Whole-tree water relations of co-occurring mature *Pinus palustris* and *Pinus elliottii* var. *elliottii*

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Abstract: The natural range of longleaf pine (*Pinus palustris* P. Mill.) and slash pine (*Pinus elliottii* var. *elliottii* Engelm.) includes most of the southeastern US Coastal Plain, and there is now considerable interest in using these species for ecological forestry, restoration, and carbon sequestration. It is therefore surprising that little information is currently available concerning differences in their ecological water relations in natural stands. In this study, we compared water use, stomatal conductance at the crown scale (G_{crown}), and whole-tree hydraulic conductance of mature pine trees growing in a naturally regenerated mixed stand on a flatwoods site in north-central Florida. We found remarkable similarities between longleaf and slash pine in stored water use, nocturnal transpiration, and whole-tree hydraulic conductance. Mean daily transpiration rate was higher for slash than for longleaf pine, averaging 39 and 26 L·tree^{-1}, respectively. This difference was determined by variations in tree leaf area. Slash pine had 60% more leaf area per unit basal sapwood area than longleaf pine, but the larger plasticity of longleaf pine stomatal regulation partially compensated for leaf area differences: longleaf pine had higher G_{crown} on days with high volumetric water content (θ_v) but this was reduced to similar or even lower values than for slash pine on days with low θ_v. There was no species difference in the sensitivity of G_{crown} to increasing vapor pressure deficit.

Résumé : L'aire de répartition naturelle du pin des marais (*Pinus palustris* P. Mill.) et du pin d'Elliott typique (*Pinus elliottii* var. *elliottii* Engelm.) comprend presque toute la plaine côtière du sud-est des États-Unis et l'utilisation de ces espèces pour la foresterie écologique, la restauration et la séquestration du carbone suscite actuellement un intérêt considérable. Il est par conséquent surprenant que peu d'information soit présentement disponible au sujet de leurs différences quant aux relations hydriques de nature écologique dans les peuplements naturels. Dans cette étude, nous comparons l'utilisation de l'eau, la conductance stomatique de la cime (G_{crown}) et la conductance hydraulique de l'arbre entier chez des pins matures croissant dans un peuplement mélangé régénéré naturellement dans une station des « flatwoods » du centre-nord de la Floride. Nous avons observé de remarquables similarités entre le pin des marais et le pin d'Elliott typique quant à l'utilisation de l'eau emmagasinée, la transpiration nocturne et la conductance hydraulique de l'arbre entier. Le taux journalier moyen de transpiration du pin d'Elliott typique était plus élevé que celui du pin des marais, soit respectivement 39 et 26 L·arbre^{-1}. Cette différence était déterminée par la surface foliaire des arbres. Le pin d'Elliott typique avait 60 % plus de surface foliaire par unité de surface terrière de l'aubier que le pin des marais. Par contre, une plus grande plasticité de la régulation stomatique chez le pin des marais compensait en partie pour les différences de surface foliaire : la valeur de G_{crown} était plus élevée chez le pin des marais les jours où la teneur volumétrique en eau (θ_v) était élevée mais elle atteignait des valeurs similaires ou même inférieures à celles du pin d'Elliott typique les jours où θ_v était faible. La sensibilité de G_{crown} à l'augmentation du déficit de pression de vapeur était la même chez les deux espèces.

[Traduit par la Rédaction]

Introduction

Pine forests once dominated the upland plant communities of the southeastern Coastal Plain (Pessin 1933). Although longleaf pine (*Pinus palustris* P. Mill.) was the dominant tree species in drier sandhills, slash pine (*Pinus elliottii* var. *elliottii* Engelm.) was an important codominant in wetter flatwoods (Pessin 1933; Abrahamson and Hartnett 1990). Flatwoods are the most extensive type of terrestrial ecosystem in the US outer coastal plain province, covering 225 000 km², about 50% of its land area (McNab and Avers 1994). Longleaf and slash pine are characteristic of pine flatwoods. More than 97% of the original land area of long-

leaf pine has been converted to other uses (Johnson and Gjerstad 2006) and some of the most species-rich areas and highest concentrations of endangered and threatened species in the Southeast are found on mesic flatwood sites (Cohen et al. 2004). These characteristics have led to increasing interest in restoration and ecological management of longleaf and slash pine forests in the region (Alavalapati et al. 2002).

The native pine species of flatwoods are well adapted to frequent, low intensity fires, but the greater fire sensitivity of slash pine (Abrahamson and Hartnett 1990) coupled with longer fire return times in flatwoods relative to sandhills is a standard explanation of slash and longleaf pine co-occurrence on these sites. Experimental fire studies indicate that

long-term persistence of longleaf pine in flatwood sites may involve complex interactions of fire, pine life history, and site water balance (Glitzenstein et al. 1995). The potential significance of water availability and plant water relations in sites with fine sand soils that have little moisture-holding capacity typical of pine flatwoods (Abrahamson and Hartnett 1990) is underappreciated. Longleaf pine diameter growth has been shown to have a high correlation with spring and summer Palmer drought severity index estimates (Van De Gevel et al. 2009). Florida oak species show distinct habitat segregation in response to soil moisture gradients (Cavender-Bares et al. 2004).

The relative densities and proportions of longleaf and slash pine depend on geographic location, climate, edaphic conditions, fire history, and human influences (Ewel 1990). Longleaf and slash pine can overlap on mesic flatwoods sites. Longleaf pine typically dominates on higher ground (drier) and better-drained sites, while slash pine dominates on lower (wetter) sites where seasonal ponding occurs. Slash pine is primarily located around or even inside the seasonal ponds, while longleaf pine dominates the higher areas between the ponds (Ewel 1990; Peet 2006).

At a global scale, water availability is one of the most important factors controlling productivity and species distributions, and interactions between water availability and water relations within species are important in determining habitat associations (Baraloto et al. 2007). Few studies exist that have examined water relations of mature longleaf and slash pine under field conditions (Teskey et al. 1994; Martin 2000; Ford and Brooks 2003; Vose et al. 2003; Addington et al. 2004, 2006; Ford et al. 2004). Whole-tree water relations characteristics, including leaf-specific hydraulic conductivity (K_{L-wt}) and stomatal conductance to water vapor at the crown level (G_{crown}), are important hydraulic architecture traits (Cruiziat et al. 2002). Variations in these traits have significant implications for patterns of transpiration and leaf water potential observed within forest canopies (Wullschleger et al. 1998) and for assessing the trade-offs between water transport and vulnerability of woody stems to xylem cavitation (Sperry et al. 1998). The objective of this study was to characterize whole-tree water relations of mature trees of these co-occurring species in terms of total daily transpiration, water storage use, leaf to sapwood area, K_{L-wt}, and adjustments in G_{crown} to varying vapor pressure deficit (D) and soil water content (θ_v) conditions. Because longleaf pine tends to dominate on drier and better-drained sites, while slash pine dominates on wetter sites, we hypothesized that (*i*) transpiration rate, water storage use, leaf to sapwood area ratio, and K_{L-wt} are higher in slash pine trees and (*ii*) longleaf pine G_{crown} is more sensitive than slash pine G_{crown} to changes in D and θ_v.

Materials and methods

Site and stand description

The study was carried out from 17 April to 9 July 2007 at the University of Florida's Austin Cary Memorial Forest located 15 km northeast of Gainesville, Florida (29°44′N, 82°09′W). Soils are classified as poorly-drained Pomona sands (sandy, siliceous, hyperthermic Ultic Aplaquods) with a discontinuous spodic horizon at 0.3–0.6 m depth and

deeper argillic horizon at 1.0–1.4 m depth (Gaston et al. 1990). The study stand consists of a naturally regenerated mixed longleaf and slash pine stand with tree ages ranging between 25 and 85 years with a mean age of 65 years. Prescribed fires have been applied since the 1950s with a 3- to 5-year return interval. The stand was thinned in 1991, removing proportionally for both species 27% of the basal area. The stand basal area at the time of measurement was 16.9 m²·ha⁻¹ (73% longleaf pine and 17% slash pine). Within the stand, slash pine tended to be clumped in the lower lying areas and along pond margins, all within a matrix of longleaf pine. The understory consisted of native species dominated by gallberry (*Ilex glabra* (L.) Gray), saw palmetto (*Serenoa repens* (Bartr.) Small), wax myrtle (*Myrica cerifera* L.), and wiregrass (*Aristida stricta* Michx) (Powell et al. 2005).

Meteorological measurements

Environmental conditions were monitored using an automatic weather station located on the top of a 30 m scaffolding tower extended approximately 5 m above the mean canopy height (Powell et al. 2005). We measured relative humidity and air temperature (HMP45C-L; Vaisala, Inc., Helsinki, Finland), photosynthetic photon flux density (PPFD) (µmol·m⁻²·s⁻¹,) (Li-190; LI-COR Inc., Lincoln, Nebraska), wind direction and velocity (03001-L; Campbell Scientific, Logan, Utah), and precipitation (TR525-I; Texas Electronics, Dallas, Texas) at 30 s intervals using an automatic datalogger (CR10X; Campbell Scientific) and stored 30 min averages. Water table depth was measured (F-68; Leupold and Stevens, Inc., Beaverton, Oregon) in a piezometer well located approximately at the midpoint between the longleaf and slash pine sectors.

Soil properties

We measured volumetric soil water content θ_v (m³·m⁻³) with vertically oriented, 200 mm long capacitive soil moisture probes (EC-20; Decagon Devices, Pullman, Washington). Probes were installed at 0.4–0.6, 0.9–1.1, and 1.4–1.6 m depths into two sectors representing the slash and longleaf pine microsites. These intervals were selected based on previous studies showing that changes in canopy conductance were better correlated with changes in θ_v between 0.3 and 0.75 m depth (Gonzalez-Benecke and Martin 2010). Estimates of water content from each probe were extrapolated to the midpoint distance between sensors. Specific calibrations were developed from soil samples taken 0.5 m away from each probe from the same depth. Soil-specific calibrations (not significantly different from the manufacturer's default calibration) were used to transform sensor output (mV) to volumetric water content: $\theta_v = -0.24508 + 0.0007958 \times$ mV. There was no difference between samples taken at each depth and the manufacturer's calibration ($P = 0.65$ and 0.82 for intercept and slope, respectively). Soil matric potential (Ψ_s) (MPa) was estimated for the 0.4–0.6 m depth measurements using previous soil water retention curves generated for local Spodosols (H.L. Gholz, unpublished data) and for the 0.9–1.0 and 1.4–1.6 m depth measurements using a computer program based on pedotransfer functions and parameterized with soil texture and bulk density data obtained at each location (Schaap et al. 2001; ROSETTA

version 1.2, US Salinity Laboratory ARS-UDA, Riverside, California). Particle size distribution was determined using the hydrometer method (Gee and Bauder 1986). Soil bulk density (ρ_s) (kg·m^{-3}) was determined using a soil core sampler (0200; Soil Moisture Equipment Corp., Santa Barbara, California). Available soil water (mm) and relative extractable soil water (REW) (%) were calculated for each microsite and day by analyzing the limits of wetting and drying of the soil through the entire study period (Ritchie 1981).

Tree selection

Four measurement trees per species were chosen from across the range of tree diameters using "quantiles of total", a stratification scheme that weights the selection of large-diameter trees more heavily than small-diameter trees (Hatton et al. 1995; Martin et al. 1997), concentrating measurement resources in tree size-classes that tend to dominate stand transpiration (Martin et al. 1997). On each tree, we measured leaf water potential, sap flow, sapwood, and leaf area. Details of biometric attributes of selected trees are presented in Appendix A.

Sap flow measurements

Twenty millimetre long Granier-type heat dissipation probes (Granier 1985) were installed approximately 0.2 m below the base of the crown (S_{crown}) of each measurement tree (see Appendix A). Briefly, the system consists of two probes inserted radially into the stem one above another about 0.1–0.15 m apart. The upper probe contains a heater and a T-type thermocouple and the lower probe contains only the thermocouple. The upper probe was heated at constant power, while the lower one was used as reference measuring the ambient temperature of the wood. The temperature difference between the heated and reference probes (ΔT) was recorded. Sap flux density (J_S) (g water·m^2 sapwood^{-1}·s^{-1}) was determined using the empirical calibration developed by Granier (1985) and confirmed by Braun and Schmid (1999) and Clearwater et al. (1999):

$$J_S = 119 \times \left(\frac{\Delta T_m - \Delta T}{\Delta T} \right)^{1.231}$$

Sap flow data were corrected to account for nocturnal transpiration by using the method proposed by Oishi et al. (2008), where ΔT_m was determined as the highest ΔT on stable days with negligible D (average, minimum 2 h $D <$ 0.05 kPa). Nocturnal transpiration (E_{night}) was determined for each tree as the total daily sap flow measured at S_{crown} when PPFD < 5 μmol·m^{-2}·s^{-1}.

To determine radial patterns J_S (Lu et al. 2000; Ford et al. 2004), variable length sap flow probes, as described by James et al. (2002), were installed at 1.8 m stem height (S_{base}). Probes were inserted at 10 mm depth intervals with the tip of the 10 mm long probes reaching 10, 20, 30, 40, 60, 80, and 100 mm depths (assuming to measure sap flux density in discrete depths, e.g., 0–10, 10–20, ..., 90–100 mm). The probe for the outermost position was installed on the north side of the stem and subsequent probes were installed clockwise around the stem at 45° intervals. Weighted average J_S at S_{base} (J_{s-b}) was calculated at each time step as the sum of the product of J_S and annulus area corresponding to each depth divided by total sapwood area to determine a unique and integrated value of J_S for each tree and time step. Weighted average J_S at S_{crown} (J_{s-c}) was calculated using sap flux density values measured at the crown base at 0–20 mm sapwood depth corrected by the radial profile in native sapwood-specific hydraulic conductivity at S_{crown} determined for each tree (Gonzalez-Benecke et al. 2010). Sap flux density was converted to sap flow by multiplying J_{s-b} and J_{s-c} by the corresponding sapwood area of each measurement point. With a chisel, bark and cambium were removed at the probe installation point to insert the sensors entirely into the xylem. Probes were coated with thermally conductive silicone grease before placement in the trees. All the sensors were protected against radiation, thermal gradients, and precipitation by reflective insulation.

Estimations of J_{s-c} were carried out with the objective to minimize water storage effects on time lags between crown transpiration and stem sap flow measurements S_{base} (Braun and Schmid 1999; Phillips et al. 2003). Daily stored water use (SWU) was computed following Goldstein et al. (1998) as the difference between J_{s-c} and J_{s-b} when $J_{s-b} < J_{s-c}$ (water storage withdrawal). SWU was calculated as the proportion of daily water stored to total sap flow at the crown base (Phillips et al. 2003; Daley and Phillips 2006).

Even though our estimates of J_{s-c} were not corrected for radial profile in J_S at that point, we believe that the use of J_{s-c} to estimate tree transpiration is appropriate because (*i*) the radial profile in stem sapwood-specific native conductance showed no significant differences between 10 and 40 mm depth ($P > 0.14$) (Gonzalez-Benecke and Martin 2010), (*ii*) the sapwood area of the outer 20 mm corresponds, on average, to 54% and 51% of total sapwood for longleaf and slash pine, respectively, and (*iii*) total daily sap flow per tree estimated at S_{base} and S_{crown} was not different ($P > 0.38$) (data not shown).

Leaf and sapwood area

At the end of the study, all four sap flow measurement trees from each species were felled to determine total tree leaf area (LA) (m^2) using a destructive determination of leaf mass (g) in conjunction with tree-specific estimations of all-sided specific LA (cm^2·g^{-1}). Trees were felled at a stump height of approximately 0.2 m and all branches were cut at the point where live needles started. All branch tips were weighed green in the field and summed to determine whole-tree branch tip fresh mass. For each tree, 20 randomly selected subsamples of branch tips were weighed, bagged, and brought back to the laboratory for separate determinations of moisture contents and dry masses of wood and needles of each branch tip. Dry mass of all living needles of the whole tree crown was estimated as the product of field-determined whole-tree branch tip fresh mass and the average dry needle to fresh branch tip ratios derived from all 20 branch tip subsamples. Needles were weighed separately into two age-classes: current year and older needles, so dry needle to fresh branch tip ratios were also calculated separately for each needle type.

All-sided specific LA was determined using the ratio between surface area and dry mass of needles. Individual needle surface area was calculated according to Niinemets et al.

(2001) from needle radius (scaled magnifier, 10×; SPI, Japan) and length (digital caliper, CD-6; Mitutoyo, Japan) on 10 needles per tree. After surface area was determined, the needles were oven-dried for 48 h at 75 °C and weighed to the nearest 0.0001 g (XA-100; Denver Instruments, Denver, Colorado). A weighted average all-sided specific LA was determined for each tree after including the proportion of leaf mass of each needle age. To estimatedaily LA for each tree, seasonal patterns were developed using published periodic measurements of leaf area index (m^2·m^{-2}) from January 2000 to January 2006 (Powell et al. 2008). LA was estimated backward in time from the LA measurement day (between 21 June and 9 July) until the sap flow installation day (17 April).

In all measured trees, at the same point where sap flow probes were installed (at S_{base} and S_{crown}), sapwood area (m^2) was estimated at the end of the study by measuring sapwood depth and stem diameter directly in disks extracted after the trees were felled. The disks were transported back to the laboratory covered with wet towels in plastic bags and stored at 5 °C for further hydraulic conductivity measurements (Gonzalez-Benecke et al. 2010). Aboveground sapwood volume below the crown base was calculated for each tree by using sapwood area measured at the stump and crown base and distance from the stump to crown base. Stem diameter and bark thickness were measured vertically along the stem every 2 m to determine stem volume. The Huber value (sapwood to LA ratio, m^2 sapwood·m^2 LA^{-1}) was calculated for each tree as sapwood area at S_{base} or S_{crown} divided by total LA.

Crown conductance

Stomatal conductance for water vapor at the individual tree crown scale (G_{crown}) (m·s^{-1}) was calculated as in Granier and Loustau (1994) from the inverted Penman–Monteith equation. After correcting for temperature changes in water density, G_{crown} was transformed to molar units (mmol water·m^2 LA^{-1}·s^{-1}). Average daily G_{crown} (G_{Cday}) (mmol·m^{-2}·s^{-1}) was estimated during daylight time (PPFD > 5 μmol·m^{-2}·s^{-1}). A reference G_{crown} (G_{Cref}) was calculated at D 1 kPa (Granier et al. 1996). The response of G_{crown} to D was quantified using boundary line analysis (Ewers et al. 2001). The upper boundary line for each tree was derived by binning G_{crown} data into 0.2 kPaD intervals (from 0.2 to 4.6 kPa) and then selecting the highest 95% G_{crown} for any interval (Gonzalez-Benecke and Martin 2010. For each tree, all upper G_{crown} values in each D interval were related to the natural logarithm of D (Granier et al. 1996):

$$G_{crown} = G_{Cref} - m \ln D$$

where m is the slope of the regression fit, representing stomatal sensitivity to D ($-dG_{crown}/d \ln D$) (mmol·m^{-2}·s^{-1}·ln kPa^{-1}). Nocturnal G_{crown} was analyzed in the same way but selecting data during nighttime (PPFD < 5 μmol·m^{-2}·s^{-1}). To reduce error due to instrument limitations on relative humidity measurements, G_{crown} was calculated only when $D \geq 0.2$ kPa. Our first approach was to use a threshold of $D \geq 0.6$ kPa, as proposed by Ewers and Oren (2000), but as the estimated values were not different if $D \geq 0.2$ kPa was included or not ($P > 0.24$) and as this informa-

tion allowed us analyze nocturnal G_{crown}, we used $D \geq 0.2$ kPa as the cutoff threshold.

To assess the effect of θ_v in the relationship between daytime G_{Cref} and $-dG_{crown}/d \ln D$, a G_{Cref} under varying soil moisture conditions was also determined for each tree as the average G_{crown} at D 1 kPa under light-saturated conditions (PPFD > 800 μmol·m^{-2}·s^{-1}) by binning G_{crown} data into 0.02 m^3·m^{-3} θ_v intervals (from 0.10 to 0.18 m^3·m^{-3}) and then calculating the average G_{crown} for any interval.

Whole-tree hydraulic conductance

Whole-tree sapwood-specific hydraulic conductance (K_{S-wt}) (mol water·m^2 sapwood^{-1}·s^{-1}·MPa^{-1}) was computed as the slope of the linear regression between J_{s-c} (transformed to molar units) and leaf water potential (Ψ_l) (MPa) (Wullschleger et al. 1998). For the day of Ψ_l measurements (17 April 2007), J_S was measured at 1 min intervals. Ψ_l was measured using a portable pressure chamber (PMS 1000; MPS Instrument Co., Corvallis, Oregon) on one shoot tip from predawn (5:00–5:30 a.m.) to late afternoon (6:00–6:30 p.m.) at intervals of 2 h approximately, completing five measurements per tree during the day. Each measurement was completed within 3 min after shoot excision, covering the sample with wet towels inside a plastic bag and maintaining inside an insulated box to minimize desiccation. Shoot sampling was carried out using a canopy lift and pole pruner.For each tree, if nighttime sap flow was detected during the night when predawn leaf water potential (Ψ_{pred}) was measured, $\Psi_s$at the root zone of each tree (Ψ_{s-est}) was estimated as the intercept of the relationship between J_{s-c} and Ψ_l. Maximum leaf water potential gradient ($\Delta\Psi$) (MPa) was calculated as the difference between midday leaf water potential (Ψ_{midday}, the minimum Ψ_l measured close to midday) and Ψ_{s-est}. Whole-tree leaf-specific hydraulic conductance K_{L-wt} (mmol water·m^2 LA^{-1}·s^{-1}·MPa^{-1}) was determined for each tree as K_{S-wt} multiplied by the corresponding sapwood to LA ratio (i.e., Huber value at S_{crown}).

Statistical analysis

Analysis of variance was used to analyze the effects of species on water relationship traits, including Bonferroni adjustments for differences in least square means (PROC MIXED; SAS Institute Inc., Cary, North Carolina). The linear model for the analysis was

$$Y_{ij} = \mu + S_i + t_{j(i)} + \varepsilon_{ij}$$

where Y_{ij} is the response value of the jth tree ($j = 1, ..., 4$) in the ith species ($i = 1, 2$), μ is the population mean, S_i is the fixed effect of species (longleaf or slash pine), $t_{j(i)}$ is the random effect of tree nested within species, and ε_{ij} is the error term ~ NID $(0, \sigma_\varepsilon^2)$ (NID, normally and independently distributed).

Repeated-measures analysis of variance was used to analyze time series data. Several covariance structure models were used for the time series analysis (power, heterogeneous first-order autoregressive, compound symmetry, heterogeneous Toeplitz, unstructured and uncorrelated models) and the model with the lowest Schwartz's Bayesian information criterion was selected for each variable analyzed (Littell et al. 2006).

Fig. 1. (*a*) Weekly average vapor pressure deficit (*D*) during daylight hours and weekly average sum of photosynthetic photon flux density (PPFD) and (*b*) available soil water (ASW) from 0.4 to 1.6 m depth, rainfall, and water table depth for longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliottii* var. *elliottii*) sites.
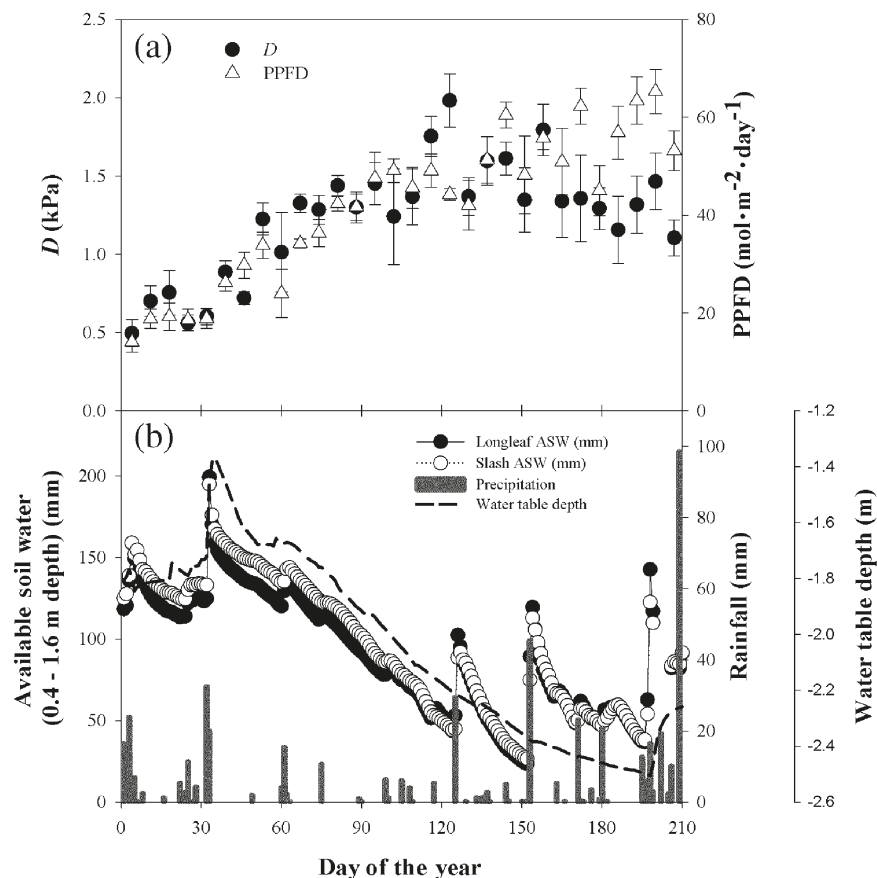
Results

Environmental conditions

During the sap flow measurement period (from 17 April to 9 July), total precipitation was 152.9 mm, corresponding to 45.7% of historic averages for the site (during a "normal" year, 334.2 mm of rainfall would occur during that period) (http://cdo.ncdc.noaa.gov/cgi-bin/climatenormals/climatenormals.pl [accessed August 2008]). Mean daily temperature increased gradually from values close to 17 °C during the third week of April to 29 °C during the first week of August. Total daily PPFD ranged from about 20 to 75 mol·m^{-2}·day^{-1} when the study was completed (Fig. 1*a*). Daily average *D* followed a similar pattern as daily PPFD but peaking approximately 1 month earlier. Both PPFD and *D* increased in variability during the summer in comparison with winter daily values (Fig. 1*a*). Available soil water from 0.4 to 1.6 m depth reached minimum values of 23.4 and 26.6 mm for longleaf and slash pine sites, respectively, corresponding to 2.6% and 5.5% REW, respectively (Fig. 1*b*). Water table depth ranged from 1.4 m at the beginning of the growing season up to 2.5 m in mid-July (Fig. 1*b*). As a difference in elevation of approximately 1.0 m was measured between the midpoint of the longleaf and slash pine trees, and assuming constant slope between both sectors, water table depth fluctuated between 1.5 and 2.0 m in slash pine and between 2.5 and 3.0 m in longleaf pine zones during the sap flow measurement period.

Sap flux density, transpiration, water storage use, and soil moisture

At 1.8 m height (S_{base}), the relationship between $J_{s\text{-}b}$ and distance from the cambium reflected a general trend that the outer probes (installed from 10 to 40 mm depth) had higher values and followed the daily *D* cycle compared with inner probes (installed at 60 and 80 mm depth), which tended to peak in late afternoon, even during night when J_S for outer probes decreased to near-zero values (data not shown). In general, after comparing $J_{s\text{-}b}$ and $J_{s\text{-}c}$ with daily courses of *D* and PPFD, it is possible to observe that $J_{s\text{-}c}$ fits better with *D* (Fig. 2) and the use $J_{s\text{-}b}$ can result in errors when the objective is to match J_S with other simultaneous meteorological or physiological measurements such as crown conductance or whole-tree hydraulic conductivity. Therefore, we used $J_{s\text{-}c}$ for further analysis of tree water use, crown conductance, and whole-tree hydraulic conductivity.

For the period analyzed from 28 April to 18 June 2007, overall daily transpiration rates (E_{day}) (L·tree^{-1}) for longleaf and slash pine were 26.1 and 39.5 L·tree^{-1} with a standard error of 5.4 and 7.6 L·tree^{-1}, respectively (coefficient of variation ~37%). The two species were not consistent in their

Fig. 2. Example of diurnal courses of (*a*) photosynthetic photon flux density (PPFD) and vapor pressure deficit (*D*) and sap flux density (J_S) measured at 1.8 m height (J_{s-b}) and at the crown base (J_{s-c}) of (*b*) the biggest longleaf pine (*Pinus palustris*) (418 mm DBH) and (*c*) the smallest slash pine (*Pinus elliottii* var. *elliottii*) (204 mm DBH) during the leaf water potential measurement day (17 April 2007).
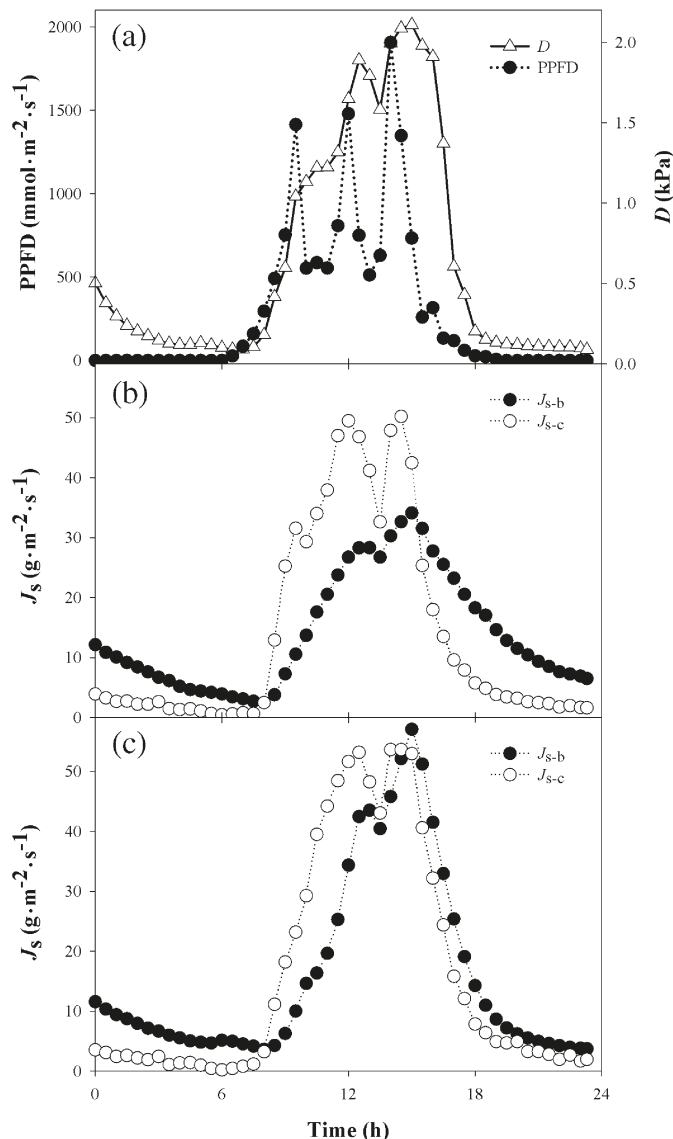
daily course of transpiration over time ($P = 0.0001$ for the species by time interaction) (Fig. 3*a*). From 28 April to 30 May (i.e., days 118 to 151), E_{day} of slash pine was significantly greater than E_{day} of longleaf pine ($P < 0.05$); this period corresponds to the time when Ψ_s of longleaf pine site reached values below –1.0 MPa from 0.4 to 0.6 m soil depth (Fig. 3*c*). After a 45 mm rainfall on 6 June (day 156), Ψ_s at the 0.4 to 0.6 m depth reached values close to –0.2 MPa and transpiration increased for both species, and E_{day} for the two species was not different ($P > 0.14$) for the rest of the measurement period. Differences in E_{day} between species reflected, on average, 50% higher water use by slash than by longleaf pine (Fig. 3*a*). That difference can be explained, at least in part, by the fact that slash pine had more LA than

longleaf pine for trees of the same sapwood area; Huber values of longleaf pine were 60% greater than those of slash pine ($P = 0.086$) (Table 1).

When E_{day} was expressed per unit LA (E_l) (L·m^2 LA^{-1}), there was also a strong interaction between species and time ($P < 0.001$) (Fig. 3*b*). It is interesting to note that when the soil was drying (during the 2 weeks before the 6 June rainfall) and Ψ_s on 0.4–0.6 m depth declined far below – 1.0 MPa (Fig. 3*c*), E_l for longleaf pine was lower than for slash pine ($P < 0.001$) (Fig. 3*b*), averaging values of 0.296 and 0.366 L·m^{-2} for longleaf and slash pine, respectively. After rainfall, this trend changed, with E_l for longleaf pine becoming higher than for slash pine ($P < 0.001$), with average values of 0.501 and 0.414 L·m^{-2} for longleaf and slash pine, respectively. Under well-watered conditions, E_l of longleaf pine was higher than for slash pine, but as the soil dried in the longleaf pine zone, this trend was reversed, with E_l of slash pine being higher than that of longleaf pine.

During the measurement period, average SWU (L·tree^{-1}) was not different between species ($P = 0.87$), averaging 8.8 and 9.6 L·tree^{-1}, with a standard error of 1.2 and 1.6 L·tree^{-1} for longleaf and slash pine, respectively (Fig. 4*a*). There was not a species by time interaction ($P = 0.99$). SWU was highly correlated with tree size; daily average SWU had a strong linear relationship ($P = 0.001$, $R^2 = 0.84$) with aboveground sapwood volume (Fig. 4*b*). SWU was not correlated with LA ($P = 0.33$; data not shown). After expressing SWU in m^3, it is possible to extrapolate from the relationship between SWU and sapwood volume that, on average, 1.7% of the sapwood volume is used for water storage. The percentage of stored water used for daily transpiration averaged 33.8% and 24.3%, for longleaf and slash pine, respectively, but the difference between species varied depending on time ($P < 0.001$ for the species by time interaction). During a dry soil period (e.g., days 139 to 151) (Fig. 3*c*), mean relative SWU was 60.2% and 26.5% for longleaf and slash pine, respectively ($P = 0.01$). During wet soil periods (e.g., days 153 to 168) (Fig. 3*c*), mean relative SWU decreased to 21.7% and 16.9% for longleaf and slash pine, respectively ($P = 0.63$). Within species, relative SWU was statistically different for longleaf pine ($P < 0.001$) but not for slash pine ($P = 0.245$) across soil moisture periods. These two subsets of time were selected based on soil moisture differences between them ($P < 0.001$) but similar among-species microsites ($P = 0.12$). Across species, θ_v and Ψ_s for "dry" and "wet" periods at 0.5 m soil depth reached values of 8.6% and 16.9% and –1.39 and –0.1 MPa, respectively; daily average D and total daily PPFD were similar between selected periods ($P = 0.266$ and $P = 0.112$, respectively).

Nocturnal transpiration (E_{night}) was not different between species ($P = 0.87$), averaging 2.43 and 2.62 L·tree^{-1} for longleaf and slash pine, respectively (Fig. 5*a*). There was no interaction between species and time ($P = 0.99$) and E_{night} accounted, on average, for 8.7% and 6.1% of E_{day} for longleaf and slash pine, respectively. Changes in E_{night} were positively correlated with changes in average nocturnal D (D_n) ($P < 0.001$, $R^2 = 0.23$) (Fig. 5*b*) and a common relationship for both species was fitted to an exponential function due to no differences between taxa ($P > 0.15$ for both curve parameters; $E_{night} = 3.51 \times (1 - e^{-3.18 \times D_n})$). Nocturnal transpiration was also positively correlated with increas-

Fig. 3. (*a*) Transpiration per tree, (*b*) transpiration per unit leaf area, and (*c*) soil matric potential at 0.4–0.6 and 1.4–1.6 m depth, rainfall, and water table depth for longleaf pine (*Pinus palustris*) (LL) and slash pine (*Pinus elliottii* var. *elliottii*) (SL). Symbols are means among four tree replicates. Error bars represent SE (*n* = 4).
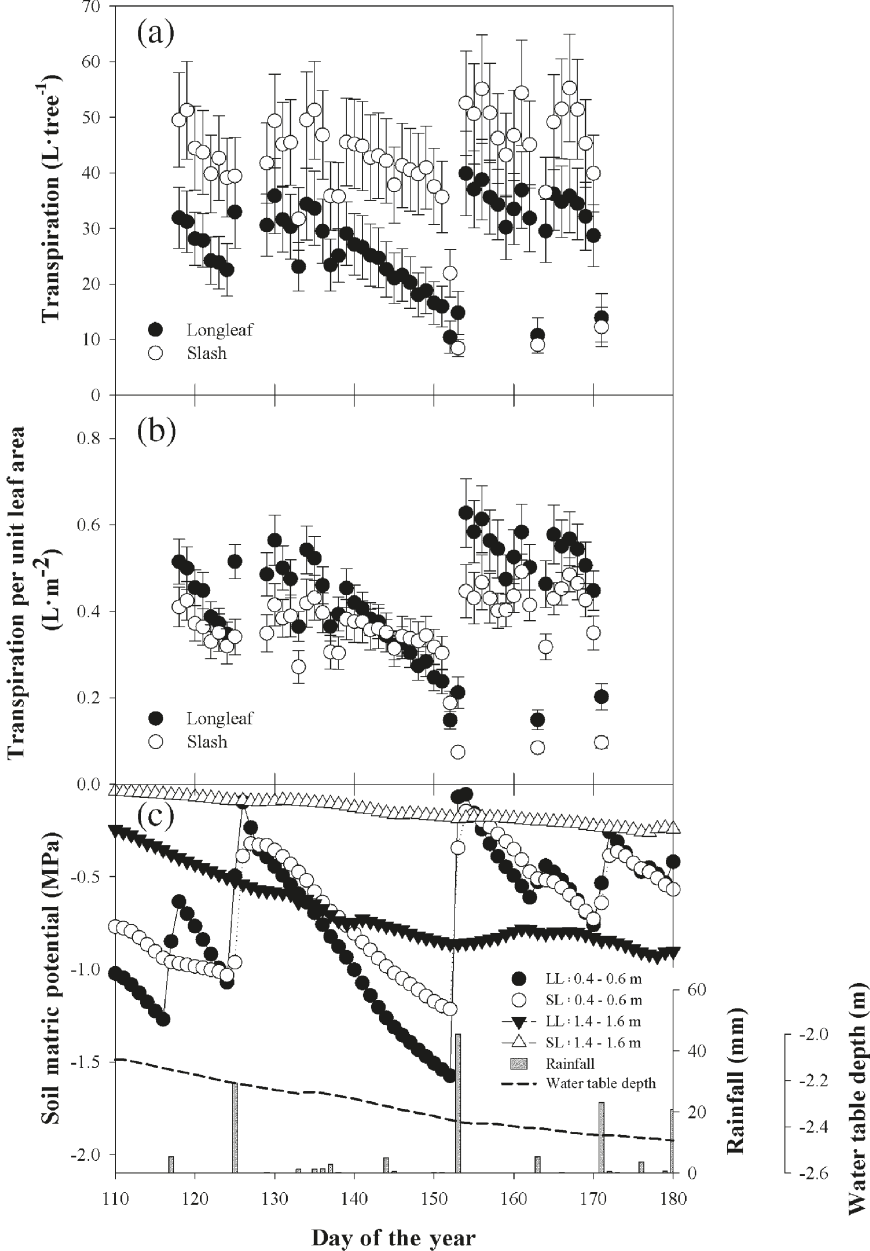
ing soil moisture ($P < 0.001$, $R^2 = 0.27$). A single relationship for both species was fit to a Weibull function, $E_{night} = 8.22 - 5.89 \times e^{-5.06} \times \left(1 - e^{-5.06 \times \theta_v^{1.034}}\right)$, because there were no differences between taxa ($P > 0.18$ for curve fit parameters). For both species, average E_{night} was 2.34 L·tree^{-1} when $\theta_v < 0.12$ m^3·m^{-3} and 3.62 L·tree^{-1} when $\theta_v > 0.14$ m^3·m^{-3} (data not shown).

Whole-tree hydraulic conductance

There were no differences in average K_{S-wt}, K_{L-wt}, Ψ_{midday}, and $\Delta\Psi$ between species ($P > 0.11$) (Table 1). Average K_{S-wt}, K_{L-wt}, Ψ_{midday}, and $\Delta\Psi$ for longleaf and slash pine were 3.37 and 4.20 mol·m^{-2}·s^{-1}·MPa^{-1}, 1.45 and 1.13 mmol·m^{-2}·s^{-1}·MPa^{-1}, –1.83 and –1.67 MPa, and 0.94

and 0.87 MPa, respectively. Average Ψ_{s-est} (that was calculated as the intercept of the relationship between Ψ_l and J_s) was different between species ($P = 0.047$), averaging values of –0.89 and –0.79 MPa for longleaf and slash pine, respectively. On the day of Ψ_l measurements, θ_v at 0.4–0.6 m depth was 0.096 and 0.105 m^3·m^{-3} at longleaf and slash pine zones, corresponding to Ψ_s of –0.96 and –0.76 MPa, respectively. These values were not statistically different from Ψ_{s-est} for each species ($P > 0.36$) and support the robustness of our measurements.

Crown conductance

Average G_{Cday} ranged between 11.4 and 58.8 and between 12.8 and 42.5 mmol·m^{-2}·s^{-1} for longleaf and slash pine, re-

Table 1. Least-square means of measured traits for longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliottii* var. *elliottii*).

Trait	Units	Species		
		Longleaf pine	Slash pine	$P > F$ species
SA_{base}	m^2	0.0401	0.0522	0.438
SA_{crown}	m^2	0.0202	0.0269	0.474
LA	m^2	61.22	104.84	0.127
HV_{base}	$m^2 \cdot m^{-2} \times 10^{-4}$	8.25	5.15	0.086
HV_{crown}	$m^2 \cdot m^{-2} \times 10^{-4}$	3.86	2.69	0.192
G_{Cref}	$mmol \cdot m^{-2} \cdot s^{-1}$	84.88	63.45	0.224
$-dG_{crown}/d \ln D$	$mmol \cdot m^{-2} \cdot s^{-1} \cdot \ln kPa^{-1}$	49.76	32.88	0.121
G_{Cref} (night)	$mmol \cdot m^{-2} \cdot s^{-1}$	22.55	18.67	0.440
$-dG_{crown}/d \ln D$ (night)	$mmol \cdot m^{-2} \cdot s^{-1} \cdot \ln kPa^{-1}$	13.48	9.140	0.221
Ψ_{midday}	MPa	−1.831	−1.668	0.111
Ψ_{pred}	MPa	−0.86	−0.72	0.004
$\Psi_{s\text{-}est}$	MPa	−0.89	−0.79	0.047
$\Delta\Psi$	MPa	0.943	0.871	0.391
$K_{L\text{-}wt}$	$mmol \cdot m^{-2} \cdot s^{-1} \cdot MPa^{-1}$	1.46	1.14	0.517
$K_{S\text{-}wt}$	$mol \cdot m^{-2} \cdot s^{-1} \cdot MPa^{-1}$	3.61	4.35	0.254

Note: SA_{base}, sapwood area at 1.8 m height; SA_{crown}, sapwood area at crown base; LA, projected leaf area; HV_{base}, Huber value at 1.8 m height; HV_{crown}, Huber value at crown base; G_{Cref}, reference crown conductance at $D = 1$ kPa under no-limiting radiation and soil moisture conditions; $-dG_{crown}/d \ln D$, crown conductance sensitivity to changes in D under no-limiting radiation and soil moisture conditions ($-dG_{crown}/d \ln D$); G_{Cref} (night), crown conductance during night at $D = 1$ kPa under no-limiting soil moisture conditions; $-dG_{crown}/d \ln D$ (night), crown conductance sensitivity to changes in D during night under no-limiting soil moisture conditions; Ψ_{midday}, midday leaf water potential; Ψ_{pred}, predawn water potential; $\Psi_{s\text{-}est}$, estimated soil matric potential at Ψ_l measurement day; $\Delta\Psi$, maximum daily water potential gradient; $K_{L\text{-}wt}$, whole-tree leaf area specific hydraulic conductance; $K_{S\text{-}wt}$, whole-tree sapwood-specific hydraulic conductance for longleaf and slash pine. P values from a mixed-model procedure ($n = 4$).

Fig. 4. (*a*) Daily water storage use (SWU) and (*b*) the relationship between sapwood volume and mean water storage use during the measurement period including linear fit (SWU = 2.327 + 10.241 × sapwood volume) for longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliottii* var. *elliottii*). Symbols are means among four tree replicates. Error bars represent SE ($n = 4$).
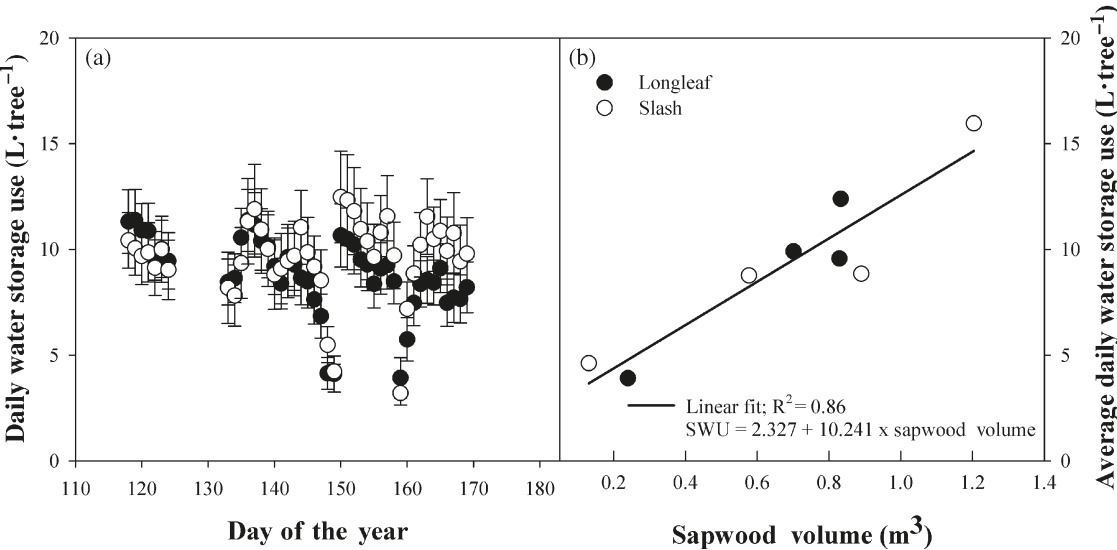

spectively. Depending on the time, there was a species effect on G_{Cday} ($P < 0.001$ for interaction between species and time). During the dry period, G_{Cday} was not different for longleaf and slash pine, but during periods of high soil moisture (after rain), longleaf pine had larger G_{Cday} values than slash pine ($P < 0.05$). Diurnal and nocturnal G_{crown} response to vapor pressure deficit was similar between species (Table 1; Fig. 6*a*). Under saturating light and nonlimiting soil moisture conditions, average G_{crown} sensitivity to D

($-dG_{crown}/d \ln D$) and average maximum G_{crown} at $D = 1$ kPa (G_{Cref}) were not different between species ($P = 0.12$ and 0.22, respectively). Nocturnal maximum G_{Cref} was 26.5% and 29.4% of daytime maximum G_{Cref} for longleaf and slash pine, respectively (Table 1).

The response of G_{crown} to increasing D was influenced by changes in soil moisture. Under low soil moisture conditions ($\theta_v < 0.11$ $m^3 \cdot m^{-3}$), G_{Cref} was highly reduced on both species. G_{Cref} averaged values 36.9% and 29.1% lower than

Fig. 5. (*a*) Nocturnal transpiration per tree and (*b*) the relationship between average nocturnal vapor pressure deficit (D_n) and nocturnal transpiration during the measurement period including the exponential saturation curve fitted ($E_{night} = 3.51 \times (1 - e^{-3.18 \times D_n})$) for longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliottii* var. *elliottii*). Symbols are means among four tree replicates. Error bars represent SE ($n = 4$).
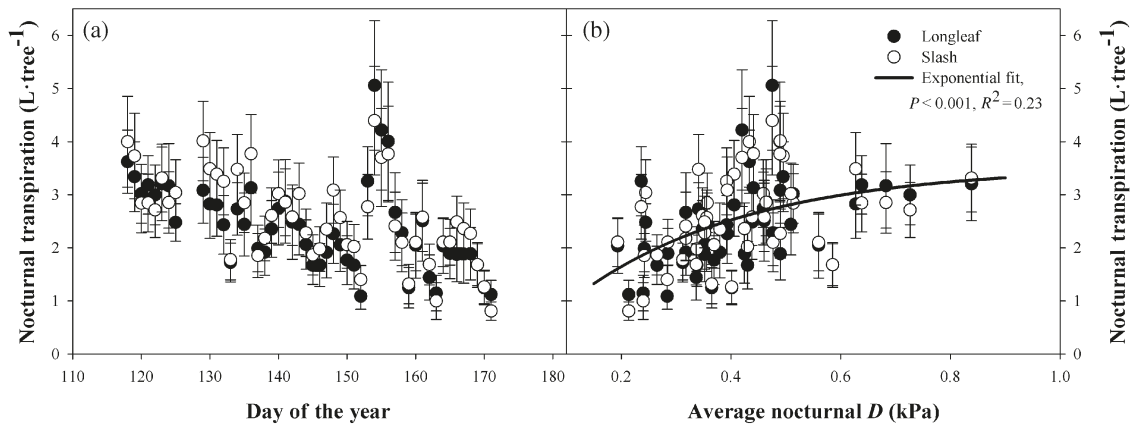
G_{Cref} for longleaf and slash pine, respectively (Table 1). There were no significant differences between species ($P = 0.83$) and soil moisture conditions ($P = 0.29$) in the relationship between $dG_{crown}/d \ln D$ and G_{Cref}, following a strong linear relationship ($P < 0.001$, $R^2 = 0.98$) (Fig. 6*b*). After pooling daytime data, the slope of that relationship was 0.626 and was no different (P 0.33) from the slope for nighttime, which was 0.647.

The relationship between G_{crown} and θ_v at 0.4–0.6 m depth was different between longleaf and slash pine (Fig. 7). An exponential saturation curve was fit separately for each species ($P < 0.05$ for curve parameters; longleaf: $G_{Cday} = 42.424 \times e^{-0.0591 \times \theta_v}$; slash: $G_{Cday} = 30.466 \times e^{-0.0744 \times \theta_v}$). Under well-watered conditions (e.g., REW > 40%), G_{Cday} of longleaf pine was larger than that of slash pine ($P < 0.001$), averaging 35.8 and 25.5 mmol·m^{-2}·s^{-1}, respectively; on the other hand, when REW was lower than 30% (threshold value corresponding to $\theta_v = 0.11$ m^3·m^{-3}, approximately), there was no difference between species in average G_{Cday} ($P = 0.45$), averaging 25.8 and 23.6 mmol·m^{-2}·s^{-1} for longleaf and slash pine, respectively. Lower minimum values of θ_v at 0.4–0.6 m depth were observed in longleaf pine compared with slash pine; this can be related to lower extraction rate at that depth on slash pine due to higher water availability at deeper profiles in slash pine due to the proximity of the water table (Fig. 3*c*). The effect of soil moisture on G_{crown} was similar for G_{Cref} and $-dG_{crown}/d \ln D$. Decreasing REW reduced proportionally both G_{crown} at $D = 1$ kPa and the sensitivity of G_{crown} to increasing D (Fig. 8).

Discussion

Longleaf and slash pine co-occur on many sites throughout their ranges and demonstrate noticeable habitat patterning where they grow together, with longleaf pine occupying the higher and better-drained microsites and slash pine predominantly found on more poorly drained microsites such as depressions and pond margins. These apparent microsite preferences are also reflected in the species' broader tolerances for site water availability: longleaf pine tolerates very dry, excessively well-drained sandhill soils, while slash pine is generally found on relatively poorly drained sites where
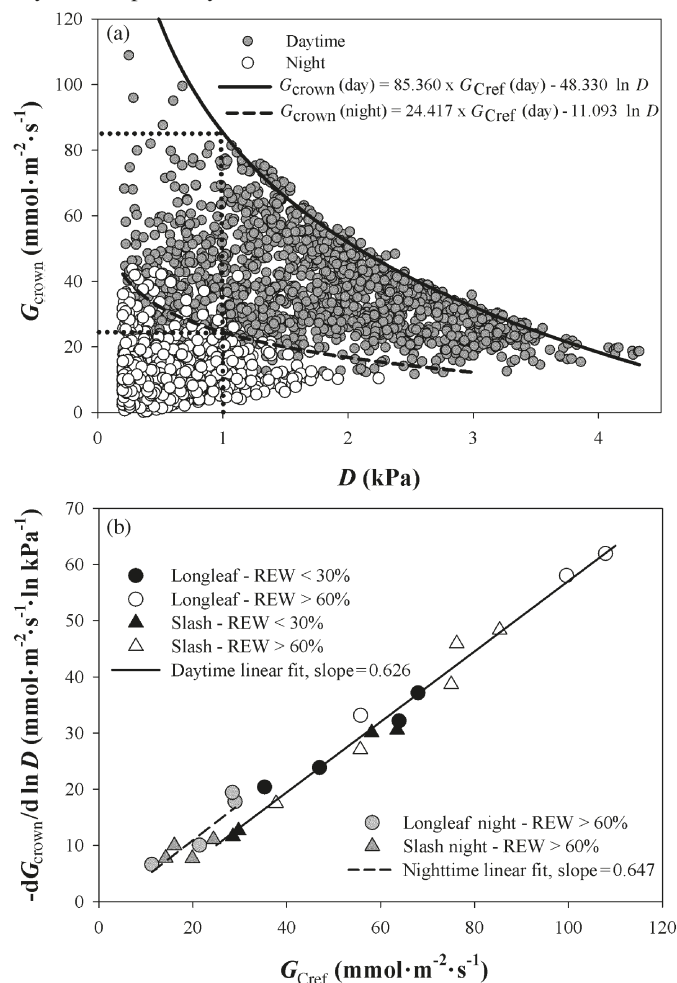
the water table can remain close to the surface for most of the year (Ewel 1990; Peet 2006). These patterns in microsite preference suggested that differences in water relations traits between the species might be associated with the relative dominance of the two species across the landscape. Our measurements were carried out in the natural habitat/microsite mosaic of the stand. Differences between the two species may reflect genetic differences and also may be explained by differences in water availability due to water table depth; therefore, the species and site effects can be confounded. We predicted that slash pine trees would have hydraulic architecture adjustments that favor higher hydraulic conductance and higher water use than longleaf pine trees. Instead, we found notable similarities between both species in water storage use, nocturnal transpiration rate, and whole-tree hydraulic conductance.

Species differences in daily water use were principally determined by differences in LA, but the greater plasticity of longleaf pine stomatal regulation partially compensated for LA differences. The differences in crown conductance adjustments to decreasing soil moisture enabled longleaf pine to function similarly to slash pine. On the other hand, the tendency of slash pine to occupy wetter zones, close to or on the fringe of small ponds, may also be related to the development of aerenchyma tissues (Fisher and Stone 1990), which enables taproot and sinkers to be submerged for weeks or even months, and perhaps to differences in root vulnerability to cavitation rather than stomatal regulation differences between species.

Our first hypothesis was not sustained by the results. Remarkable similarities were found between longleaf and slash pine in use of stored water, nocturnal transpiration, and whole-tree hydraulic conductance. Daily transpiration of slash pine was higher than that of longleaf pine only on days with decreasing soil moisture. This last result is related to the fact that slash pine has a larger LA and a lower stomatal sensitivity to reducing θ_v.

Daily tree transpiration rates were comparable in similar-sized longleaf and slash pine evaluated in other studies. Vose et al. (2003) reported mean sap flow between 30 and 80 L·tree^{-1} for longleaf and slash pine trees ranging from

Fig. 6. Example of the relationship between vapor pressure deficit (D) and stomatal conductance for water vapor at the individual tree crown scale (G_{crown}) for (*a*) nocturnal and diurnal periods and (*b*) the relationship between the reference G_{crown} at $D = 1$ kPa (G_{Cref}) and G_{crown} sensitivity to increasing vapor pressure deficit ($-dG_{crown}/d\ln D$) for nighttime and daytime and different conditions of soil moisture (REW, relative extractable soil water). In Fig. 6*a*, the data correspond to a slash pine (*Pinus elliottii* var. *elliottii*) tree of 493 mm DBH and 29.4 m height. The upper lines represent boundary line analysis fitting for nighttime and daytime G_{crown} and the vertical dashed line at $D = 1$ kPa intersects the boundary line at G_{Cref}, which was 24.4 and 85.3 mmol·m^{-2}·s^{-1} for nighttime and daytime, respectively.

Fig. 7. Average daily crown conductance (G_{Cday}) and volumetric soil water content (θ_v) at 0.4–0.6 m depth for longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliottii* var. *elliottii*) including exponential saturation curves fitted for both species (longleaf pine: $G_{Cday} = 42.424 \times e^{-0.0591 \times \theta_v}$; slash pine: $G_{Cday} = 30.466 \times e^{-0.0744 \times \theta_v}$. Symbols are means among four tree replicates. Error bars represent SE ($n = 4$).
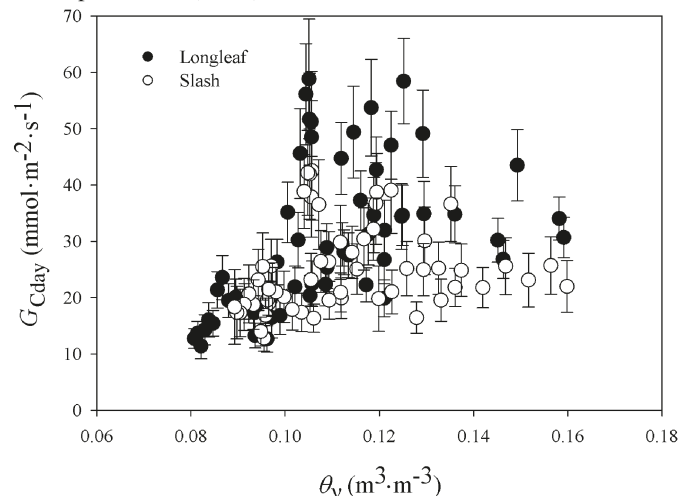
most active portion of the crown is the most important source of free stored water, accounting for 91.1% of the total free water volume. Čermák et al. (2007) carried out that study in old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with a large living crown of 31 m. In contrast, the pine trees in our study had crown lengths that averaged 7.1 and 11.1 m for longleaf and slash pine, respectively. Stem volume without bark above the S_{crown} probes averaged only 10.4% and 11.7% of the total stem volume for longleaf and slash pine, respectively; therefore, it is highly unlikely that the sapwood above the S_{crown} probes had a significant impact on total daily SWU compared with the sapwood volume below the live crown. The use of water stored in stem averaged across time and species 1.7% of sapwood volume, so the larger the tree, the larger the SWU.

SWU was not different between species and accounted for 24%–34% of total daily water use. The larger LA of slash pine does not affect daily bole water recharge cycles. Our results demonstrated that SWU depended on bole size rather than on LA of the tree. Meinzer et al. (2004, 2006), working with different species of angiosperms and gymnosperms, concluded that storage characteristics were species independent and linearly related to tree size. In our study, average SWU was 8.84 and 9.62 L·tree^{-1} for longleaf and slash pine, respectively. Phillips et al. (2003) reported mean SWU of 6.5 and 16.7 L·tree^{-1} for 25 and 36 m tall Garry oak (*Quercus garryana* Dougl.) and ponderosa pine (*Pinus ponderosa* P. & C. Lawson), respectively, averaging up to 20% of daily sap flow. In angiosperm tropical tress, Goldstein et al. (1998) reported average daily SWU between 4.0 and 8.7 L·tree^{-1} for trees between 160 and 270 mm DBH, pointing out a common relationship between sapwood area or tree height and diurnal storage capacity independent of taxa. Čermák et al. (2007) also found that about 20% of daily sap flow came from stored water in old-growth Douglas-fir

350 to 450 mm diameter at breast height (DBH). In a 14-year-old slash pine plantation, Martin (2000) determined average and maximum winter daily transpiration rate of 28.3 and 71.6 L·tree^{-1}, respectively, for 240 mm average DBH trees. On a natural regenerated longleaf pine savanna, Ford et al. (2004) reported average daily water use from 36.8 to 218.3 L·tree^{-1} for trees ranging between 190 and 1180 mm DBH for longleaf pine and 99.3 L·tree^{-1} for a single slash pine tree of 700 mm DBH.

Our estimates of SWU are based on the lag between bole sap flow at the crown base and bole sap flow at 1.8 m height; this rationale is in agreement with Čermák et al. (2007), who concluded that the xylem sapwood below the

Fig. 8. Relationship between (*a*) stomatal conductance for water vapor at the individual tree crown scale (G_{crown}) at $D = 1$ kPa (G_{Cref}) and (*b*) G_{crown} sensitivity to increasing vapor pressure deficit ($-dG_{crown}/d \ln D$) to changes in soil moisture at 0.4–0.6 m depth (expressed as relative extractable water (REW)) for longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliottii* var. *elliottii*). Symbols are means among four tree replicates. Error bars represent SE ($n = 4$).
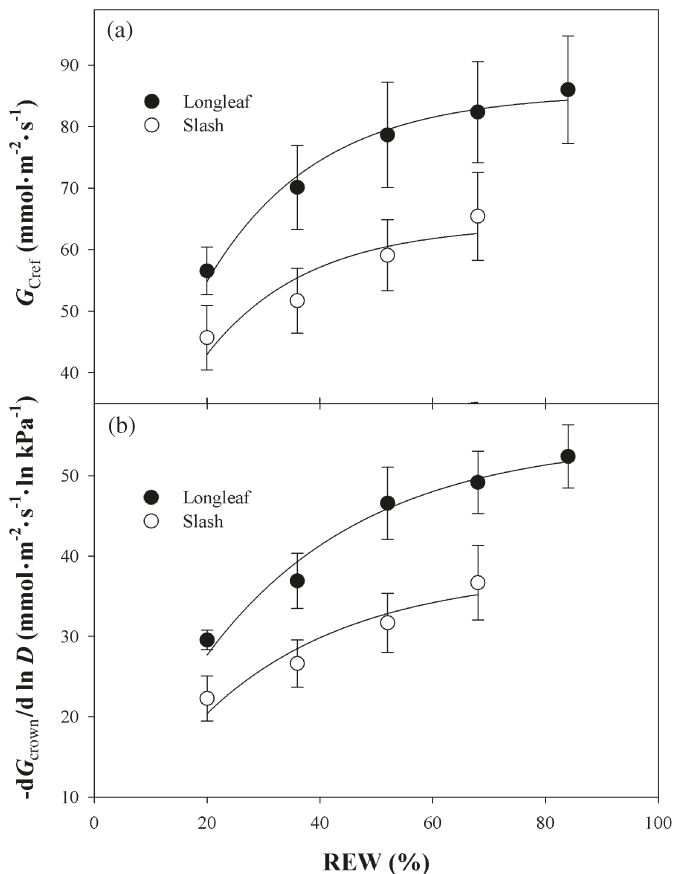
trees, ranging from 25 to 55 L·tree^{-1}. The same authors also indicated that the deeper zone in the sapwood can serve as a source of stored water, concurring with our observations of time lags with depth in the radial profile in sap flux density. As was reported in Gonzalez-Benecke et al. (2010), there were no differences in sapwood-specific hydraulic conductivity along the sapwood radius for either species. This high reliance of mature longleaf and slash pine on short-term stem water storage is a confirmation of the important role of sapwood water storage in maintaining high transpiration rates and limiting diurnal fluctuations in leaf water potential (Meinzer et al. 2004).

Both species showed similar E_{night} that accounted for, on average, 6%–8% of total daily water use. Several authors have reported similar proportions of nocturnal transpiration in trees. For example, Benyon et al. (1999) reported that nighttime transpiration accounted for 5% of total daily water use in grand eucalyptus (*Eucalyptus grandis* W. Hill ex Maid.), and Oishi et al. (2008) found that E_{night} was 11% of total daily transpiration in loblolly pine (*Pinus taeda* L.). Daley and Phillips (2006) reported 10%, 8%, and 2% for white birch (*Betula papyrifera* Marsh.), red oak (*Quercus*

rubra L.), and red maple (*Acer rubrum* L.), respectively. In our study, longleaf and slash pine's E_{night} values were positively correlated with nocturnal D and soil moisture and no differences between species were found in those relationships. As we did not measure sap flow in branches, our E_{night} estimates should be interpreted with caution. They may partially reflect water refilling of crown bole sapwood during night in addition to nocturnal transpiration from needles. On the other hand, the positive relationship between E_{night} and nocturnal D indicates that sap flow during night occurs due to stomata opening. More research in this area is needed to clarify these results.

Whole-tree hydraulic conductance (expressed on both a sapwood area and LA basis) was similar between longleaf and slash pine. To compare our estimates of K_{L-wt} with the results obtained by Addington et al. (2004, 2006) on mature longleaf pine, K_{L-wt} was expressed in kilograms of water and in an hour basis (kg·m^2 LA^{-1}·h^{-1}· MPa^{-1}). Our average estimates of K_{L-wt} for longleaf and slash pine were 0.088 and 0.071 kg·m^{-2}·h^{-1}·MPa^{-1}, respectively, when θ_v at 0.4–0.6 m depth averaged 0.10 m^3·m^{-3} (data not shown). These values were similar to the observations of Addington et al. (2004, 2006) (maximum K_{L-wt} close to 0.075 kg·m^{-2}·h^{-1}·MPa^{-1}), but θ_v was close to 7% at the time of their measurement. Longleaf and slash pine measured in this study both have higher K_{S-wt} than values reported for loblolly pine. Samuelson and Stokes (2006) and Gonzalez-Benecke and Martin (2010) reported for non-soil-water-limited conditions an average K_{S-wt} of 3.0 and 2.9 mol·m^{-2}·s^{-1}·MPa^{-1}, respectively. Maximum root-to-leaf water potential gradient ($\Delta\Psi$) was not different between species and concordant with values reported by Teskey et al. (1994) for 23-year-old slash pine; visual estimations of the difference between their estimations of Ψ_{midday} and Ψ_{pred} indicate that average $\Delta\Psi$ was 0.94 MPa across the whole season, showing a strong similarity between both species in stomatal control, resulting in relatively constant $\Delta\Psi$, allowing Ψ_l to fluctuate in synchrony with Ψ_s, reflecting an isohydric regulation of water potential. This response of leaf water potential corresponds to that presented by Franks et al. (2007) as "isohydrodynamic" where strong stomatal control maintains relatively constant $\Delta\Psi$ but at the same time allows Ψ_l to fluctuate in synchrony with Ψ_s. This suggests stomatal control that allows maintenance of high rates of carbon gain while at the same time avoiding excessive xylem cavitation.

Our second hypothesis was partially supported by the results: there were differences in stomatal response to θ_v and, to a lesser extent, to D. Stomatal conductance responses to increasing D and decreasing θ_v are necessary adjustments to regulate Ψ_l and avoid excessive xylem cavitation (Oren et al. 1999). The relationship between G_{crown} and θ_v was different between longleaf and slash pine, but the decline in G_{Cref} and $-dG_{crown}/d \ln D$ with decreasing soil moisture followed the same curvilinear shape for both species, maintaining the proportionality of the trade-off between potential stomatal conductance under low D (1 kPa) and stomatal closure as D increases. Soil moisture did not affect the ratio between $-dG_{crown}/d \ln D$ and G_{crown}; lower θ_v caused a decrease in G_{Cref} with a proportional drop in $-dG_{crown}/d \ln D$. Our results are in agreement with other studies that confirm this relationship (Oren et al. 1999; Domec et al. 2009) where

G_{crown} sensitivity to D was attributable to the variation in G_{Cref}. Domec et al. (2009) reported, for loblolly pine, a steep decline in G_{Cref} and $-dG_{crown}/d\ln D$ up to 30% of their maximum value when REW declined from 80% to 10%; in our study, when REW declined up to 21% and 26% (average REW at G_{Cref} ("dry") for longleaf and slash pine sites, respectively), G_{Cref} declined up to 37% and 29% of maximum G_{Cref}. We found that the sensitivity of G_{Cref} to increasing D was not increased at night, as Daley and Phillips (2006) reported for white birch. The slope of the relationship between G_{Cref} and $-dG_{crown}/d\ln D$, which was not different between species and daylight and soil moisture conditions, was concordant with the theoretical slope of 0.6 proposed by Oren et al. (1999). This relationship implies that trees with overall high stomatal (crown) conductance will tend to be more sensitive to D, showing higher stomatal closure as D increases.

Under well-watered conditions, E_l of longleaf pine was higher than that of slash pine, but as the soil dried, this trend was reversed. This response can be related to species differences in G_{crown} sensitivity to θ_v and D. Our results agree with those of Addington et al. (2006) who concluded that hydraulic adjustment of longleaf pine enables it to maintain large hydraulic conductance when soil moisture conditions are adequate in xeric sites. The differences in water relationship traits per unit LA are largely compensated for by the larger LA per unit sapwood area of slash pine. Our results suggest that whole-plant hydraulic adjustments are well coordinated with one another and with the environment.

Conclusion

We found remarkable similarities between longleaf and slash pine in use of stored water, nocturnal transpiration, and whole-tree hydraulic conductance but differences in other important traits including leaf to sapwood area ratio, stomatal response to θ_v, and, to a lesser extent, stomatal response to D. Differences in leaf to sapwood area ratio, where slash pine produces much more LA per unit basal sapwood than longleaf, are partially compensated for by the large plasticity of G_{crown} response to θ_v and to some extent to D in longleaf pine. More research is needed to better understand microsite preferences of each species, such as relationships between hydraulic architecture and tracheid anatomy traits, and more integrated traits such as crown conductance and whole-tree hydraulic conductance of each species.

Acknowledgements

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Appendix A

Table A1 appears on the following page.

Table A1. Biometric parameters of measured longleaf pine (*Pinus palustris*) and slash pine (*Pinus elliottii* var. *elliottii*) trees.

Species	DBH (mm)	H (m)	H_{crown} (m)	LA (m^2)	Vol (m^3)	SLA (cm$^2 \cdot$g^{-1})	SVol (m^3)	NM (kg)	SA$_{base}$ (m^2)	SA$_{crown}$ (m^2)	ST$_{base}$ (mm)	ST$_{crown}$ (mm)
Longleaf pine	198	22.76	14.85	28.9	0.398	119.3	0.191	8.45	0.0191	0.0066	4.42	3.95
	308	25.03	19.35	45.1	0.954	105.1	0.564	15.96	0.0392	0.0192	5.45	6.27
	370	23.04	16.85	37.6	1.203	133.4	0.528	12.79	0.0432	0.0194	5.00	6.30
	418	24.87	15.32	95.1	1.840	119.3	0.723	31.02	0.0589	0.0355	5.97	5.92
Slash pine	204	22.64	10.40	42.2	0.346	110.2	0.146	11.58	0.0181	0.0102	4.22	3.45
	320	26.01	17.38	110.1	1.151	110.2	0.693	35.63	0.0550	0.0250	9.15	7.57
	390	29.5	17.50	169.4	1.844	114.7	0.802	56.49	0.0607	0.0312	6.85	5.67
	453	30.95	18.75	97.6	2.452	105.7	1.092	35.41	0.0753	0.0413	7.47	6.75

Note: DBH, stem diameter at breast height; H, total tree height; H_{crown}, stem height at 0.2 m below crown base; LA, projected leaf area; Vol, total stem volume over bark; SLA, all-sided specific leaf area; SVol, stem sapwood volume; NM, needle mass; SA$_{base}$, sapwood area at 1.8 m stem height; SA$_{crown}$, sapwood area at 0.2 m below crown base; ST$_{base}$, sapwood thickness at 1.8 m stem height; ST$_{crown}$, sapwood thickness at 0.2 m below crown base.