

Winter Season Tree Sap Flow and Stand Transpiration in an Intensively-Managed Loblolly and Slash Pine Plantation

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INTRODUCTION

On the lower gulf coastal plain of the southeastern United States, meteorological conditions during the winter months of November to February remain conducive to aboveground physiological activity, with frequent periods of high radiation, and temperatures seldom falling below freezing. While a number of studies have investigated southern pine physiology during the winter months (Drew and Ledig,

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The author thanks Tom Hinckley for loaning the sap flow systems, and the University of Florida Department of Agricultural and Biological Engineering for providing the meteorological data. The author acknowledges the help of Jeff English, Robert McGarvey and Duncan Wilson with fieldwork, and the helpful discussions and reviews provided by Eric Jokela and Duncan Wilson.

This study was funded by the Forest Biology Research Cooperative at the University of Florida. The research was conducted on land managed by Jefferson Smurfit Corporation.

Florida Agricultural Experiment Station Journal Series Number XXXX.

[Haworth co-indexing entry note]: "Winter Season Tree Sap Flow and Stand Transpiration in an Intensively-Managed Loblolly and Slash Pine Plantation." Martin, Timothy A. Co-published simultaneously in *Journal of Sustainable Forestry* (Food Products Press, an imprint of The Haworth Press, Inc.) Vol. 10, No. 1/2, 2000, pp. 155-163; and: *Frontiers of Forest Biology: Proceedings of the 1998 Joint Meeting of the North American Forest Biology Workshop and the Western Forest Genetics Association* (ed: Alan K. Mitchell et al.) Food Products Press, an imprint of The Haworth Press, Inc., 2000, pp. 155-163. Single or multiple copies of this article are available for a fee from The Haworth Document Delivery Service [1-800-342-9678, 9:00 a.m. - 5:00 p.m. (EST). E-mail address: getinfo@haworthpressinc.com].

1981; Boltz et al., 1986; Day et al., 1991; Teskey et al., 1994; Murthy et al., 1997), most of these studies have focused on organ-level responses. Few, if any, have examined physiological processes at the whole-tree or stand level. The primary objective of this study was to quantify winter season transpiration rates of trees and stands of loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pine. Transpiration is an important process, both in terms of hydrology (Whitehead and Kelliher, 1991; McNulty et al., 1996) as well as tree and stand physiology (e.g., Monteith 1995), and is closely linked to productivity at various scales (Leuning, 1995; Le Maitre and Versfeld, 1997). As such, measurements of winter transpiration rates will be useful for understanding the environmental limits to southern pine productivity. In addition, by conducting measurements in plantations that have undergone intensive cultural treatments, we will gain insight into the water balance of stands under management scenarios that are becoming increasingly common (Sedjo and Botkin, 1997).

METHODS

This research was conducted in one stand of *P. taeda* and one stand of *P. elliottii* planted in 1983, 20 km northeast of Gainesville, Florida as part of a larger experiment investigating the effects of intensive weed control and fertilization on growth of southern pines (Swindel et al., 1988). The sap flow measurements took place on 468 m² study plots that contained 56 *P. taeda* or 52 *P. elliottii* trees (approximately 1150 trees ha⁻¹). After planting, understory vegetation was permanently excluded with herbicide and mechanical treatments, and fertilizer containing micro- and macronutrients was applied one to three times per year from establishment until 1993. Basal areas of the *P. taeda* and *P. elliottii* stands were 40.5 and 34.8 m² ha⁻¹, respectively. Average tree height in the *P. taeda* and *P. elliottii* plots were 18.8 and 17.1 m, respectively (range 14.3-20.6 m and 14.6-19.3 m, respectively) at the time of sap flow measurements. Average *P. taeda* and *P. elliottii* diameter at breast height (DBH) were 20.5 and 19.8 cm, respectively (range 10-29.7 cm and 15.2-25.7 cm, respectively).

Tree sap flow was measured using the tissue heat balance technique described in detail by Cermák et al. (1973, 1982), Kucera et al. (1977), and Cermák and Kucera (1981). Gauges were installed on four sample trees in each stand. Sample trees were chosen so that each tree repre-

sented one fourth of the total basal area of the stand (sample trees were at the 16th, 59th, 78th and 93rd percentile of the cumulative stand basal area for *Pinus taeda*, and at the 30th, 50th, 70th and 94th percentile for *Pinus elliottii*). Gauges were installed and insulated as described in Martin et al. (1997). On the two largest sample trees in each stand, two gauges were installed on opposite sides of the stem to account for possible circumferential variation in sap flow rates (Cermák and Kucera, 1985) and sap flow was calculated as the average of the two sides. Sap flow was logged each second and saved as 15 minute averages. Measurements continued from early November 1997 until late February 1998.

Tree-level sap flow data were integrated to the stand level as described by Cermák and Kucera (1990) and Martin et al. (1997). This was accomplished by quantifying the relationship between size of the sampled sap flow trees (in this case, individual tree basal area) and daily total tree sap flow. This relationship was then applied to the basal area distribution of the stand to calculate transpiration for each day.

To evaluate the environmental evaporative demand (i.e., the maximum transpiration rate possible given the meteorological conditions and no limitations due to reductions in stomatal conductance), a physiologically-based potential transpiration (T_{pot}) was calculated from weather station data using the Penman-Monteith equation:

$$T_{pot} = \frac{sR + \rho_a C_p D g_a}{\lambda [s + \gamma(1 + g_a/g_{crown})]} \quad (1)$$

where:

T_{pot} is in mm s^{-1}

s is the slope of the saturated vapor pressure versus temperature curve (kPa K^{-1})

R is incoming radiation (W m^{-2}), (ρ_a is the density of dry air (kg m^{-3}))

C_p represents the specific heat capacity of air ($\text{J kg}^{-1} \text{K}^{-1}$)

λ is the latent heat of evaporation of water (J kg^{-1})

γ is the psychrometer constant (kPa K^{-1}).

Because there is little or no information in the literature on the micro-meteorology of southern pines, canopy and aerodynamic conductances

(g_{crown} and g_a) were set to 25 and 200 mm s^{-1} , respectively, the maximum values for conifers given in Kelliher et al. (1993). This had the effect of simulating transpiration from a tree canopy with high leaf area with stomata fully open during all daylight hours. Potential transpiration was calculated hourly during daylight hours, and summed for each day.

RESULTS AND DISCUSSION

Tree Sap Flow

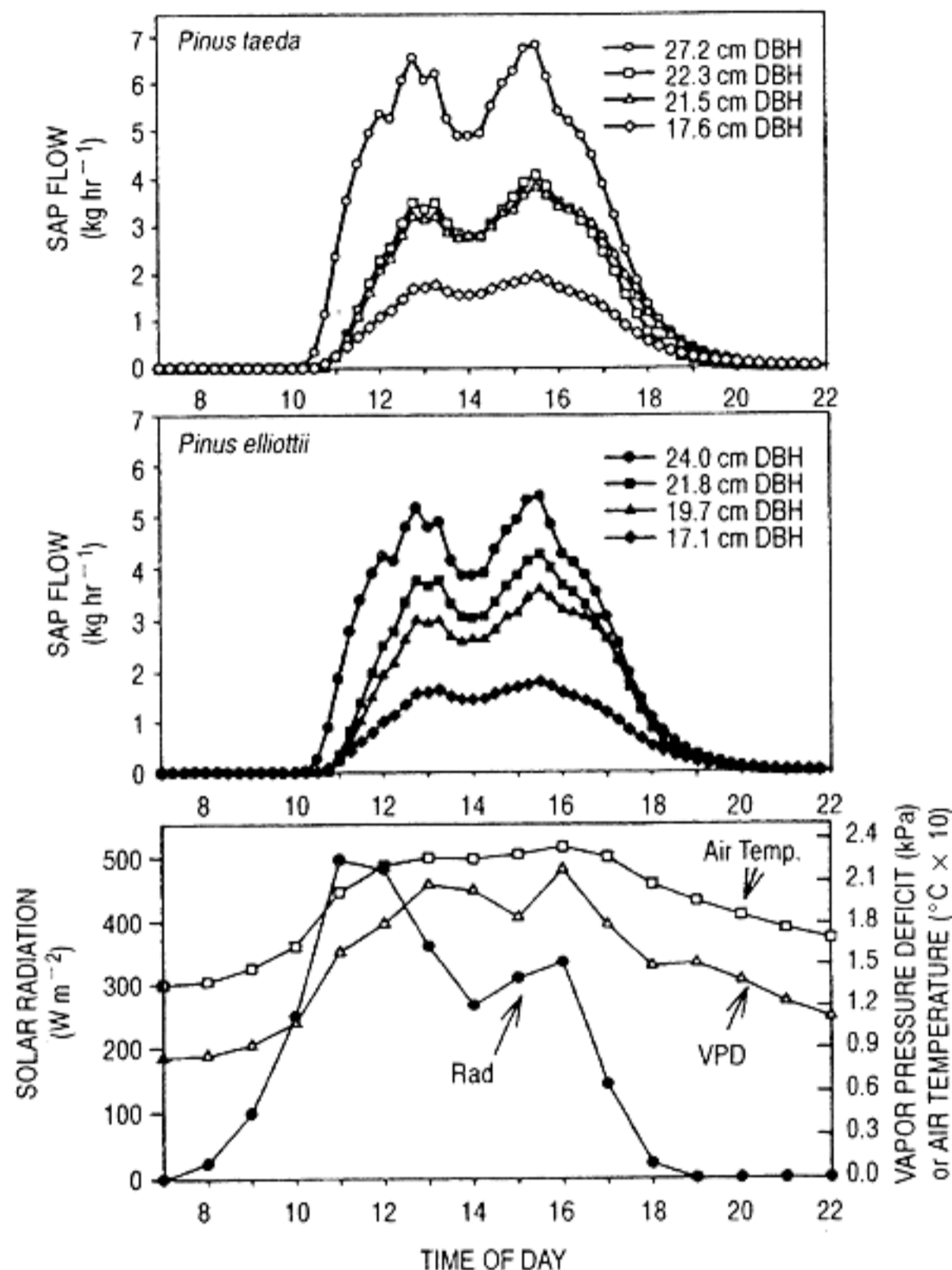
Sap flow rate throughout the day was very responsive to meteorological changes. For example, on January 3, patterns of sap flow closely mirrored changes in solar radiation (Figure 1).

These sensitive responses to radiation are most likely the result of radiation-mediated changes in crown-level stomatal conductance, rather than the direct effects of radiation on transpiration (the R term in Equation 1). This is because, in conifers, boundary layer conductance is much larger than stomatal conductance, making vapor pressure deficit and stomatal conductance the primary controllers of transpiration rate; changes in radiation have little direct effect on transpiration in these "well coupled" systems (Meinzer, 1993).

Daily water loss from individual trees had a strong linear correlation with tree basal area (Figure 2), with R^2 values of this relationship usually exceeding 0.80. The use of a linear scaling relationship with these data produces a positive x-intercept, which implies that trees with basal areas smaller than this intercept have zero transpiration. In this study, the x-intercept almost always fell below the basal area of the smallest tree in the study plots. Only on days with very low transpiration rates (cool, moist, cloudy days) did the x-intercept slightly exceed the basal area of the smallest tree in the plots (i.e., December 27, 1997, Figure 2). In these cases, for the purposes of scaling water loss to the stand scale, the one or two trees with basal areas smaller than the intercept were assumed to have no water loss. Stand transpiration estimated with this method differed on average by less than 3% from an independent non-regression method, which scaled transpiration upward, based on four tree basal area size classes (data not shown).

Regressions between tree daily water loss and tree basal area were not significantly different between the species on any day measured.

FIGURE 1. Diurnal patterns of *Pinus taeda* and *Pinus elliottii* tree sap flow and environmental variables on January 3, 1998.



Average daily transpiration ranged from 8.1 kg for the smallest tree measured (17.1 cm DBH) to 35.3 kg for the largest tree (27.2 cm DBH). Maximum rates of water loss for the largest trees measured exceeded 75 kg (Table 1). These winter rates of daily tree water loss are comparable to spring and summer tree water loss measured in *Pinus halapensis* Mill., *Pinus pinaster* Ait. and *Pinus sylvestris* L. trees of similar size (Granier et al., 1990; Schiller and Cohen, 1995; Granier et al., 1996).

Stand Transpiration

Stand transpiration during the 108 day measurement period ranged from effectively zero on rainy days to over 4 mm day⁻¹ on warm, dry

FIGURE 2. Relationship between tree size and tree water loss for *Pinus taeda* and *Pinus elliottii* trees on days with differing potential transpiration (T_{pot} , Equation 1).

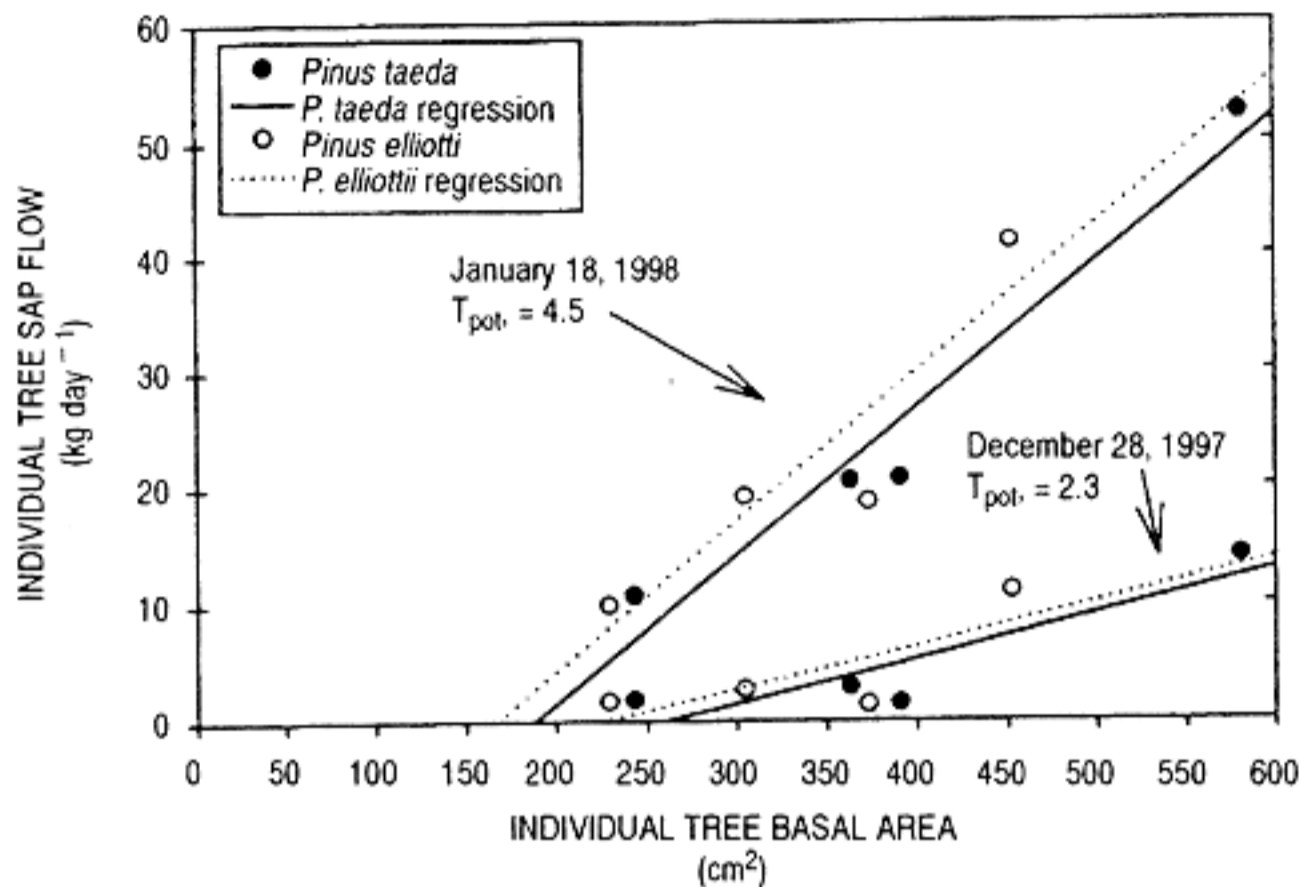


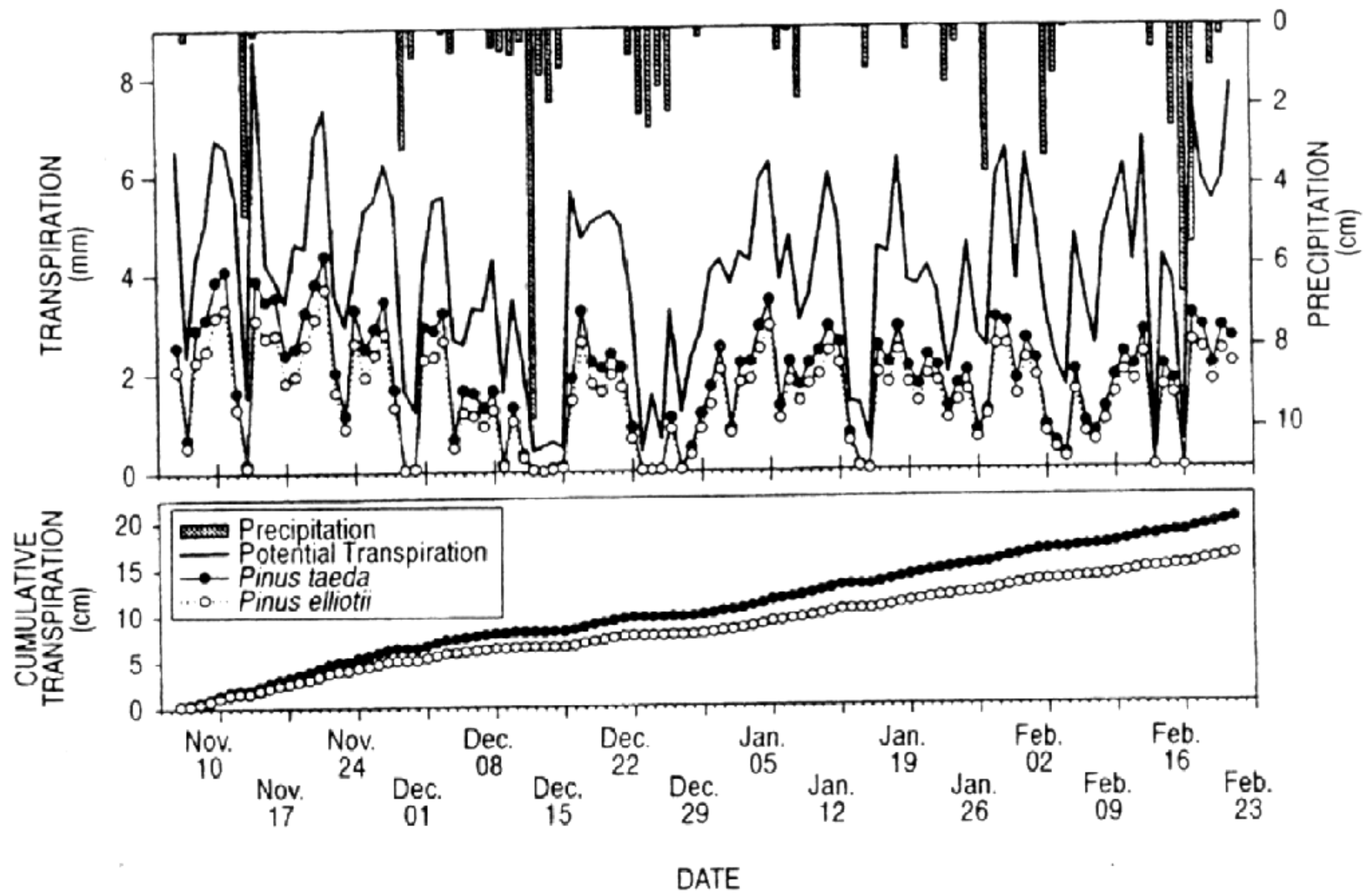
TABLE 1. Biometric parameters and sap flow statistics for eight *Pinus taeda* and *Pinus elliottii* trees in north-central Florida, U.S.A.

Species	Diameter at 1.37 m (cm)	Basal Area (cm ²)	Projected Crown Area (m ²) ^a	Maximum Daily Transpiration (kg)	Average Daily Transpiration (kg)
<i>Pinus taeda</i>					
	27.2	581	20.0	75.1	35.3
	22.3	391	13.1	50.9	19.4
	21.5	363	6.5	45.3	18.6
	17.6	243	4.2	17.0	8.1
<i>Pinus elliottii</i>					
	24.0	452	12.9	71.6	28.3
	21.8	373	8.5	42.3	14.3
	19.7	305	5.5	38.4	14.7
	17.1	230	3.6	28.4	8.1

^a Area of an ellipse calculated from measurements of crown diameters in two directions

days (Figure 3). As was the case with tree-scale transpiration, these winter stand transpiration rates were comparable to spring and summer season stand transpiration measured with sap flow methods in European pine forests (Granier et al., 1990; Granier et al., 1996) and in a less intensively managed loblolly pine forest in North Carolina

FIGURE 3. Daily and cumulative stand transpiration in *Pinus taeda* and *Pinus elliotii* stands, and potential transpiration and precipitation during the winter of 1997-1998.



(Oren et al., 1998; tree age = 12, stand basal area = $15.9 \text{ m}^2 \text{ ha}^{-1}$). It should be noted that throughout the measurement period, the water table remained within 1.3 m of the soil surface, suggesting that soil water deficits were not an important influence on tree transpiration.

While the relationship between tree size and tree water loss was identical for the two species (Figure 2), *P. taeda* stand transpiration was consistently 20 to 25% higher than transpiration of the *P. elliotii* stand. Mean *P. taeda* stand transpiration was 1.8 mm day^{-1} , compared to the *P. elliotii* average of 1.5 mm day^{-1} . Over the three months of measurement, this translated into a 3.8 cm difference in cumulative water loss between the stands (19.8 and 16.0 cm cumulative *P. taeda* and *P. elliotii* stand transpiration, respectively, Figure 3). The contrasts in stand transpiration were the result of differences in tree size distributions between the two species, and are consistent with trends in canopy leaf area for the two stands. Litterfall and destructive sampling data show that all-sided leaf area index (LAI) in the *P. taeda* stand ranged from $7.9 \text{ m}^2 \text{ m}^{-2}$ in November to $5.9 \text{ m}^2 \text{ m}^{-2}$ in February, while *P. elliotii* LAI ranged from 6.2 to $5.0 \text{ m}^2 \text{ m}^{-2}$ over the same period, demonstrating between-species LAI differences on the order of 20% (E. Jokela and T. Martin, unpublished data).

CONCLUSIONS

Due to the mild winter climate conditions in northern Florida, intensively-managed *P. taeda* and *P. elliottii* stands transpire during the winter at rates observed in more northern pine forests during the spring and summer. Because transpiration and productivity are linked, this suggests that considerable carbon gain takes place during the winter months in this region.

The relationship between tree basal area and daily water loss was not statistically different between *P. taeda* and *P. elliottii*, indicating similar rates of water loss per unit stem or sapwood area. More research needs to be done to determine whether transpiration rates per unit leaf area (and therefore canopy conductance) remains the same between species.

The *P. taeda* stand transpired approximately 20% more water than the *P. elliottii* stand under identical climate conditions, partially due to species differences in stand structure (diameter distributions and leaf area index). However, species differences in canopy conductance could also partially explain these results. Further work is needed to investigate potential canopy conductance differences between the species.

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