#### ARTICLE





## The influence of climate and management on transpiration of residential trees during a bark beetle infestation

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#### **Abstract**

Trees in residential environments are affected by a unique combination of environmental and anthropogenic factors, including occasional insect outbreaks that are increasing in frequency and severity due to climate change. We studied loblolly pine trees infested by bark beetles in a residential backyard in a southeastern US city. We investigated the responses of tree and stand-level transpiration to environmental factors (solar radiation, atmospheric vapor pressure deficit, and soil moisture), severe weather events (strong winds and heavy storms), bark beetle infestation, and human actions (insecticide treatments and tree removals). We used constant heat dissipation probes to make continuous sap flux measurements  $(J_0)$  in tree boles. Over 22 months of the study,  $J_0$  of trees with confirmed infestation decreased from ~90 to ~60 g cm<sup>-2</sup> day<sup>-1</sup> and  $J_0$  of the rest of the trees increased from ~60 to ~80 g cm<sup>-2</sup> day<sup>-1</sup>. One infested tree died, as its  $J_0$  steadily declined from 110 g cm<sup>-2</sup> day<sup>-1</sup> to zero over the course of 2 months, followed by a loss of foliage and visible signs of severe infestation 6 months later.  $J_0$  was sensitive to variations in incoming solar radiation and atmospheric vapor pressure deficit. In most trees,  $J_0$  linearly responded to soil water content during drought periods. Yet despite complex dynamics of  $J_0$  variations, plot-level transpiration at the end of the study was the same as at the beginning due to compensatory increases in tree transpiration rates. This study highlights the intrinsic interplay of environmental, biotic, and anthropogenic factors in residential environments where human actions may directly mediate ecosystem responses to climate.

#### KEYWORDS

ecohydrology, insect attack, insect outbreak, outdoor water use, residential ecosystems, urban forest transpiration

## INTRODUCTION

Interactions of trees with their environment are strongly influenced by land cover change (Grimmond et al., 2016; Hall et al., 2016; Mahmood et al., 2014; Payn et al., 2015) and global climate change (Adams et al., 2010; Dale et al., 2001; Hartmann et al., 2022; Lee et al., 2023; Overpeck et al., 1990). One of the most prominent climate

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change-induced disturbances currently affecting trees is the increased frequency and severity of insect outbreaks (Anderegg et al., 2015; Seidl et al., 2017). Insect attacks are among the most important causes of widespread forest mortality across the globe (Fettig et al., 2022; Hlásny et al., 2021; Raffa et al., 2008). While warmer temperatures are favorable for the occurrence and development of insect outbreaks (Bentz et al., 2010; Hartmann et al., 2022), exposure to multiple environmental and anthropogenic stressors (Kleinman et al., 2019) contributes to the vulnerability of trees to insect attacks. Besides forests and tree plantations, trees in cities are also subject to devastating insect attacks, with the losses of trees jeopardizing aesthetics, recreation quality, property values, and other aspects of urban livability (Berland & Elliott, 2014; Korányi et al., 2022; Laćan & McBride, 2008).

Eighty percent of the US population lives in cities (www.census.gov), where about one third of the cumulative urban area is covered by tree canopies (Dwyer et al., 2000). Cities are areas of immediate interactions between people and trees. Tree species composition, spatial arrangement, appearance, health, and lifespan are directly affected by human decisions, which interplay with a variety of environmental factors (Jenerette et al., 2016; Padullés Cubino et al., 2020). Cities are unique ecological environments, where landscape and soil properties, water inputs, and even atmospheric temperatures and humidity are strongly dependent on human actions (Hall et al., 2016), driven both by individual choices (Avolio et al., 2018) and broader societal and institutional mechanisms (Cook et al., 2012; Groffman et al., 2014).

Even though trees in cities do not consume enough CO<sub>2</sub> to compensate for a notable fraction of urban emissions, they may effectively mitigate harsh urban microclimates and provide a variety of local-scale ecological benefits (Pataki et al., 2021). Shade from tree canopies lowers summer temperatures (Armson et al., 2012; Shiflett et al., 2017), reduces water losses from grass lawns (Litvak et al., 2013; Shashua-Bar et al., 2009), and curbs residential energy consumption for air conditioning (Akbari, 2002; Simpson, 2002). Trees may also provide a dramatically positive effect on human physical and mental health (Donovan et al., 2013; Ulmer et al., 2016).

Trees have a significant impact on the hydrology and water budgets of cities (Kuehler et al., 2017; Litvak, Manago, et al., 2017). However, predicting transpiration of trees in cities remains a challenge as it exhibits high species- and site-specific variability (Pataki et al., 2011). A detailed study of tree species commonly grown in greater Los Angeles (California, USA) revealed a large variability in sap flux (from ~4 to ~300 g cm<sup>-2</sup> day<sup>-1</sup>) and tree-level transpiration (from ~3 to ~180 kg day<sup>-1</sup>; Pataki et al., 2011). In particular, a comparison of sap flux of

Canary Island pines among nonirrigated and irrigated sites showed that sap flux and tree-level transpiration of irrigated trees may be as high as ~20 times larger than nonirrigated trees (Pataki et al., 2011). Another in situ sap flux study conducted in Minneapolis–Saint Paul (Minnesota, USA) showed that seasonal and annual transpiration of coniferous trees in a residential setting was about two times larger than deciduous broadleaf trees (Peters et al., 2011). While tree transpiration highly depends on species composition, environmental conditions, and landscape management, the set of variables affecting transpiration of trees in cities is yet to be fully understood and quantified.

This study investigates sap flux and transpiration of trees at a residential location in a southeastern US city. While residential areas occupy ≥50% of the areas of US cities (Akbari et al., 2003; Akbari & Rose, 2008)—much larger than commercial, industrial, and any other type of urban land cover—very few studies reported sap flux of residential trees in the US. Sap flux measurements in residential trees pose significant logistical challenges, as they require homeowners' permissions for long-term placement of scientific equipment on their property, adjustments to the setup design to keep minimal interference with the aesthetics and use of the property, and other constraints on research activities based on homeowner preferences.

We conducted continuous sap flux measurements in loblolly pine trees (Pinus taeda L.) located in a residential backyard within its native region. Some studied trees exhibited the signs of bark beetle (*Ips* spp.) infestation. Over the course of the study, the homeowners undertook active interventions to limit infestation with insecticide treatments and tree removals. Intensive management of urban residential trees is common, yet its interactions with tree ecophysiology have been rarely studied. Therefore, we continued to monitor tree ecophysiology and microclimate during these management actions to address the following questions: How much water do loblolly pines transpire in an unirrigated residential setting in their native region? How does bark beetle infestation affect tree transpiration and its responses to environmental drivers of transpiration, such as solar radiation and atmospheric vapor pressure deficit (VPD)? To what extent do human actions (i.e., insecticide treatment and tree removal) affect transpiration of the tree stand? We expected transpiration of healthy trees to be similar to natural tree stands and plantations, and transpiration of unhealthy trees to decrease over time. We also hypothesized that dying-off and clearing trees would result in the increase in transpiration of remaining trees due to better coupling with the atmosphere and increased access to sunlight, soil water, and other resources.

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#### **METHODS**

## Study site

We studied a stand of loblolly pine trees growing in a residential backyard in the northeast of Tallahassee. Tallahassee is a humid subtropical city located north of the peninsula, in the Florida Panhandle region. The mean annual temperature is 20°C (NOAA National Weather Service; https://www.weather.gov/wrh/climate? wfo=tae). The city receives abundant precipitation of 145 cm year<sup>-1</sup> (annual average, NOAA National Centers for Environmental Information; https://www.ncei.noaa. gov/access) in the form of rain, thunderstorms, hurricanes, and tropical depressions. The rainfall has high seasonal variability, with about half of the annual rainfall occurring between June and September. Tallahassee is a fast growing city: from 1970 to 2017, the population increased by a factor of seven and the area of the city nearly quadrupled; the current population is approaching 200,000 (US Census Bureau; https://data.census.gov). Tree canopy cover in Tallahassee is 74%, one of the highest among US cities (McLean et al., 2020).

The studied backyard was located in an area developed in the late 1970s. In addition to the loblolly pine trees, which were ~84 years old, the site contained several water oaks, small fruit trees, woody shrubs, and flowerbeds, and the groundcover consisted of turfgrass, Asiatic jasmine, and Virginia creeper. The site was not regularly irrigated or fertilized. Some of the plantings were occasionally irrigated, and the ground cover was regularly mowed. The appearance of the yard, microclimate, and canopy coverage were typical of northeast Tallahassee. This site was examined as part of a larger study of Tallahassee urban forest transpiration.

## Sap flux measurements

We installed Granier-type thermal dissipation probes (hereafter sap flux sensors; Granier, 1987) at ~1.35 m height in the outer 2 cm of sapwood in 11 loblolly pine trees. Each tree was equipped with one heated sap flux sensor and one unheated/reference sap flux sensor inserted below the heated one and connected with a thermocouple that continuously measured the temperature difference between the sensors ( $\Delta T$ , in degrees Celsius; Lu et al., 2004). The voltage difference from each thermocouple (in millivolts) was measured every 30 s by a datalogger (CR3000; Campbell Scientific, Logan, UT, USA), and the averages were calculated and logged every 30 min. We calculated sap flux density in the outer 2 cm

of sapwood ( $J_0$ , in grams per square meter per second) following Granier (1987) as:

$$J_0 = 119 \left( \frac{\Delta T_{\text{max}} - \Delta T}{\Delta T} \right)^{1.231},\tag{1}$$

where  $\Delta T_{\rm max}$  is the maximum temperature difference between the sap flux sensors in each tree observed at night when  $J_0 \approx 0$ . The calculations of  $\Delta T$ ,  $\Delta T_{\rm max}$ , and  $J_0$  from thermocouple data series were performed using the open source software Baseliner (Oishi et al., 2016). We calculated daily  $J_0$  (in grams per square meter per day) as the sums from 5:30 am to 5:00 am the next day.

### **Environmental parameters**

Air temperature (T, in degrees Celsius) and relative humidity (RH, in percentage) were measured every 30 min by a HOBO T/RH MX2302A Data Logger with an external T/RH sensor covered by a solar radiation shield RS3-B (Onset Computer Corporation, Bourne, MA) and mounted at 2 m height on the trunk of one of the studied trees (Tree 3; Table 1). Because measuring the overstory solar radiation was not feasible at our study site, we downloaded the hourly intensity of solar radiation ( $I_0$ , in watts per square meter) from the Montford Middle WeatherSTEM weather station located at 1.6 km from the study site (https://leon.weatherstem.com). The volumetric soil moisture content of the top 30 cm (VWC, in cubic meters of H<sub>2</sub>O per cubic meter) was measured continuously by soil water content reflectometers (CS616; Campbell Scientific, Logan, UT, USA) every 30 s and averaged every 30 min by a datalogger (CR3000; Campbell Scientific).

We used air T and RH to compute VPD. We extracted daytime VPD using the time series of  $I_0$  and calculated daytime averages of VPD. We calculated day length-corrected VPD (D, in kilopascals) by multiplying VPD by light day length and dividing by 12 h (Oren et al., 1996). We calculated daily averages of VWC and  $I_0$  from 5:30 am to 5:00 am the next day.

## Plot area and tree canopy cover

We estimated the ground area of the studied backyard ( $A_{\rm G}$ , in square meters) and tree canopy cover before and after tree removals using satellite images from April 2020 and April 2021 (Google Earth Pro 7.3.6.9345). To analyze tree canopy cover, we used ImageJ software (Schneider et al., 2012).

**TABLE 1** The characteristics of studied trees, including dbh, bark thickness  $(d_B)$ , sapwood depth  $(d_S)$ , and sapwood area  $(A_S)$ .

Tree ID	dbh (cm)	d <sub>B</sub> (cm)	d <sub>s</sub> (cm)	$A_{\rm S}$ (cm <sup>2</sup> )	Confirmed infestation	Sap flux record period	Additional information
1.0	34.8	0.7	7.8	626.1	Yes	4/19/2020-5/26/2020	Cut down on 5/28/2020
1	44.9	2.0	8.5	864.5	Yes	6/1/2020-1/10/2021	Cut down in January 2021
2	43.3	1.3	11.0; 9.0	963.1	No	5/11/2020-10/23/2021	
3	62.6	2.5	12.7; 12.0	1753.6	Yes	5/17/2020-10/23/2021	Intensive insecticide treatment July 2020 <sup>a</sup>
4	50.6	0.7	12.0; 10.0	1318.1	No	5/18/2020-2/19/2022	
5	60.8	1.5	16.5; 15.0	2080.9	Yes	5/17/2020-2/19/2022	Intensive insecticide treatment July 2020
6	46.1	1.3	12.0	1190.2	No	9/22/2020-1/19/2022	
7	44.5	0.4	11.5	1162.2	No	9/22/2020-1/19/2022	
8	44.5	2.0		963.6 <sup>b</sup>	Yes	9/23/2020-1/18/2022	Zero sap flux starting 11/30/2020
9	61.9	2.0	14.3	1956.5	No	9/22/2020-2/19/2022	
10	60.6	2.0	16.5	2080.6	No	9/22/2020-2/19/2022	

<sup>&</sup>lt;sup>a</sup>For the details of insecticide treatment, see *The timeline of events* in the text.

## Scaling to whole-tree and plot-level transpiration

After the end of the sap flux measurements, we determined sapwood depths from tree cores. We collected the cores from each tree except Trees 1.0 and 1, which were cut, and for which we measured sapwood depth using cross-sections of the trunks. We used sapwood depths and tree dbh (at ~1.35 m height; in centimeters) to estimate sapwood areas ( $A_{\rm S}$ , in square centimeters) of each tree. We could not determine the sapwood depth of Tree 8 where bark beetles completely destroyed the wood. We estimated  $A_{\rm S}$  of Tree 8 using the following empirical relationship derived from the dimensions of the rest of the studied trees ( $R^2 = 0.95$ ; p < 0.0001):  $A_{\rm S} = 2.35(0.5\,{\rm dbh} - d_{\rm B})^2$ .

Estimating whole-tree transpiration requires the knowledge of radial distribution of sap flux density throughout the sapwood of each tree (Baiamonte & Motisi, 2020; Berdanier et al., 2016; Fan et al., 2018). Because measuring sap flux density along tree radii was not a feasible option in this study, we estimated tree-level transpiration of studied trees using Gaussian functions (Ford et al., 2004):

$$J = J_0 e^{-\frac{1}{2} \left(\frac{x - x_0}{\beta}\right)^2}, \tag{2}$$

where J (in grams per square centimeter per second) is a sap flux density at the sapwood depth of x (in centimeters),  $\beta$  is the parameter determining the rate of decrease of J with depth, and  $x_0$  is the sapwood

depth at which the maximum  $J = J_0$  is detected. Here, we posit  $x_0 = 1$  cm as the mean of 0–2 cm depths sensed by sap flux sensors. Equation (2) was shown to capture the shape of the radial distribution of sap flux density reasonably well (Ford et al., 2004; Pataki et al., 2011). Thus, Ford et al. (2004) empirically measured the radial profiles of sap flux density in several pine species including loblolly pine that had dimensions similar to the trees in this study. The analysis of multiple published data of radial sap flux density profiles by Pataki et al. (2011) demonstrated a good performance of this method in other coniferous tree species as well. The resulting equation for the daily whole-tree transpiration ( $E_{\rm T}$ , in kilograms of H<sub>2</sub>O per tree per day) is as follows (Litvak, Mccarthy, et al., 2017):

$$E_{\rm T} = 6.4 \times 10^{-4} A_{\rm S} J_0. \tag{3}$$

Assuming the density of water to be  $\approx 1000 \text{ kg m}^{-3}$ , we calculated plot-level transpiration of each tree per ground area of the site ( $E_{\rm G}$ , in millimeters per day) as  $E_{\rm G} = E_{\rm T}/A_{\rm G}$  and plot-level transpiration per ground area of the entire tree stand as the sum of individual tree  $E_{\rm G}$ .

## Statistical analyses and curve fitting

We used R 4.1.0 (R Core Team, 2021) for all statistical analyses except curve fitting that we performed in SigmaPlot version 10.0 (Systat Software).

<sup>&</sup>lt;sup>b</sup>The inner part of Tree 8 was completely destroyed; neither the collection of a core nor visual determination of  $d_S$  from the stub was possible.  $A_S$  was studied using an empirical relationship derived from the dimensions of the rest of the studied trees (see *Methods* for details).

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#### THE TIMELINE OF EVENTS

This section provides a detailed description of the timeline of events; the summary is shown in Table 2. In April-May 2020 we installed sap flux sensors in five loblolly pine trees (Trees 1.0, 2, 3, 4, and 5; Table 1). Soon after the installation was completed, the homeowner made a decision to cut down Tree 1.0, which was leaning over the house. After the tree was cut down, a section of the trunk at the height of the sensors was separated to measure sapwood depth. The trunk section showed no signs of infestation until ~1.5 months later, when the wood became visibly stained revealing the presence of a bluestain fungus, which is associated with bark beetle attacks (Paine & Stephen, 1987; Yearian et al., 1972; Figure 1a). We disconnected all sap flux instrumentation during the felling of Tree 1.0. After the felling, four remaining trees were re-instrumented and one more tree (numbered Tree 1), located in close proximity to the place of Tree 1.0, was instrumented to replace it.

In early July 2020, a loblolly pine tree in the study yard, which was not part of the sap flux measurements, apparently died from the bark beetle infestation. By this time, Trees 3 and 5 had multiple boreholes and discharge from the bark, which indicated infestation (Figure 1b,c). Treatment with the insecticide Onix (bifinthrin) was administered by a tree care service on July 6 and July 13; ~ 15 L (4 gallons) of the insecticide was applied to each

**TABLE 2** Short summary of *The timeline of events* (see text for more details).

more details).	
Month/ year	Event
4/2020	• Sap flux sensors were installed in Trees 1.0, 2, 3, 4, and 5
5/2020	<ul><li>Tree 1.0 was cut down</li><li>Sap flux sensors were installed in Tree 1</li></ul>
7/2020	<ul> <li>Trees 3 and 5 exhibited the signs of bark beetle infestation</li> <li>All loblolly pine trees in the yard received insecticide treatment</li> <li>A loblolly tree that was not instrumented with sap flux sensors died and was removed</li> </ul>
9/2020	• Sap flux sensors were installed in Trees 6–10
1/2021	<ul> <li>Tree 1 was cut down</li> <li>Several more trees located close to the house were removed</li> </ul>
6/2021	<ul> <li>New sap flux sensors were installed in Trees 2, 3, 4, and 5</li> <li>Tree 8 exhibited excessive signs of severe infestation</li> </ul>
1/2022	Tree 8 was cut down

pine tree in the yard. Additionally, Trees 3 and 5 were wrapped in burlap and plastic wrap after the second insecticide application, which was meant to intensify the treatment (Figure 1d). On July 24, the tree killed by the bark beetles was removed.

In September 2020, we obtained the homeowner's permission to instrument five more trees and installed sap flux sensors in Trees 6–10.

In late January of 2021, the homeowner removed several more trees located close to the house. To avoid the damage from tree-cutting activities, the sap flux instrumentation was removed again on January 11. Tree 1 and several more trees that were not part of this study were cut down. On February 8, all study trees except Trees 1 and 5, which were also planned to be cut down, were re-instrumented.

On June 15, 2021, one year after the beginning of the measurements, we removed sap flux sensors from Trees 2 and 3 and installed new sap flux sensors on the opposite sides of the boles. This was done to prevent measurement errors associated with the long-term use of sap flux sensors (Moore et al., 2010). On June 29, 2021, we did the same with Tree 4, and installed new sap flux sensors on the opposite side of Tree 5, which ended up still not cut down at that time.

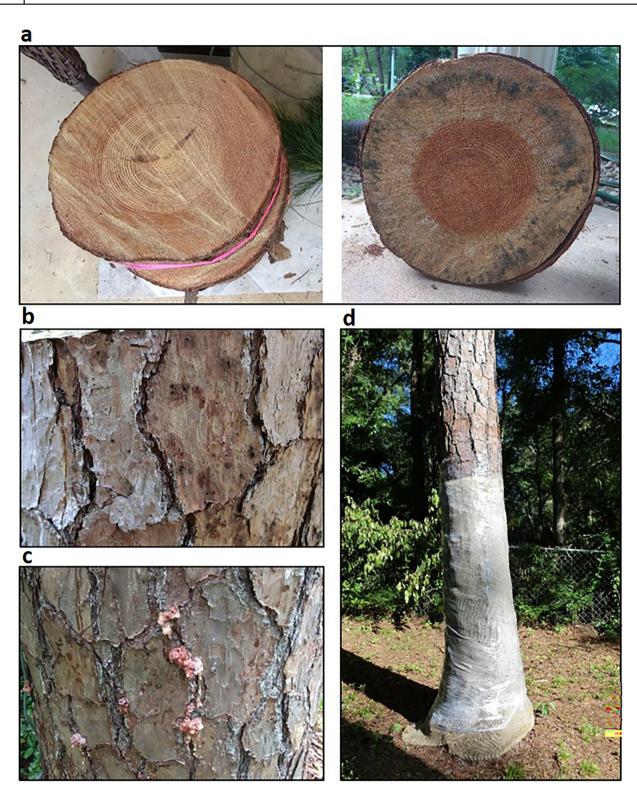
By late June 2021, Tree 8 had no foliage and exhibited excessive signs of severe infestation on its trunk. Tree 8 was cut down on January 20, 2022.

### **RESULTS**

#### Sap flux and environmental conditions

The time series of  $J_0$  (Litvak & Pataki, 2023) is shown in Figure 2 along with the environmental parameters.  $J_0$  shows a clear seasonal pattern, similar to both  $I_0$  and D, which were also strongly correlated with each other (linear regression,  $R^2=0.81$ , p<0.0001, not shown).  $I_0$  varied from  $253\pm76~\rm W~m^{-2}$  in May 2020 to  $97\pm57~\rm W~m^{-2}$  in January 2021 (Figure 2a), and then from  $258\pm65~\rm W~m^{-2}$  in May 2021 to  $92\pm39~\rm W~m^{-2}$  in December 2021 (Figure 2b). D varied from  $1.6\pm0.6~\rm kPa$  in May 2020 to  $0.4\pm0.3~\rm kPa$  in January 2021 (Figure 2a) and, very similarly, from  $1.6\pm0.6~\rm kPa$  in May 2021 to  $0.4\pm0.2~\rm kPa$  in December 2021 (Figure 2b).

During the measurements, six severe weather events affected the area (Table 3; Figure 2). The most extreme of these weather events were (1) a tornado, which did not affect the study site directly, but brought the winds up to 42.5 m s<sup>-1</sup> on April 23, 2020, and (2) Hurricane Sally, which caused heavy rainfall (98.8 mm day<sup>-1</sup>; Figure 2a) and wind gusts up to 18 m s<sup>-1</sup> on September 16, 2020. After heavy rains and strong winds, trees lost multiple

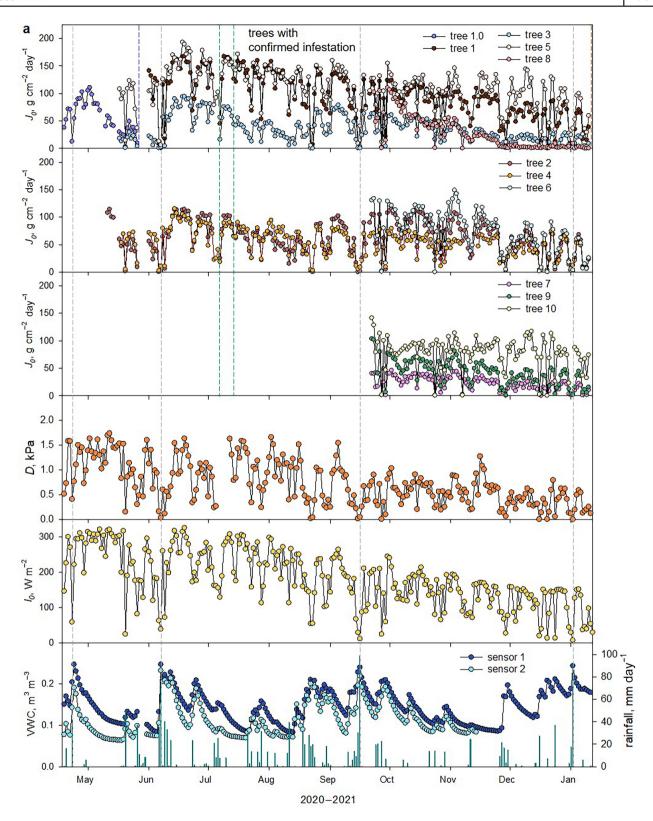


**FIGURE 1** (a) Trunk sections of Tree 1.0 right after cutting on May 28, 2020 and on July 17, 2020; the later image reveals the presence of a bluestain fungus. (b) Multiple boreholes in the bark indicating bark beetle infestation. (c) Discharge from the bark indicating severe infestation. (d) A tree treated with bifenthrin insecticide and wrapped in burlap fabric and plastic wrap. Photo credit: Elizaveta Litvak.

branches and foliage. A branch that fell during Hurricane Sally damaged our datalogger enclosure, with no damage to the instruments and no interruption to the data collection (Appendix S1: Figure S1).

Overall,  $J_0$  varied from nearly zero to ~190 g cm<sup>-2</sup> day<sup>-1</sup>, with the lowest  $J_0$  values observed during rainy days with very low D. To analyze  $J_0$  and its changes, we considered the following time periods:

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**FIGURE 2** Data records (a) before and (b) after the break in data collection in January–February 2021 caused by the removal of Tree 1: daily sap flux in the outer 2 cm of sapwood ( $J_0$ ), mean day-length corrected atmospheric vapor-pressure deficit (D), intensity of the incoming shortwave solar radiation ( $I_0$ ), and volumetric water content in the upper 30 cm of soil (VWC; shown with the daily rainfall from NOAA National Weather Service at Tallahassee Regional Airport, www.weather.gov/wrh/climate?wfo=tae).  $J_0$  records of trees with confirmed infestation are shown in the uppermost panel. Occasional near-zero  $J_0$  values correspond to very low D during rains and fog. Error bars are not shown to avoid clatter; SDs are:  $15 \pm 5\%$  of  $J_0$ ,  $3 \pm 2\%$  of D,  $3 \pm 0\%$  of  $I_0$ , and  $3 \pm 4\%$  of VWC. Vertical dashed lines: gray lines indicate severe weather events (listed in Table 3); purple and dark red lines (top panel only) indicate the timing of Trees 1.0 and 1 felling (see Table 2 and text for details); green lines (top three panels) indicate insecticide treatments (see Table 2 and text for details).

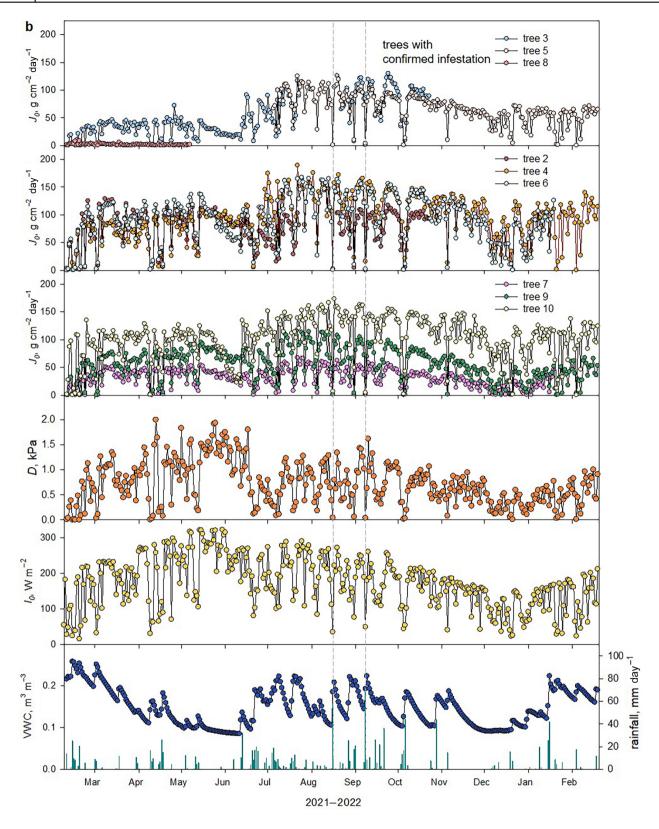


FIGURE 2 (Continued)

- (1) from the beginning of sap flux measurements in Trees 1–5 on May 11, 2020 until five more trees (Trees 6–10) were instrumented on September 21, 2020,
- (2) from September 22, 2020 until the removal of sap flux equipment on January 10, 2021, and (3) from reinstallation of sap flux measurements on February

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**TABLE 3** Severe weather events that affected the study site during measurements; data from NOAA Weather Service at Tallahassee Regional Airport (www.weather.gov/wrh/climate?wfo=tae) and FSU WeatherSTEM (https://leon.weatherstem.com).

Date	Event	Rainfall (mm day <sup>-1</sup> )	Max wind speed (m s <sup>-1</sup> )
4/23/2020	Tornado	41.7	42
6/7/2020	Tropical Storm Cristobal	72.9	7
9/16/2020	Hurricane Sally	98.8	18
1/2/2021	Severe thunderstorm	89.7	6
8/16/2021	Tropical Storm Fred	57.9	13
9/8/2021	Tropical storm Mindy	71.7	18

9, 2021 until the end of sap flux data record on February 19, 2022 (Appendix S1: Table S1). The first two time periods are shown in Figure 2a and the third time period is shown in Figure 2b.

 $J_0$  of the trees with confirmed infestation (Trees 1, 3, and 5) decreased from  $93 \pm 51 \text{ g cm}^{-2} \text{ day}^{-1}$  during the first time period to  $64 \pm 41 \text{ g cm}^{-2} \text{ day}^{-1}$  during the second time period (ANOVA; p < 0.0001) and did not significantly change from the second to the third time period  $(J_0 = 59 \pm 32 \text{ g cm}^{-2} \text{ day}^{-1}; p = 0.73)$ .  $J_0$  of the rest of the trees did not significantly change from the first to the second time period  $(J_0 = 62 \pm 29 \text{ g cm}^{-2})$  $day^{-1}$  and  $54 \pm 33$  g cm<sup>-2</sup>  $day^{-1}$ , respectively; p = 0.05), yet significantly increased from the second to the third time period, reaching  $76 \pm 43 \text{ g cm}^{-2} \text{ day}^{-1}$ (p < 0.0001). This dynamic resulted in higher  $J_0$  of the trees with confirmed infestation than  $J_0$  of the rest of the trees during the first and second time periods (p < 0.0001 and p = 0.003) and significantly lower than $J_0$  of the rest of the trees during the third time period (p < 0.0001).  $J_0$  of Tree 8 showed a steady decline from 110 g cm<sup>-2</sup> day<sup>-1</sup> on September 30, 2020 to zero on November 30, 2020, indicating the death of the tree (Figure 2a, upper panel). We did not include Tree 8 in the analysis above to avoid underestimation of  $J_0$  of trees with confirmed infestation.

## Sap flux responses to environmental conditions

Overall,  $J_0$  of the studied trees showed a strong linear correlation with  $I_0$  (Figure 3). The slopes of these relationships changed significantly over the course of the study (ANOVA; p < 0.0001), with the only exception of Tree 1, which had a stable slope until the tree was cut down (Figure 3a).  $J_0$  was also correlated with D. We fitted logarithmic functions ( $J_0 = a + b \times \ln(D)$ ; Appendix S1: Figure S2) with parameters that were changing at the same time with the slopes of  $J_0$  relationships with  $I_0$ .

There was no long-term correlation of  $J_0$  with VWC. However,  $J_0$  of several trees—both with and without confirmed infestation—was linearly correlated with VWC during dry episodes in May 2020 (19-day long) and May-June 2021 (28-day long; Figure 4). These dry periods (hereafter, spring droughts) may be classified as "precipitation deficit flash droughts" (Mo & Lettenmaier, 2016); they resulted from a combination of the maximum daily  $D (1.4 \pm 0.2 \text{ kPa in } 2020 \text{ and } 1.5 \pm 0.3 \text{ kPa in } 2021)$ , very low precipitation, and low VWC (Figure 2). Both trees that were instrumented before May 2020 (Trees 1.0 and 2) showed a strong correlation of  $J_0$  with VWC during the spring drought in 2020; also, five out of seven trees in which  $J_0$  was measured in May–June 2021 showed strong correlation of  $J_0$  with VWC during the spring drought in 2021 (Figure 4).

We did not observe any clear responses of  $J_0$  to insecticide treatments (Table 1) or severe weather events (Table 3).

### Plot area and tree canopy cover

The estimated  $A_{\rm G}$  was 1000 m<sup>2</sup>, with tree canopy entirely covering the ground before tree removals. After tree removals, the tree canopy cover was  $\approx$ 670 m<sup>2</sup> or 67% of  $A_{\rm G}$  (Figure 5a).

## Whole-tree and plot-level transpiration

 $E_{\rm T}$  varied from 22 ± 12 to 165 ± 55 kg tree<sup>-1</sup> day<sup>-1</sup>. We compared  $E_{\rm T}$  changes over the three time periods defined above.  $E_{\rm T}$  of the trees with confirmed infestation (Trees 1, 3, and 5) decreased from 94 ± 65 kg tree<sup>-1</sup> day<sup>-1</sup> during the first time period to 66 ± 54 kg tree<sup>-1</sup> day<sup>-1</sup> during the second time period (ANOVA; p < 0.0001) and did not significantly change from the second to the third time period ( $E_{\rm T} = 72 \pm 39$  kg tree<sup>-1</sup> day<sup>-1</sup>; p = 0.3).  $E_{\rm T}$  of the rest of the trees did not

**FIGURE 3** Daily sap flux in the outer 2 cm of sapwood ( $J_0$ ) plotted against the intensity of the incoming shortwave solar radiation ( $I_0$ ) for (a) trees with confirmed infestation and (b) the rest of the trees. Regression lines are shown for significant relationships (p < 0.0001). Panels marked as "spring droughts" indicate time periods of dry weather conditions when  $J_0$  was strongly correlated with volumetric water content in the upper 30 cm of soil (Figure 4).

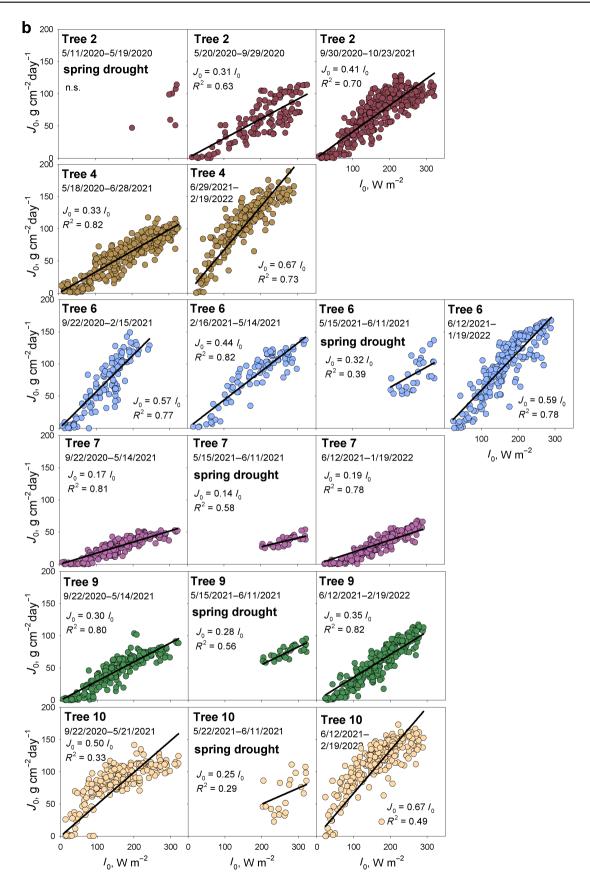
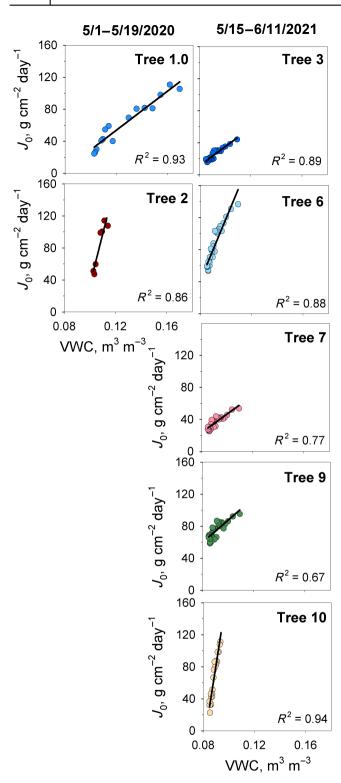


FIGURE 3 (Continued)



**FIGURE 4** Daily sap flux in the outer 2 cm of sapwood  $(J_0)$  plotted against volumetric water content in the upper 30 cm of soil (VWC) during prolonged dry periods in the spring of 2020 (on the left) and 2021 (on the right). Regression lines are shown for significant relationships (p < 0.0001).

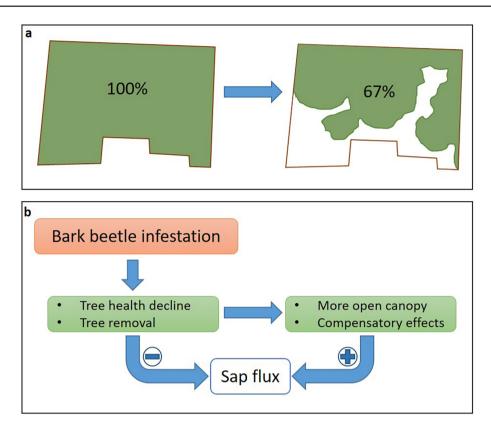
significantly change from the first to the second time period ( $E_T = 48 \pm 23 \text{ kg tree}^{-1} \text{ day}^{-1}$  and  $52 \pm 37 \text{ kg tree}^{-1} \text{ day}^{-1}$ , respectively; p = 0.2), yet it significantly

increased from the second to the third time period, reaching  $73 \pm 49 \ \mathrm{kg} \ \mathrm{tree}^{-1} \ \mathrm{day}^{-1} \ (p < 0.0001)$ . These changes resulted in higher  $E_{\mathrm{T}}$  of the trees with confirmed infestation than  $E_{\mathrm{T}}$  of the rest of the trees during the first and second time periods (p < 0.0001), but similar  $E_{\mathrm{T}}$  during the third time period (p = 0.2). Tree 8 was not included in this analysis to avoid underestimation of  $E_{\mathrm{T}}$  of the trees with confirmed infestation.

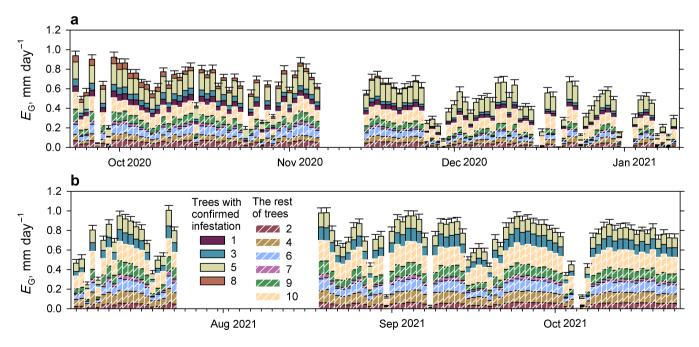
 $E_{\rm G}$  of individual trees varied from 0.02  $\pm$  0.01 to  $0.17 \pm 0.06 \text{ mm day}^{-1}$  (Figure 6; Appendix S1: Table S2). The patterns and temporal changes of  $E_G$  were similar to  $E_{\rm T}$ . The evaluation of cumulative  $E_{\rm G}$  and its temporal changes was constrained by data availability. We aimed to compare cumulative  $E_{\mathrm{G}}$  during the following time periods: (1) from September 22, 2020, when 10 studied trees were instrumented with sap flux sensors, until the removal of sap flux equipment on January 10, 2021, and (2) the corresponding time period from September 22, 2021, to January 10, 2022. However, the complete data records for all studied trees within both time periods were only available from September 23 to October 23 of 2020 and 2021, respectively. During these 31-day-long periods, cumulative  $E_G$  did not significantly differ between 2020 and 2021 (ANOVA; p = 0.4) and the relationships of  $E_G$  with  $I_0$  and D were nearly identical with the same parameters (Figure 7).

#### DISCUSSION

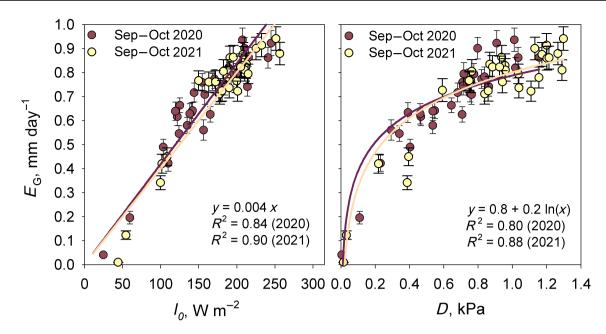
Continuous in situ measurements of  $J_0$  in loblolly pine trees in a residential yard captured a bark beetle infestation coinciding with the homeowner's actions of insecticide treatments and removal of trees that posed safety risks. According to our observations, five of the studied trees were infested by bark beetles (Table 1). In the rest of the trees, infestation, while also likely, was not confirmed with certainty. It is hard to distinguish the reasons underlying varying degrees of infestation of different trees. Hypothetically, these differences might have been caused by the timing of bark beetle intrusion in each tree, that is, some trees might have been infested earlier than others and thus demonstrated more prominent signs of infestation. It is also possible that the trees have varying vulnerability to infestation based on nonstructural carbohydrates, carbon allocation, water stress, anatomical structure (such as the number and size of resin ducts), or production and release of defensive chemicals (Ferrenberg et al., 2014; Franceschi et al., 2005). The results of the present study do not allow us to determine the role of tree fitness in the degree and probability of infestation, which would be highly desirable for developing a more detailed and accurate understanding of the dynamics of tree- and stand-level transpiration.



**FIGURE 5** (a) Schematic outline of studied backyard with tree canopy cover shown before and after the study. (b) Conceptual diagram of the opposite effects of bark beetle infestation on sap flux of studied trees.



**FIGURE** 6 Time series of daily plot-scale transpiration ( $E_G$ ) shown with SD (a) before and (b) after the break in data collection caused by the removal of Tree 1. The bars representing "trees with confirmed infestation" are stacked on top of "the rest of trees", which are also highlighted by hatching. Note that Tree 8 (died in late November 2020) and Tree 1 (cut down in January 2021) are not present in panel (b).



**FIGURE 7** Cumulative plot-scale transpiration of the loblolly pine stand ( $E_G$ ) on September 23–October 23, 2020 and September 23–October 23, 2021 plotted against the intensity of the incoming shortwave solar radiation ( $I_0$ ) and atmospheric vapor pressure deficit (D).

 $J_0$  of studied trees was strongly correlated with  $I_0$  and D most of the time (Figure 3; Appendix S1: Figure S2); additionally,  $J_0$  of seven trees was strongly correlated with VWC, but only during spring droughts (Figure 4). Our records indicate  $J_0$  decline and recovery periods in most studied trees (Figure 3) and the death of Tree 8 (Figures 2 and 3).  $J_0$  of Tree 8 steadily declined over the course of 2 months (Figure 2), followed by a loss of foliage and visible signs of severe infestation 6 months later. As expected, we observed a decline of  $J_0$  in the trees with confirmed infestation. We also observed an increase of  $J_0$  in the rest of the trees after tree clearings, resulting in similar plot-level transpiration before and after canopy loss (Figure 5a,b).

## Water use by loblolly pines

Loblolly pine is native to the southeastern US, where it is the most commercially important forest tree species (Domec et al., 2012). The water use of loblolly pine has been previously studied in forests and timber plantations within the region. Transpiration of loblolly pines was found to depend on the age and size of trees (Aguilos et al., 2021; Domec et al., 2012). A long-term study based on eddy covariance found that transpiration of a pine plantation in North Carolina increased until the age of 10 years, after which it remained stable (Aguilos et al., 2021).

Summertime transpiration of loblolly pine stands grown for timber could reach or exceed 5 mm day<sup>-1</sup>

(Domec et al., 2012; Sun et al., 2010). However, sap flux-derived transpiration of nonirrigated 12-year-old loblolly pine stand at the Tree Research and Education Site in North Carolina did not exceed 1 mm day<sup>-1</sup>, with  $J_0$ ranging from 0 to 60 g m<sup>-2</sup> s<sup>-1</sup> (Ewers et al., 1999). These values are similar to  $E_G$  and  $J_0$  of nonirrigated residential trees in this study (Figures 2 and 6). This similarity demonstrates a remarkably good agreement in  $E_G$  and  $J_0$  of loblolly pines of different ages (12 years old in a previous study and ~84 years old in a current study) and at different settings. Also, monthly averaged transpiration of healthy loblolly pine trees in a forest in Mississippi, which reached ~2000 kg month<sup>-1</sup> (Hornslein et al., 2018), is in good correspondence with our estimates for trees without confirmed infestation before tree clearings  $(1900 \pm 900 \text{ kg month}^{-1})$ ; after tree clearings, our estimates increased by ~1000 kg month<sup>-1</sup>.

## Sap flux responses to environmental factors and infestation

## The intensity of solar radiation and atmospheric VPD

The sensitivity of  $J_0$  to  $I_0$  and D observed in this study (Figure 3; Appendix S1: Figure S2) is in good correspondence with previous studies of transpiration of loblolly pine in forest and plantation settings (Aguilos et al., 2021; Ewers et al., 1999). Linear responses of transpiration to  $I_0$  indicate efficient use of light across a range of

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intensities (Figure 3). Similar patterns were observed in loblolly pine plantations of different ages (Aguilos et al., 2021) and many other coniferous tree species (e.g., Ewers et al., 2005; Litvak et al., 2011; Tang et al., 2006). Strong saturation responses to *D* (Appendix S1: Figure S2) indicate partial closure of leaf stomata in response to increasing *D*. Such stomatal responses, intrinsic to physiology of trees and many other plant species, prevent excessive water loss that could otherwise disable water-conducting tissues (Sperry, 2000; Sperry et al., 2008; Sperry & Tyree, 1988).

#### Soil water content

The absence of a correlation between  $J_0$  and VWC is common in trees that do not experience soil water limitations (Lagergren & Lindroth, 2002; Litvak, Mccarthy, et al., 2017; Pereira et al., 2006). The trees in this study were not irrigated yet appeared to receive ample rainfall most of the year (Figure 2). However, during two spring drought episodes, VWC became the major factor determining  $J_0$  in most trees (Figure 4), indicating a strong dependence of  $J_0$  on VWC. During these periods, transpiration switched from an "energy-limited" regime, when it was mainly controlled by solar radiation and atmospheric thermal energy, to a "water-limited" regime, when it was mainly controlled by soil moisture availability. These regimes are important modes of ecosystem functioning that determine the patterns of carbon and water fluxes in natural environments (Denissen et al., 2022; Seneviratne et al., 2010 and references therein). In contrast to irrigated tree stands in dry southwestern cities, where tree transpiration is essentially energy-limited (Bush et al., 2008; Litvak et al., 2011, 2012; Pataki et al., 2011), the shift of this tree stand to a water-limited mode in response to soil water limitations highlights the functional similarity of these unirrigated residential trees to natural forests. However, the observed patterns of  $J_0$ responses to soil water limitations do not necessarily fully represent all studied trees because of limited spatial and depth coverage of VWC data (0-30 cm depth, while the rooting depth of loblolly pine trees may reach up to 3 m; Ewers et al., 1999).

### Remaining variability of sap flux

In this study,  $I_0$  and D were strongly correlated with each other, and  $J_0$  was linearly correlated with both  $I_0$  and  $\ln(D)$ , with similar temporal patterns of declines and increases of the slopes (Figure 3; Appendix S1: Figure S2). The relationships between  $J_0$  and  $I_0$  have zero

origins, so we may use changes in their slopes as direct indicators of additional  $J_0$  variability.

The changes in slopes of the relationship between  $J_0$ and  $I_0$  had different patterns in trees with and without confirmed infestation (Figure 3). Across the trees without confirmed infestation, slope changes were consistent and showed two distinct trends. The first trend was a decline of the slope and/or significance of the relationship between  $J_0$  and  $I_0$  during spring droughts (Figure 3b; observed in all trees except Tree 4), when VWC explained most of  $J_0$  variability (Figure 4). The second trend was an increase in the slope of the relationship between  $J_0$  and  $I_0$  starting in June 2021 or earlier (Figure 3b). The only exception to this pattern was a decline in slope for Tree 6 in February-May 2021 (Figure 3b). This decline co-occurred with the increase in the range of D from 0-1 kPa to 0-2 kPa (Appendix S1: Figure S2b), likely indicating the adjustment of stomatal regulation to higher evaporative demand. Overall, these patterns are common and characteristic of healthy trees.

In trees with confirmed infestation, the patterns were different and not consistent among trees. Thus, Trees 1.0 and 3 responded to the spring droughts similar to the trees without confirmed infestation (Figures 3a and 4). However, while for Tree 3 the slope of the relationship between  $J_0$  and  $I_0$  increased afterward, for Tree 1.0 it decreased (Figure 3a). From mid-May 2020 through mid-May 2021, the slope of the relationship between  $J_0$ and  $I_0$  for Tree 3 increased and decreased twice (Figure 3a). These slope changes were not co-occurring with any environmental stressors, insecticide treatments, or changes in D ranges. Therefore, they most likely indicate physiological responses to bark beetle damage and consequent partial recovery, with possible delayed contributions of the insecticide treatments (Fettig et al., 2006). For Tree 1, the slope of the relationship between  $J_0$  and  $I_0$ remained the same until the tree was cut down in January 2021. For Tree 5, the slope was declining starting in July 2021 until the end of the study. For Tree 8, the fast decline of the slope in October-November 2020, reaching zero in December 2020, indicated mortality (Figure 3a). These differences among trees may reflect different degrees or stages of infestation, individual patterns of anatomical damage, and consequent differences in physiological responses and coping with stress.

Sap flux decline in infected trees has been reported in many studies (e.g., Børja et al., 2016; Kirisits & Offenthaler, 2002; Parke et al., 2007; Preisler et al., 2021; Urban & Dvořák, 2014). Our results specifically support the observations by Hornslein et al. (2018), who used girdling and inoculation with blue stain fungi to simulate bark beetle damage in loblolly pine trees. Similar to our study, different trees in the simulation exhibited different

timings of health decline, yet the same general pattern of sap flux changes: initially, sap flux of damaged trees was higher than control trees, and later it declined by 600 kg month<sup>-1</sup> (Hornslein et al., 2018). Higher sap flux of infected trees in both previous and current studies (by ~300 and ~270 kg month<sup>-1</sup>, respectively) likely signals the first stage of tree-level water transport dysfunction, manifesting in weaker stomatal regulation and excessive water loss via transpiration. The subsequent decrease in sap flux indicates degradation of the whole-tree water transport system, manifesting in excessive embolism and inability to maintain sufficient water transport to the canopy, while physical damage from bark beetle activity continues to destroy the sapwood.

## Sap flux cessation and tree mortality

When the cessation of whole-tree water transport is not associated with temporary responses to environmental factors, it is a definitive indicator of tree death (Børja et al., 2016; Preisler et al., 2021). The transport of water from roots to canopy is critical for maintaining such essential functions of trees as stomatal control of CO<sub>2</sub> uptake and H<sub>2</sub>O loss, photosynthesis, and sugar transport via phloem (Brodribb, 2009). Therefore, sap flow is a "vital sign" of a tree, and its cessation is a sign of an irreversible failure of physiological processes. The cessation of sap flux may occur weeks to months before the appearance of visual signs of severe health decline (Børja et al., 2016; Kirisits & Offenthaler, 2002). This time lag arises from the complexity of trees as organisms, in which cell and tissue-level processes may continue without being properly connected and coordinated with each other (Anderegg et al., 2012). In our study, sap flux in Tree 8 ceased about 6 months before the signs of fatal damage became apparent. Browning and loss of the foliage may have been delayed by stomatal closure, which kept leaf water losses to a minimum. However, over time, the lack of water transport from roots to leaves inevitably caused the failure of the canopy when it ran out of stored water and carbon.

# Impact of tree removal and die-off on plot-level transpiration

Tree clearings and foliage loss by infested trees resulted in the loss of about one-third of the canopy (Figure 5). Canopy loss is known to trigger compensatory increases in leaf stomatal and hydraulic conductance, which help maintain adequate photosynthetic rates despite reduced leaf area (Pataki et al., 1998; Reich et al., 1993). This is a possible cause of transpiration increase of the remaining canopy. In addition, canopy loss immediately resulted in

greater exposure of the remaining canopy to sunlight and atmospheric conditions, likely leading to a better coupling of the canopy with ambient air (Jarvis & McNaughton, 1986). Higher exposure to  $I_0$  and D, which were the major controlling factors of  $J_0$  during most of the study (Figure 3; Appendix S1: Figure S2), is another possible cause of transpiration increase of the remaining canopy.

In the long run, in addition to the light, the remaining trees gained increased access to other freed-up resources, such as soil water, nutrients, and room for canopy growth. Each of these factors or their combination may have contributed to the observed increase of  $J_0$  and  $E_{\rm T}$  of the trees without confirmed infestation and one tree (Tree 3) with confirmed infestation (Figure 5; Appendix S1: Table S1). These increases of  $J_0$  and  $E_T$ resulted in similar cumulative  $E_{\rm G}$  in September–October of 2020 and 2021 despite tree clearings and canopy reductions (Figures 6 and 7). Such compensatory effects are common at individual, stand, and population levels after insect attacks, diseases, and other disturbances, such as fires, floods, hurricanes, lightning strikes, grazing, and thinning (Li et al., 2021). At a stand level, increased basal and height growth of the trees (Bose et al., 2018) and accelerated production of leaves (Rea & Massicotte, 2010) and roots (Baskin, 2012) were observed to follow disturbances associated with tree mortality.

In forest ecosystems, compensatory processes usually continue over several decades after the disturbance until a state similar to pre-disturbed conditions is reached and a closed canopy is restored (Li et al., 2021). However, in a residential yard, tree placement and species composition largely depend on the homeowner's decisions and preferences, which are driven by socioeconomic factors and local nursery offerings (Avolio et al., 2018; Conway, 2016; Kloster et al., 2021).

Our results indicate a large role of compensatory effects on tree transpiration in the studied tree stand, as plot-level transpiration was restored pre-disturbance levels, despite a substantial reduction of canopy cover (Figures 5-7). However, in case of a larger canopy reduction, the potential strength of compensatory effects remains uncertain, as the potential for compensatory effects is not unlimited (i.e., at 100% canopy reduction, tree transpiration would certainly cease), as well as the relative importance of environmental, biological, and human factors in a future plant composition and ecohydrological functioning of the yards.

## Role of climate change

Regardless of whether they are located in a natural or human-dominated environment, trees are now subjected ECOSPHERE 17 of 21

to an increasingly higher likelihood of insect attacks and other disturbances, which also increase in frequency and severity due to climate change (Berland & Elliott, 2014; Edburg et al., 2012). Shifts in temperature and precipitation regimes driven by climate change exacerbate and increase the frequency of the major sources of tree stress, such as severe droughts, fires, winds, and pest attacks, and cause widespread tree mortality globally (Anderegg et al., 2015; Seidl et al., 2017). In the over 80-year lifespan of the studied trees, mean monthly maximum temperatures of their environment increased by about 1°C along with a notable increase in frequency of hurricane winds and tropical storms affecting the city of Tallahassee (NOAA National Weather Service; https://www.weather.gov/tae). Just during the duration of this study, studied trees underwent six severe weather events (Table 3). While our  $J_0$  dataset does not show any direct responses of trees to heavy storms and strong winds, they may have weakened the ability of trees to resist infestation (Anderegg et al., 2015; Seidl et al., 2017). Additionally, wind damage makes trees a target for insect attacks (Fettig et al., 2022; McNichol et al., 2019).

Notably, climate change affects trees and bark beetles simultaneously, yet in opposite ways. When warmer and dryer conditions exert additional stresses on trees, they accelerate the metabolism and reproductive rates of bark beetles (Davis, 2022; Mitton & Ferrenberg, 2012). When windstorms physically damage trees, they create more beneficial conditions for the spread of bark beetles (Fettig et al., 2022; McNichol et al., 2019). All in all, the co-occurrence of these climate change-induced stress factors might have weakened the defensive mechanisms of studied trees, and—consequently—reduced their chances of survival in case of a disturbance.

## **Conclusions and implications**

We studied sap flux and transpiration of unirrigated residential loblolly pines within their natural range. Both sap flux and transpiration of the trees without confirmed infestation were in close agreement with previous findings for loblolly pines in natural conditions. In accordance with our expectations, transpiration of infested trees generally decreased over time. However, each infested tree exhibited its own pattern of sap flux responses to environmental drivers (Figure 3a). Also in accordance with our expectations, transpiration of the trees without confirmed infestation increased after tree clearings and die-off. We attributed this increase to compensatory increases of leaf stomatal conductance, stronger coupling of the opened-up canopy with the atmosphere, and stand-level compensatory effects due to higher resource availability (Figure 5).

The fate of the studied trees was strongly dependent on the homeowner's decisions about tree removals. Trees in close proximity to the house and trees severely damaged by infestation posed safety risks as they had an increased likelihood of dropping branches or falling, especially in case of strong winds (Gilman et al., 2006; McLean et al., 2018). The homeowner's decisions were made under a high level of uncertainty regarding the effectiveness of insecticide treatment, the degree of physical damage to the trees, and the likelihood, timing, and severity of future weather events that may affect the yard. These uncertainties are specific to the study area and, in general, to the US southeast; in other regions, uncertain risk factors affecting decision-making may concern floods, droughts, fires, pest attacks, etc.

The results of this study highlight the complexity and nonlinearity of the response of tree stand transpiration to insect infestation and human actions that addressed both infestation and the possibility of hazardous weather conditions. Thus, Tree 1.0 was cut even before the discovery of the infestation to avoid safety hazards related to the increasing frequency of hurricane winds in the study area. Our results demonstrate that the effects of climate change-induced disturbances on urban water balance are not straightforward and strongly tied to human decisions and actions. These decisions are currently made under high levels of uncertainty due to the lack of information and support for homeowners facing emergencies on their property. Hence, scientifically based guidelines for tree management under climate change-related emergencies are urgently needed.

As climate change-induced disturbances gain momentum, it is necessary to understand complex ecosystem responses to the upcoming changes and their effects on the environment. In human-dominated environments, this knowledge is critical for informed risk assessment and decision-making on the scales from household to nationwide. Our study highlights that a comprehensive understanding of changing plant composition and eco-hydrologic functioning of residential environments—the environments where humans and nature affect each other in the most direct way-requires not only consideration of environmental, socioeconomic, and cultural factors, but also human decision-making under a high level of uncertainty. These factors and their interactions are determining the future appearance, sustainability, and resilience of residential environments in the face of further climate change-induced impacts, extremes, and disturbances.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data (Litvak & Pataki, 2023) are available from Hydroshare: https://doi.org/10.4211/hs.d774a78c24ce499 4a4871660f8d1879f.

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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