

TECHNICAL REPORT

# Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species

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## ABSTRACT

We investigated radial patterns of sap flux density and wood properties in the sapwood of young loblolly pine (*Pinus taeda* L.), mature white oak (*Quercus alba* L.) and sweetgum (*Liquidambar styraciflua* L.), which represent three major classes of wood anatomy: non-porous (coniferous), ring-porous and diffuse-porous. Radial measurements of xylem sap flux density were made in sections of xylem extending to 20 mm and 20–40 mm from the cambium. These measurements were compared with measurements of the relative water content ( $R_s$ ) and sapwood specific gravity ( $\rho_f$ ) of corresponding radial sections. In both hardwood species, sap flow differences were rarely significant between the two depth intervals. In pine, a 59% reduction in daily sap flux density from outer to inner sapwood was found. This could not be accounted for by a 3% drop in  $R_s$ ; rather, an accompanying 9% reduction in  $\rho_f$  indicated a transition between the depth intervals from mature to juvenile sapwood, and is the probable cause of the lower flux rate in the inner xylem of pine.

**Key-words:** *Liquidambar styraciflua*; *Pinus taeda*; *Quercus alba*; soil moisture; transpiration; xylem.

## INTRODUCTION

In sap flow experiments utilizing heat pulse velocity (e.g. Edwards & Booker 1984) or constant-heat flow sensors (Granier 1987; Oren *et al.* 1993), failure to account for radial and angular trends in xylem hydraulic characteristics may introduce significant errors in scaling of sap flux density measurements to the whole-tree or stand scales (Edwards & Booker 1984; Hatton, Moore & Reece 1995). The identification of radial trends may also provide insight into physiological adaptations of wood water storage and movement. In this study we examined radial sap flow, relative water content and wood density trends in 12-year-old loblolly pine (*Pinus taeda* L.) with little or no heartwood formation, and two mature hardwood species, white oak (*Quercus alba* L.) and sweetgum (*Liquidambar styraciflua* L.). The objective of this study was to test the assumption

of radially uniform sapwood transport across the conducting xylem of these species.

Additionally, in order to provide physically based explanations for any radial patterns we may observe in sap flow, the sapwood relative water content ( $R_s$ ) and specific gravity ( $\rho_f$ ) were both measured at the same depth intervals as the sap flow measurements. Sapwood hydraulic conductivity may be influenced by  $R_s$  (Comstock 1965; Kininmonth 1970; Booker & Kininmonth 1977) and  $\rho_f$  (Booker & Kininmonth 1977). Sapwood permeability has been shown to decrease exponentially with  $R_s$  (Edwards & Jarvis 1982; Waring & Running 1978; Waring, Whitehead & Jarvis 1979; Pothier *et al.* 1989), and to be inversely correlated with  $\rho_f$  (Booker & Kininmonth 1977). However, juvenile wood, with lower  $\rho_f$  than mature wood, may have lower hydraulic conductivity due to shorter tracheid lengths (Pothier *et al.* 1989).

## MATERIALS AND METHODS

### Species, site and experimental conditions

Sites for all three species were located at Duke Forest near Durham, NC, USA (35°52'N, 79°59'W), a transitional zone between the coastal plain and the Piedmont plateau. The surrounding terrain is rolling, with an average elevation of ≈130 m above sea level. Mean annual temperature for this region is 15.5 °C, and mean annual precipitation is 1140 mm. Rainfall is well distributed throughout the year. July has the highest average amount of rainfall, and November the lowest. Minimum soil moisture usually occurs in spring and summer. Rainfall in 1994 totalled 940 mm, about 100 mm less than the 10 year average for this region.

### Loblolly pine

The stand was located in the Blackwood Division of Duke Forest, on soil classified in the Enon Series as low-fertility, acidic Hapludalfs (D.D. Richter, Duke University, unpublished results) subject to minimal erosion because of a less than 2% slope. Ten trees in a plot within a uniform, managed stand of loblolly pine were chosen for study, and had a mean diameter (1.3 m above-ground) of 89 mm (range 53–137 mm). Measurements of sap flux density were made continuously over nine clear, dry and warm days beginning

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**Table 1.** Stand parameters for experimental sites in Duke Forest, NC

Division of Duke Forest	Pine <i>P. taeda</i>	Hardwood <i>Q. alba</i> <i>L. styraciflua</i>
Stand age (year)	12	approx 80
Stand density (trees ha <sup>-1</sup> )	5240	1330
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	24.8	22.1
Sapwood area (m <sup>2</sup> ha <sup>-1</sup> )	22.6	6.19
DBH (mm)	55	103
Average height (m)	7.1	45
Leaf area index (m <sup>2</sup> m <sup>-2</sup> )	2.7	5.5

on 8 September 1994. Table 1 summarizes information about the stands.

### White oak and sweetgum

The stand was located in a mature, mixed hardwood forest in the Eno Division of Duke Forest on soil classified as a Georgeville silt loam, with 6–10% slopes. The forest developed on abandoned pasture land ≈80 years ago. The average diameter of the trees was 344 mm (range 185–506 mm) for oak, and 180 mm (range 54–282 mm) for sweetgum. Sap flux density measurements during four clear, warm days were made continuously on 10 dominant white oak trees beginning on 16 October 1994, and seven dominant sweetgum trees beginning on 27 October 1994. Throughout the course of these measurements we observed no end-of-season discoloration on intact canopy leaves. Continuous air temperature data recorded in Duke Forest c. 6 km from this forest showed that the first frost of the season occurred on 12 November 1994.

### Constant heating sap flow probe implementation and meteorological measurements

Sap flux density measurements within two radial depth intervals in the xylem were made with a constant heat-flow method using heated and unheated thermocouple pairs as described by Granier (1987). The apparatus consisted of a pair of fine-wire copper–constantan thermocouples joined at the constantan leads so that voltage measured across the copper leads represented the temperature difference ( $\Delta T$ ) between the thermocouples. Each thermocouple was installed in the midpoint of a 1.5-mm-diameter, 21-mm-long, hollow steel needle, around which electrically insulated constantan heating wire had been coiled. The probes were coated with thermally conducting silicon grease and inserted into aluminum tubes installed in the bole of the tree, separated vertically by c. 150 mm. The upper heating coil received 200 mW power which was dissipated as heat into the sapwood and vertical sap flux surrounding the probe. The lower coil was left unheated. During conditions of

zero sap flux density, the temperature difference between upper and lower thermocouples stabilized and represented the steady-state temperature difference resulting solely from the dissipation of heat into non-transporting sapwood. This  $\Delta T$  served as a baseline from which any sap flow caused a decrease in  $\Delta T$ . After subtracting the baseline  $\Delta T$ , sap flux density was then calculated from the corrected  $\Delta T$  as described by Granier (1987).

Heated probes were inserted into the xylem at a height of 1.15 m above the ground at two depths, in the 0–20 mm interval and the 20–40 mm interval inside the cambium of each tree. The installation of the probes in the 20–40 mm interval was accomplished by scraping off bark and drilling a 12-mm-diameter, 20-mm-deep hole in the xylem. The heated probes were positioned ≈50 mm circumferentially from each other. To provide reference for both heated probes, a reference probe was positioned 150 mm below the heated probes in the 10–30 mm interval from the cambium so that it overlapped both depths. A single reference probe was used after verifying that there was no diurnal, radial stem temperature gradient by monitoring unheated probe systems over a diurnal course before beginning heated measurements. All probes were placed on the north-facing side of trees. Silicon gel was applied to all excess space in drilled holes and over all sensor housings to provide thermal insulation.

In order to calculate vapour pressure deficit, relative humidity and temperature were recorded continuously with an RHA1 probe (Delta-T Devices Ltd, Cambridge, UK). In addition, photosynthetically active quantum flux (PFD) was measured above the canopy (LI-193SA Spherical Quantum Sensor, Li-Cor, Lincoln, NE). These measurements included reflected canopy radiation and therefore are useful for comparative purposes only. Both xylem flow and micrometeorological data were sampled with a multi-channel data logger (Delta-T Devices Ltd, Cambridge, UK) at 30 s intervals and averaged and recorded every 30 min.

### Relative water content and sapwood specific gravity

Subsequent to the xylem sap flux density measurements, cores for estimation of  $R_s$  and  $\rho_f$  were taken with a 12-mm-diameter increment borer at a height of 1.3 m across the whole diameter of each tree for pines, and to a depth of 60 mm for hardwoods. For the pines, cores were taken less than 48 h after a 4 mm rainfall, when average leaf water potential of current-year needles was -0.1 MPa ( $n = 3$ ) measured with a Scholander-type pressure chamber (PMS Instrument Corp., Corvallis, OR). Because of the height of the hardwoods, water potential was not measured, although cores were taken less than 48 h after a 5 mm rain event.

Immediately after coring, samples were placed in pre-cut, transparent 'Tygon' tubing (13 mm inner diameter),

sealed at the ends and placed in an ice chest. Upon return to the laboratory, all samples were transferred to a refrigerator set at 4 °C. Total core lengths minus bark were measured to the nearest 1·0 mm while still in the transparent tubing.

Samples 20 mm long were cut from each core by sliding the core out from the tubing. Immediately after cutting, the fresh mass of each sample was obtained with a draft-shielded electronic balance (Model BA-6100, Sartorius Corp., Bohemia, NY). Fresh, and all subsequent, mass measurements were made to the nearest 0·1 mg. Sample lengths were then measured with a micrometer to the nearest 0·1 mm.

In order to obtain the saturated mass of the sapwood, samples were placed in glass vials and submerged at room temperature in de-gassed water. All samples were left submerged for at least 48 h before weighing. Samples were removed from vials, excess surface water was removed with a moist cloth and then the samples were re-weighed. After saturated masses were recorded, samples were placed in a forced-draught oven set at 80 °C and dried to a constant mass. Samples were then re-weighed to obtain dry mass.

The relative water content,  $R_s$ , was computed as

$$R_s = \frac{W_f - W_d}{W_s - W_d}, \quad (1)$$

where  $W_f$ ,  $W_s$  and  $W_d$  are the fresh, saturated and dry sample masses, in grams, respectively. The sapwood specific gravity,  $\rho_f$ , was computed as

$$\rho_s = \frac{W_d}{V_{wb}}, \quad (2)$$

where  $V_{wb}$  is the green volume of the sample.

## Statistical analysis

The dependence of  $R_s$  and  $\rho_f$  on the depth of sapwood samples was examined using one-way ANOVA and pair-wise Tukey's Studentized Range (HSD) tests (Statistical Analysis Systems, Cary, NC) after verifying that tree diameter class main effects and tree diameter–sapwood depth interaction effects were not significant at  $P = 0\cdot05$  in a two-way ANOVA.

Statistical analysis of sap flux density measurements consisted of  $t$ -tests (Statistical Analysis Systems, Cary, NC) for the difference between the means of outer and inner sap flux density at each point in the time series. It should be noted that repeated measurements of sap flux density are autocorrelated and thus the assumption of independence between temporally adjacent sample sets is invalid. However, proper methods for analysing such data (e.g. time-series analysis, and ANOVA with repeated measurements) cannot be used to identify the time intervals in which two trends are different or similar. In order to identify these intervals, we used Student's  $t$ -test for each measurement period in the time series.

## RESULTS AND DISCUSSION

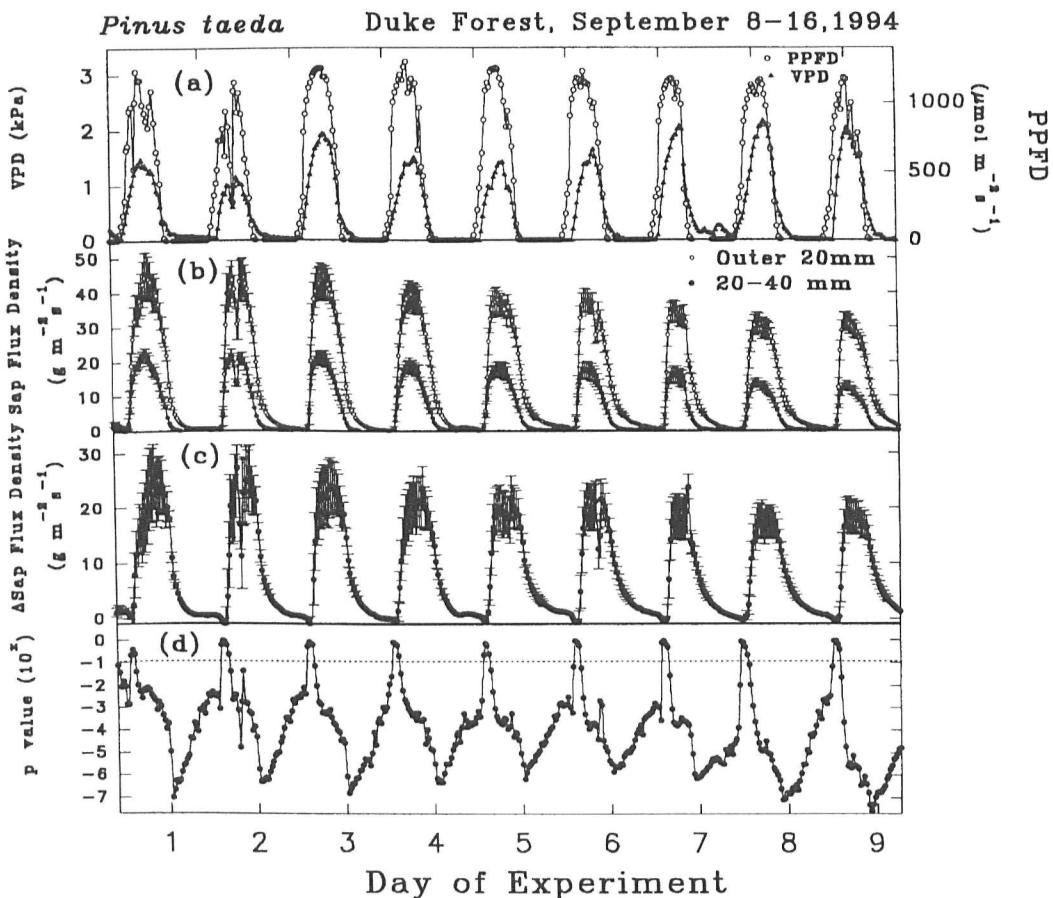
While a decrease in sap flux density radially towards the pith was found in loblolly pine, no changes in flux were found in white oak or sweetgum. Here we interpret these results on the basis of corresponding  $\rho_f$  and  $R_s$  data.

### Pine

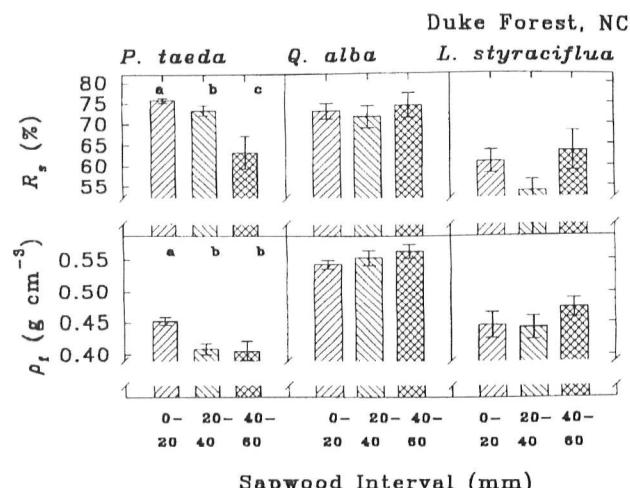
For pine, inner sapwood sap flux density measurements were consistently less than outer sapwood measurements over the diurnal courses (Fig. 1), with average integrated daily values of inner sapwood sap flux density only 41% of the outer sapwood measurements. Table 2 compares these sap flow patterns with those found in other conifer species. Sapwood specific gravity,  $\rho_f$  and  $R_s$  were observed to decrease radially in loblolly pine (Fig. 2), with mean values of  $\rho_f$  close to published values for loblolly pine (Paul & Smith 1950; Megraw 1985) and decreasing radially inwards as previously found (Zobel & McElwee 1958; Wahlenberg 1960; Panshin & de Zeeuw 1970). The sapwood relative water content,  $R_s$ , was also in the range of published values for other conifer species (Waring & Running 1978; Waring, Whitehead & Jarvis 1979; Edwards & Jarvis 1982). The decrease in  $R_s$  with distance from outer xylem to pith (Fig. 2) confirms similar findings in conifers (e.g. Trendelenburg 1939; Choong & Fogg 1989). Moreover, the small decrease in  $R_s$  found in those studies between the outer and inner sapwood, in relation to the much larger drop in  $R_s$  in the innermost sapwood, has also been confirmed. The decrease in  $R_s$  with distance from the cambium was more pronounced than decreases found in Douglas fir (*Psuedotsuga menziesii*) (Waring & Running 1978; Chalk & Bigg 1956).

However, the 3% radial decrease in  $R_s$  from outer (0–20 mm) to inner (20–40 mm) xylem depths alone cannot explain the large reduction in sapflux density with depth. Using data from *Abies grandis* (Waring & Running 1978), it is estimated that a 3% drop in  $R_s$  could have reduced conductivity by 10% at most. Furthermore, the radial decrease in  $\rho_f$  found in this study is typically associated with increasing hydraulic conductivity (Booker & Kininmonth 1977), so that the combined effect of the radial decreases in  $\rho_f$  and  $R_s$  would have led to, at most, a marginal decrease in the sap flux density of the inner xylem.

It is more likely that there was a much lower sap flux density in the inner xylem because the inner xylem was composed of juvenile wood, while the outer growth rings were mature xylem. A transition between the two types of sapwood from the 0–20 mm to the 20–40 mm interval is suggested by the decrease in  $\rho_f$  and the absence of a further decrease in  $\rho_f$  from the 20–40 mm to the 40–60 mm interval. Juvenile wood in loblolly pine usually occurs until the 7th to 10th rings from the pith, and differs from mature wood by having lower specific gravity and greater mean lumen diameters as a result of greater proportions of large-diameter earlywood tracheids (Megraw 1985; Larson 1969). Juvenile wood is also characterized by



**Figure 1.** Time series of the environmental conditions and average sap flux density of 10 loblolly pines monitored at 0–20 mm and 20–40 mm depths from 8 to 16 September 1994. (a) Vapour pressure deficit and photosynthetically active radiation. (b) Sap flux density per unit sapwood area. (c) Difference between outer and inner sap flux density values. (d) *P* value for the difference between outer and inner sap flux density values. Note the exponential vertical scale. The horizontal line represents *P* = 0.10. Differences between the two time series were not significant only during brief morning periods when absolute values of sap flux density were minimal. All vertical bars represent two standard errors.



**Figure 2.** Wood relative water content ( $R_s$ ) and sapwood specific gravity ( $\rho_t$ ) as functions of depth from the cambium towards the pith, in loblolly pine, white oak and sweetgum. Bars with different letters are significantly different (Tukey's  $P < 0.05$ ).

shorter tracheids and greater fibril angles (Seth 1981; Megraw 1985). According to the Hagen–Poiseuille law, increased lumen diameter increases hydraulic conductivity (Jarvis 1975). However, increased lumen diameter may have less influence on bulk hydraulic conductivity than decreased tracheid length (Petty & Puritch 1970; Whitehead, Sheriff & Greer 1983; Pothier *et al.* 1988; Milota *et al.* 1994) because the primary resistance in tracheids is in their bordered pit interfaces, producing a higher resistance for shorter tracheids than for longer tracheids over the length of the tree. Using data on tracheid length in *Pinus taeda* from Megraw (1985), and a relationship incorporating the effects of both larger lumen diameter and shorter tracheids in juvenile xylem derived from *Pinus banksiana* from Pothier *et al.* (1989), we estimated that the hydraulic conductivity in juvenile loblolly pine sapwood is 40% less than that in mature sapwood of the same tree. Thus, low hydraulic conductivity of juvenile relative to mature wood is the likely cause of the reduced sap flux density with depth in the xylem.

**Table 2.** Comparison of results of studies of radial trends in sapwood hydraulic conductivity, heat pulse velocity (HPV) or heat flux density

Source	Species	Technique	Radial increments studied	Pattern from outer/inner xylem
<i>Coniferous</i>				
Comstock (1965)	<i>Tsuga canadensis</i>	hydraulic conductivity	categorical <sup>2</sup>	d; >50% decrease
Sipchanov & Baurenska (1965)	<i>Picea excelsa</i>	staining	unknown	d; max flow in first two rings
Swanson (1967a, 1967b, 1971)	<i>Picea excelsa</i>	HPV	6×5 mm+1×10 mm	g; 0.3:0.0:1.0:0.9:1.0:0.8:0.5 <sup>3</sup>
	<i>Pinus contorta</i>	same	same	g; 0.0:0.3:0.5:1.0:0.9:0.8:0.7
Kininmonth (1970)	<i>Pinus radiata</i>	hydraulic conductivity	unknown	e; 1.0 conductance ratio
Markstrom & Hann (1972)	<i>Pseudotsuga menziesii</i>	hydraulic conductivity	categorical	d; 27% decrease
	<i>Pinus contorta</i>	same	same	d; 24% decrease
Mark & Crews (1973)	<i>Picea engelmannii</i>	same	same	d; 43% decrease
	<i>Picea engelmannii</i>	HPV	5×6 mm+21 mm+3×13 mm+37 mm	g; 0.1:0.1:0.5:1.0:1.0:0.3:0.3:0.2:0.1:0.1
	<i>Pinus contorta</i>	same	5×6 mm+3×10 mm+20 mm+4×10 mm	g; 0.1:0.2:0.7:1.0:0.5:0.3:0.3:0.3:0.1:0.1:0.1
Booker & Kininmonth (1977)	<i>Pinus radiata</i>	hydraulic conductivity	categorical	e; 1.0 conductance ratio
Booker (1984)	<i>Pinus radiata</i>	staining	continuous	g/d; max flow 3 mm in; 70% drop 8 mm
Cermák <i>et al.</i> (1992)	<i>Picea excelsa</i>	heat balance, staining	continuous (staining)	g; max flow ~30 mm depth, 20 mm tails
This study	<i>Pinus taeda</i>	heat balance	2×20 mm	d; 1.0:0.4
<i>Diffuse-porous</i>				
Cohen, Fuchs & Green (1981)	<i>Citrus sinensis</i>	HPV	6×10 mm from 10 mm in	d; 1.0:0.8:0.4:0.2:0.1:0.0
Edwards & Booker (1984)	<i>Populus deltoides</i>	HPV, dye staining	8×11 mm	e/d; 1.0:0.9:1.0:0.5:0.7:0.6:0.1:0.1
	<i>Populus yunnanensis</i>	same	same	e/d; 1.0:0.4:0.6:0.8:0.6:0.6:0.1:0.1
This study	<i>Liquidambar styraciflua</i>	heat balance	2×20 mm	e; 1.0:1.0
<i>Ring-porous</i>				
Miller, Vavrina & Christensen (1980)	<i>Quercus velutina</i>	HPV	6×12 mm	s; 1.0:0.9:0.7:0.5:0.4:0.3:0.0
Ellmore and Ewers (1986)	<i>Ulmus americana</i>	hydraulic conductivity	6 growth rings	s; 1.0:0.1 (next five rings)
Cermak <i>et al.</i> (1992)	<i>Quercus robur</i>	heat balance, staining	continuous (staining)	s; decrease to zero in 20 mm
Granier <i>et al.</i> (1994)	<i>Quercus robur</i>	HPV, heat balance	3×11 mm	s; 1.0:0.2:0.1
This study	<i>Quercus alba</i>	heat balance	2×20 mm	e; 1.0:1.0

<sup>1</sup> d = decreasing; g = Gaussian; e = even; s = sharply decreasing.

<sup>2</sup> Inner and outer sapwood depths were not specified.

<sup>3</sup> Percentage normalized by maximum value.

<sup>4</sup> Maximum conductivity within each growth ring was also measured and was more even than across the increments shown.

## Hardwoods

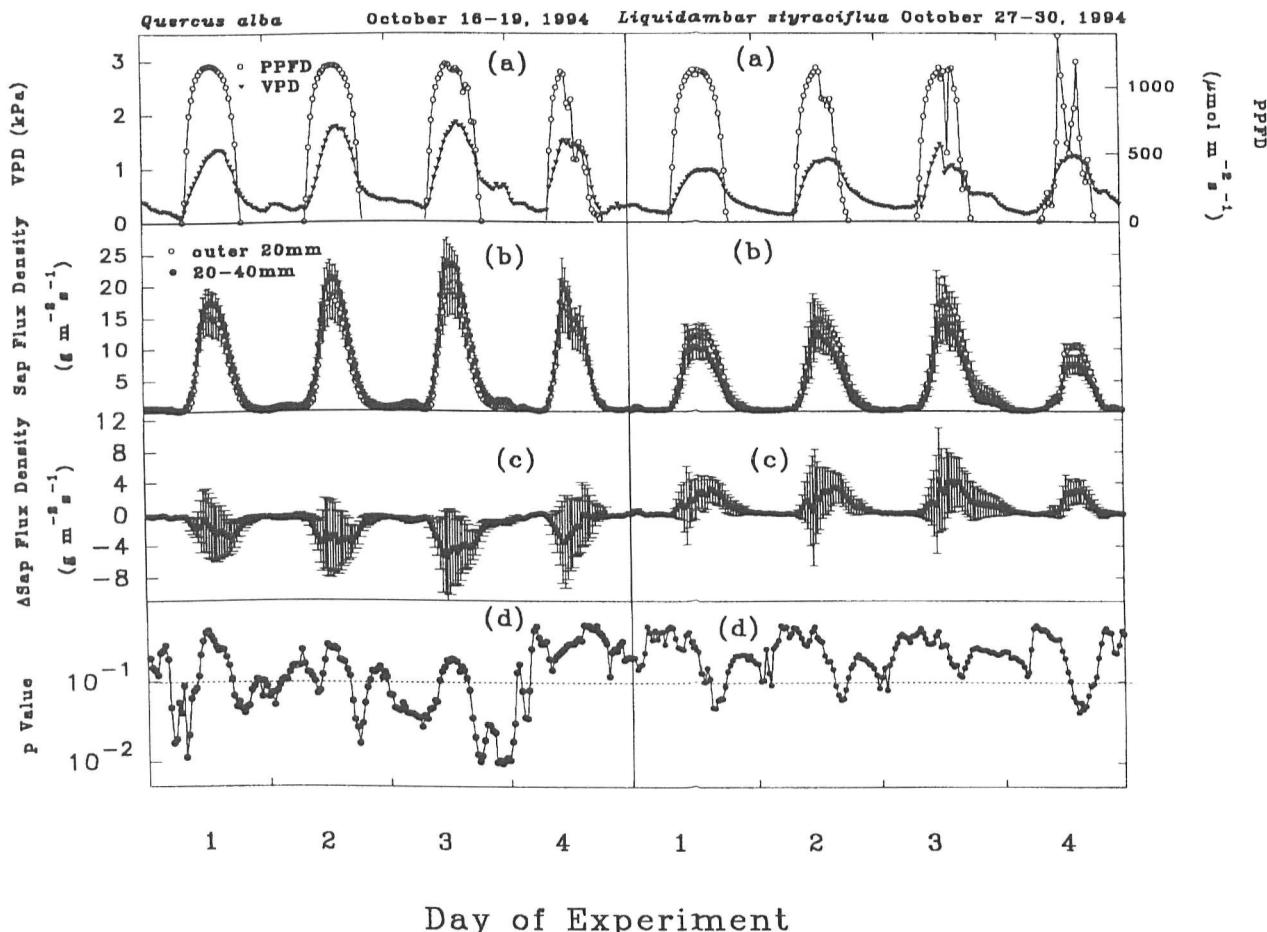
For sweetgum, differences in sap flow were rarely statistically significant, except for the period from late evening to early morning, when sap flux densities were close to zero (Fig. 3a). In oak too, differences between the means of sap flow measurements at different depths were also minimal, and were only statistically significant during the night at very low sap flux densities (Fig. 3b). However, over the 4 d of measurement, inner sapwood sap flux densities were consistently higher than those measured across the outer sapwood. Table 2 compares the results from this study with those obtained for other ring- and diffuse-porous species.

In both white oak and sweetgum, no effect of sapwood depth on  $R_s$  was found across the 60 mm examined ( $P=0.05$ ). Specific gravity was also unaffected by depth in either hardwood species ( $P=0.05$ ). Specific gravity values

agreed well with average values reported for both species; for sweetgum  $\rho_f$  was reported to be  $0.46 \text{ g cm}^{-3}$  while values of  $\rho_f$  for white oak range from  $0.55$  to  $0.64 \text{ g cm}^{-3}$  (Panshin & de Zeeuw 1970). A general trend towards decreasing  $\rho_f$  from pith to bark in white oak is consistent with previous findings in *Quercus falcata* L. (Hamilton 1961). Our measured values of  $\rho_f$  for any sapwood segment were within  $0.02 \text{ g cm}^{-3}$  of reported values (Panshin & de Zeeuw 1970).

Our results for sweetgum (Fig. 3) are consistent with those of Edwards & Booker (1984), who found slight decreasing trends in *Populus deltoides* cv. 'ANU 60/129' and *Populus yunnanensis* across 80 mm of conducting sapwood. Because neither  $R_s$  nor  $\rho_f$  was significantly different among sapwood depth intervals in this study, the lack of a strong gradient in radial sap flux density may reflect the

## Duke Forest, North Carolina



**Figure 3.** Time series of environmental conditions and average sap flux density of 10 white oak and seven sweetgum trees monitored at 0–20 mm and 20–40 mm depths during October 1994. (a) Vapour pressure deficit and photosynthetically active radiation. (b) Sap flux density is expressed as in Fig. 1. (c) Difference between outer and inner sap flux density values. (d) *P* value for the difference between outer and inner sap flux density values. The horizontal line represents *P* = 0.10. Differences between the two time series were never greater than *P* = 0.01 and were greater than *P* = 0.10 only during conditions of very low absolute sap flux densities. All vertical bars represent two standard errors.

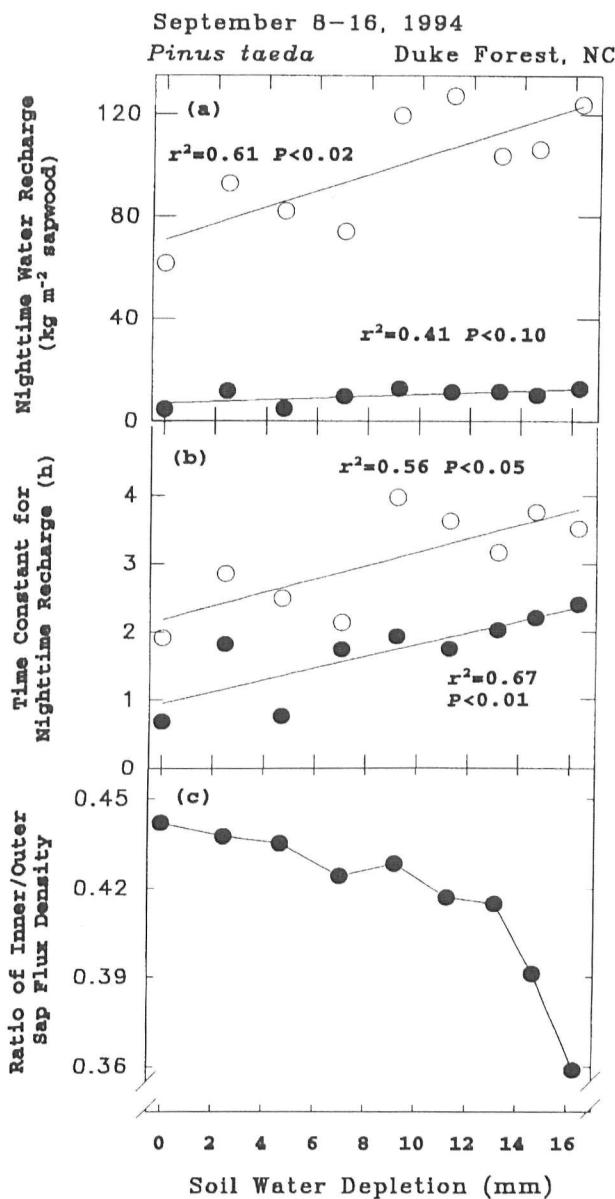
evenness of the sapwood characteristics across the intervals studied.

Our results for white oak, however, contradict those of other studies examining radial trends in xylem sap flow in ring-porous species (Fig. 3 & Table 2). It is likely that the reason for the similarity in sap flux in the outer and inner xylem is that, in the slow-growing, large-diameter trees used in this study, the earlywood of the current year was very thin ( $3 \pm 1$  mm) and thus was under-represented in the 20-mm-long sap flux probe. The effect of the youngest earlywood on the sensor reading was probably diluted by sapwood rings more than 1 year old. The peak sap flux densities recorded across both zones were similar ( $\approx 20 \text{ g m}^{-2} \text{ s}^{-1}$ ) to those reported by Granier *et al.* (1994) for *Quercus petraea* across 11–33 mm zones in the sapwood, but were much less than those recorded across a 0–11 mm zone ( $\approx 65 \text{ g m}^{-2} \text{ s}^{-1}$ ). This indicates that the sap flux measured in our experiment in both inner and outer xylem probably

occurred in latewood vessels across several growth rings, and explains the absence of radial patterns of sap flow in this study. The significant sap flux density at a depth of 40 mm inside the cambium observed in these large-diameter white oak trees is not surprising because it is known that, while earlywood vessels of white oak embolize and readily form tyloses after the year of development (Miller, Vavrina & Christensen 1980), latewood vessels continue to function or are re-activated, thus providing a back-up hydraulic system (Granier *et al.* 1994).

#### Effects of soil drying on pine sap flux

Because there was no precipitation input at the site during the period of the pine study, it was possible to examine sapwood water transport as a function of both radial position and reduction in soil water availability, as inferred from accumulated daily transpiration loss. Daily transpi-



**Figure 4.** Nighttime stem recharge in loblolly pine over a drying period, calculated from the time at which above-canopy photosynthetic radiation became zero. (a) Nighttime uptake for both inner (solid circles) and outer (open circles) xylem intervals. (b) Time constant for nighttime recharge, calculated as the time required to reach  $(1 - e^{-1})$  of zero transpiration, for both inner (solid circles) and outer (open circles) xylem intervals. In all cases, linear regressions had lower  $P$  values than quadratic regressions. (c) Ratio of inner to outer sap flux density over the drying period.

ration was estimated by scaling xylem sap flux densities by stand-scale xylem cross-sectional areas per unit ground area (Dunn & Conner 1993; Thorburn *et al.* 1993).

The total amount of water taken from the soil during the night for recharge of stem water storage was calculated as the integrated uptake, beginning in the evening when PFD reached zero, and ending when sap flux reached zero at night. Nighttime recharge increased with increasing soil

moisture depletion (Fig. 4a); nighttime uptake by a tree of inside-bark diameter similar to the average of the trees in this study (94 mm at 1.3 m above the ground) would have amounted to 3.85 kg at the beginning and 7.75 kg at the end of the drying period.

The time constant for nighttime stem recharge was calculated as the length of time taken for the average sap flux density of inner or outer xylem to drop by  $e^{-1}$  from its value when above-canopy PFD dropped to zero. These time constants were obtained from linear regressions performed on natural-log-transformed time series. The time taken for recharge increased with decreasing soil moisture, as apparent from the relationship between the time constant and soil moisture depletion (Fig. 4b). Thus, the rate of recharge decreased with soil moisture, while both the amount of water absorbed and the time required for completing the nighttime recharge increased. Furthermore, the ratio of the daily integrated flux density in the inner:outer xylem decreased with soil moisture from 0.44 to 0.36 (Fig. 4c). Thus, when scaling measurements of sap flux density using heat pulse or constant-heat sensors to whole-tree or stand scales, it is important to consider the presence of radial patterns of sap flux density as well as how such patterns may change as a result of changing soil moisture availability.

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