, 2003). Teasing out the relative importance of height and canopy position relative to

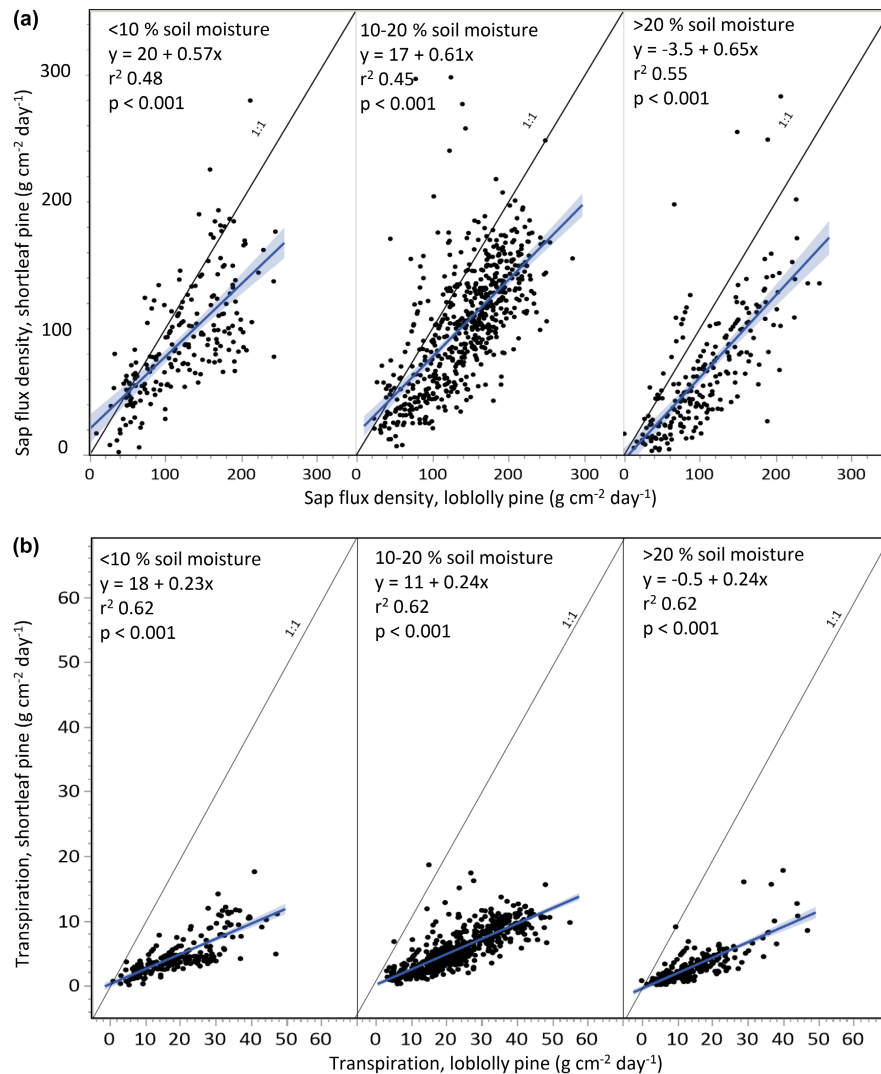


FIGURE 5 Relationship between LP and shortleaf pine (a) daily sap flux density and (b) daily transpiration during three soil moisture periods (<10%, 10%–20%, and >20%). The shaded area depicts 95% confidence interval for the trend.

the amount of water transpired by dominant and suppressed trees can be complex and was not a specific objective of this project. However, research has shown that canopy exposure and the ratio of sapwood area to the basal area can directly affect transpiration rates (Aparecido et al., 2016).

The higher J_s in loblolly when compared to shortleaf (Figure 4A) also appears to hold as the pines reach maturity. In a nearby 80-year-old mixed pine-hardwood stand, Boggs et al., (unpublished) measured J_s in three mature loblolly pines (averaging 53.7 cm in diameter and 28.9 m height) and three mature shortleaf pines (averaging 45.5 cm in diameter and 23.6 m in height) for 26 days during the growing season in 2019 (June 27–July 22). J_s was 44% higher in the loblolly pines than in the shortleaf pines (112 vs. 62 g/cm²/day).

4.2 | Species- and watershed-level transpiration

Daily T_s in the 8-year-old loblolly pine was significantly higher than the shortleaf pines but their WUE was statistically the same (Table 1; Figure 4). WUE in this study was similar to values found in Maier et al. (2017), 1.72 kg biomass m³ H₂O/year. The observed inter-species similarities in WUE suggest that shortleaf and loblolly pines when growing together, may share similar degrees of structural or physiological coordination when exposed to the range of climate and moisture conditions in this study. The lower T_s in the shortleaf pines when compared to the loblolly pines was likely a result of differences in hydraulic capacity driven by thinner growth rings, higher wood density, and shorter needles (Wang et al., 2019). In addition, the increase in leaf hydraulic conductance was likely related to a larger mean hydraulic diameter and

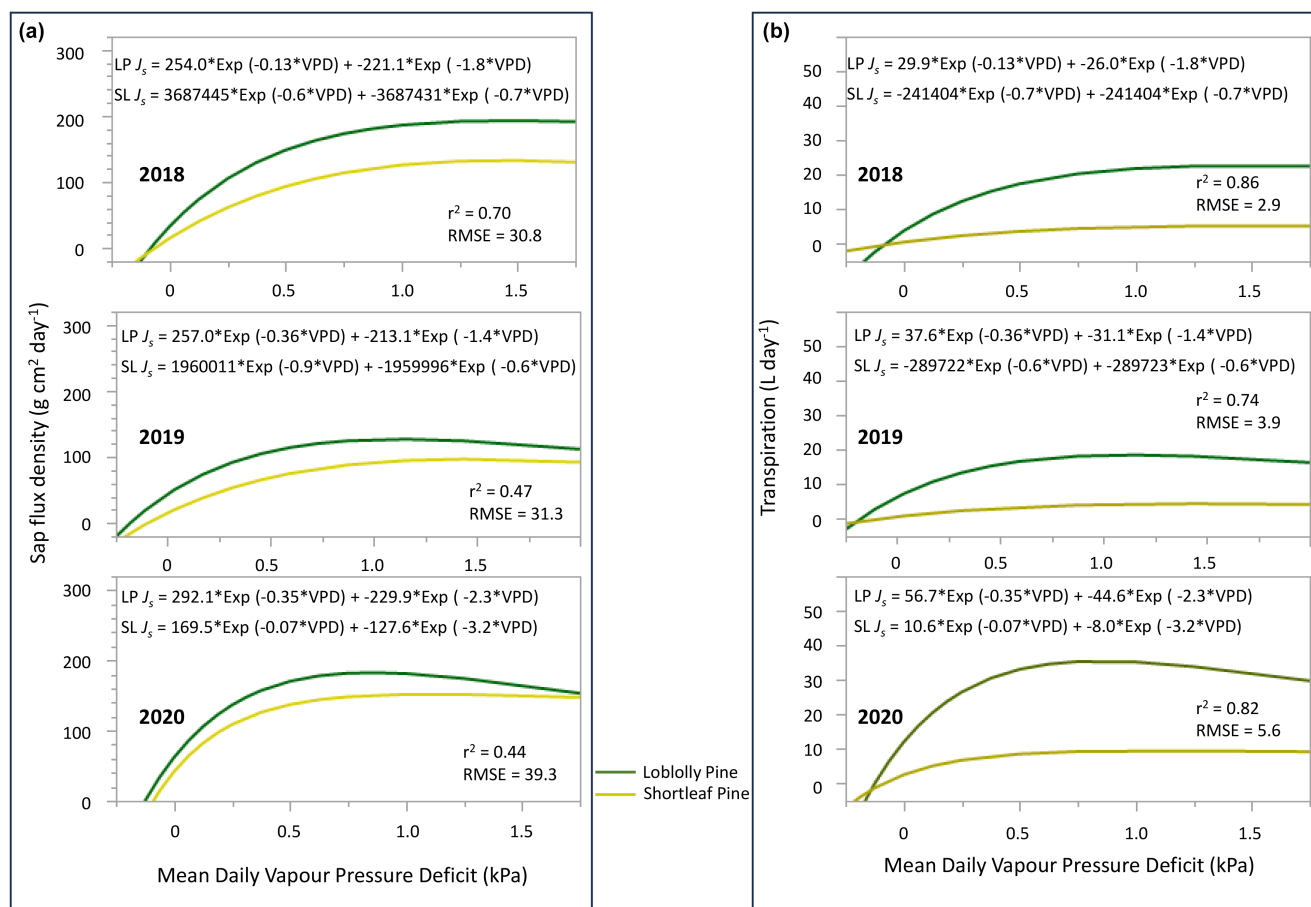


FIGURE 6 Bi-exponential 4P decay fit of mean daily vapor pressure deficit (VPD), and (a) sap flux density and (b) daily transpiration in LP and SL before (2018 and 2019) and after (2020) the thinning.

shorter pathway for water movement through the mesophyll (Scoffoni et al., 2016). Leaf hydraulic conductance tends to increase with increasing needle length in pine trees due to the relationship between leaf morphology (xylem hydraulic conductance) and water transport efficiency (Domec et al., 2016). In addition, differences in canopy position and depth of root of the two species can also explain the lower water uptake of shortleaf pines (Brewer, 1975; Carlson & Harrington, 1987). Choat et al. (2012) found that differences in root architecture and hydraulic conductivity played a major role in determining the WUE of different tree species. Dominant canopy trees, like loblolly, typically have higher transpiration rates than co-dominant trees (i.e., shortleaf) as a result of higher input radiation into the tree crown (Aranda et al., 2012; Horna et al., 2011; Martin et al., 1997). Although the subordinate canopy position could make it harder for shortleaf pine to make use of the available resources when compared to loblolly, understanding the relative transpiration rates between shortleaf and loblolly can play an important role in determining the final water budget in forested systems. However, water limitations can increase root mass relative to leaf area. This is advantageous for dry conditions but during abundant soil water, a low shoot/root ratio would disproportionately reduce the tree's ability to fully utilize the resource (e.g., shortleaf pine in this case).

Given that the watershed in this study was a planted loblolly pine plantation and was managed for loblolly, it was not surprising that loblolly dominated basal area, sapwood, and T_w (Tables 1 and 2). T_w reached a maximum of 240 mm in 2019 with shortleaf pine accounting for 3.3 mm of the total T_w . The lack of canopy openness before the thinning likely disproportionately influenced the contribution of shortleaf pine to T_w . After the thinning, the proportion of the contribution from shortleaf to T_w increased from 1.4% to 2.5%. The canopy opening likely provided an opportunity for the shortleaf pines to respond competitively, and radial growth and water use increased in response to canopy exposure.

The absolute contribution of transpiration by shortleaf to T_w was small (Table 2) but the relative change in transpiration after the thinning was larger than loblolly (Figure 4). Although this small contribution could be a result of noise in the data caused by variability in measurements or a response to subtle changes in environmental conditions, it was worth noting that T_s increased by 100% after the thinning in shortleaf whereas T_s increased by 60% in loblolly pine (Figure 4B). This could suggest that canopy exposure (not only tree height) may have influenced transpiration at the species level. In pine-dominated managed or thinned forests where shortleaf represent 15% to 20% of the basal area (Matusick et al., 2020), shortleaf contribution to T_w will likely be greater than what was observed in this study where the basal area was only 4%.

Loblolly pines grow exceptionally well in the southern United States and will double the productivity of most other pines (VanderSchaaf & Kushla, 2022). Basal area stem growth in shortleaf pine is related to root development, and the shortleaf pine rooting system is structured for drier sites with poorer soil conditions than loblolly pine (Carlson & Harrington, 1987). Shortleaf pine seedlings tend to grow slowly during the first few years to establish their root system with most of the above-ground growth occurring early in the growing season (Lawson, 1990). During this study, shortleaf pine grew much slower than loblolly pines; the shortleaf added $0.85 \text{ cm}^2/\text{year}$ of wood (or an average of 8 kg of biomass/year) while the loblolly pines added $1.5 \text{ cm}^2/\text{year}$ of wood (or an average of 28 kg of biomass/year) (Figure 3). A recent study showed that stomatal conductance and carbon assimilation are higher in pine species bearing long needles such as loblolly pine or longleaf pine (Wang et al., 2019). These structural differences between species may allow shortleaf pines to use less water and occur on sites with low water or nutrient availability (Lawson & Kitchens, 1983), and might make them more resilient to changes in climate (e.g., drought) and precipitation patterns than loblolly. McNulty et al. (2014) proposed that fast-growing, fully canopied, non-chronically stressed trees, like loblolly pine, may be more vulnerable to drought stress and climate impacts. The slower growth of shortleaf pine could suggest a potential resilience to changes in soil moisture, suggesting a nuanced aspect of forest dynamics in response to prolonged environmental changes. The total number of shorter needles have a smaller surface area than loblolly from which water can evaporate, thus allowing shortleaf pines to conserve water and potentially exhibit higher WUE than other species during drier conditions. Drought effects on species' growth and stand health depend on a range of factors including the length of drought, root traits, physiological characteristics, and species composition (Clark et al., 2016).

4.3 | Effects of soil moisture on transpiration

Shortleaf has the largest natural range of the southern pines, with loblolly pine having the second largest (Schultz, 1997). Shortleaf pine is presumed to be more drought tolerant than loblolly pine given the wide coverage of its natural range and occurrence on xeric sites (Lawson, 1990). We found that the mean slope was 0.6 between shortleaf J_s and loblolly J_s across the range of soil moisture conditions in the study, suggesting that water use (J_s) in both young pine species was similarly coupled to the amount of available soil water during the study period (Figure 5a). There is a slight decreasing trend in the relationship between soil moisture and J_s . Thus, this suggests that as soil moisture increases, there is a corresponding decrease in J_s . However, when VPD is high ($\sim 0.75 \text{ kPa}$) J_s and T_s increased with soil moisture. This pattern can likely be attributed to an increase in T_s rates in response to higher atmospheric demand that is driven in part by the amount of available soil moisture. Increases in VPD has also been shown to compensate for any potential drought-induced reduction in sap flux density (Boggs et al., 2021). This underscores the importance of considering multiple environmental factors when assessing plant water relationships. As this stand ages, variations in T_s will likely increase, altering the relationship between carbon, soil moisture, and T_s (Birdsey & Heath, 1995). Domec et al. (2012) found that a 5-year-old loblolly pine stand in the coastal plain of North Carolina used 125–290 mm less water than a 19-year-old stand. Bradley and Will (2017) reported that although transpiration in shortleaf pine was similar to loblolly pine when exposed to water stress, shortleaf pine partitioned more coarse roots than loblolly pine which may allow shortleaf to better withstand drought due to greater potential belowground carbohydrate supply. Chronic water stress in a young loblolly pine plantation may affect T_s even during wet conditions, resulting in a carryover effect of water availability on T_s (Ewers et al., 1999). Drought and thinning have been shown to have limited impacts on ET in the energy-limited coastal plain (Liu et al., 2018).

4.4 | Effects of VPD on transpiration

Atmospheric dryness, characterized by VPD, is an important driver of species transpiration, particularly when plant available water is not severely limited or during average precipitation (Wang et al., 2017). Precipitation was at or above the 30-year norm for this region during the study period, 2018–2020. Daily J_s and T_s formed a nonlinear relationship with VPD in both shortleaf and loblolly pine (Figure 6a,b). The magnitude of the difference between T_s in loblolly and shortleaf pine increased with increasing VPD (Figure 6b) but this difference was not observed for J_s , (i.e., when the data are normalized by sapwood area). The sapwood area plays a crucial role in the comparison of J_s and T_s . J_s is the rate of sap flow per unit area of sapwood, while T_s is the overall water loss by the tree. When considering sapwood area, it helps normalize the comparison by accounting for variations in tree size (which is reflected in J_s). Comparing T_s alone might lead to biased conclusions, as larger trees typically have more sapwood (*Quercus* spp. can be an exception to this, Boggs et al., 2021) and, therefore, higher absolute flux. By considering this, we assessed the efficiency of water use on a standardized/normalized basis, enabling a more accurate comparison of water loss across species.

Seventy-five percent of the days monitored in this study had a mean daily VPD of 0.7 kPa or less. This range is similar to values found in Domec et al., 2015. An increase in the number of low VPD days and uniform wetness through the canopy, due to increased precipitation, could reduce the T_s difference between the two species (Aparecido et al., 2016). T_s in loblolly pine indicated a saturation trend (i.e., saturation response to VPD) when VPD was between 0.75 to 1.0 kPa while T_s in shortleaf pine saturated between 1.0 and 1.5 kPa during the monitoring

years. Whelan et al. (2015) found that stomatal closure in a coastal longleaf pine ecosystem was between 1.75 and 2.0 kPa, suggesting a difference in species stomatal control when compared to loblolly and shortleaf pine in the Piedmont. Once T_s reached saturation in our study, T_s began to decrease or became less responsive to changes in atmospheric and environmental conditions. The lowest VPD saturation point for T_s for both species was in 2020, following the thinning.

Our study only captured 1 year of daily J_s and T_s data after the thinning, but research has shown that annual water loss in loblolly pine stands with shallow groundwater can recover (increase) within a few years after a thinning due to rapid canopy closure of the overstory trees and rapid regrowth of understory species (Liu et al., 2018). Annual tree transpiration and soil evaporation changes and recovery from thinning will likely be different in the Piedmont which is much drier than forests along the coasts of Florida, Georgia, and the Carolinas (Jordan et al., 2008). Monitoring of the trees on this Piedmont site over the long term will provide additional information about the variability of J_s and T_s after the thinning. Shallow versus deep rooting patterns, water exploitation strategies, and specific physiological traits in certain trees may explain the accessibility of water by those trees and the relations between water use and environmental drivers such as VPD and soil moisture (Fabiani et al., 2021; Fan et al., 2017).

5 | CONCLUSIONS

This study provides a comparative analysis of sap flux and transpiration of two co-occurring and ecologically important southern pines, shortleaf pine, and loblolly pine in the headwater watershed. We discovered that in a closed canopy pine plantation, loblolly pines used significantly more water than shortleaf, in part, because of the subordinate canopy position and competitive disadvantage of shortleaf to make use of the available resources. WUE, however, was not significantly different between the species, suggesting that there might be a strong water and carbon coupling among pine species.

This study has important implications for forest water management enhancement. Thinning the stand might increase tree-level transpiration by a larger percentage in shortleaf compared to loblolly because canopy exposure (not primarily tree height) had an influence on transpiration at the individual level. Species that use less water than others might increase the availability of stored soil moisture in the subsurface zone during periods of drought. Thus, keeping soil water content above a certain threshold or minimum can be a key metric in forest planning and management (i.e., manage species, thin the stand, or create an open forest). As spatial data on species-specific water use becomes more widespread, and ecosystem models' ability to capture plant responses to forest management improves, precision forestry (e.g., site-specific management) can be used more as an option to improve watershed management and water storage capacity—despite the complexities of how species respond to the interactions between available water, light, and nutrients. Overall, we suggest that planting shortleaf pines might save water when compared to loblolly pine. However, the impacts of increasing climate variability will likely create environmental conditions that exceed those found in this study, and a non-antecedent species response is possible (McNulty et al., 2024). Future studies should focus on stand-level shortleaf pine forest water balances to quantify hydrologic benefits of forest management (e.g., species change) at a broader scale.

AUTHOR CONTRIBUTIONS

Johnny Boggs: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; supervision; writing – original draft; writing – review and editing. **Ge Sun:** Conceptualization; formal analysis; funding acquisition; methodology; writing – original draft; writing – review and editing. **Jean-Christophe Domec:** Conceptualization; formal analysis; methodology; writing – original draft; writing – review and editing. **Steve McNulty:** Writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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

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