WHOLE-STEM WATER RELTIONS IN WHITE OAK (*QUERCUS ALBA L.)*

by

CAROL ELAINE GORANSON

(Under the Direction of Robert O. Teskey)

ABSTRACT

While many tree species rely on sapwood capacitance to store and release water for transpiration, heartwood has never been considered to be a water storage reservoir. This research project investigated diurnal and seasonal changes in heartwood water content of white oak (*Quercus alba* (L.)) using automated TDR probes, and related the results to tree water use, measured using sap flux sensors, and environmental variables. Sap flux data were recorded from June to November, 2004, and heartwood water content was monitored from June 2004 to May 2005. *Q. alba* heartwood had daily and seasonal water content fluctuations that were correlated with temperature and the availability of soil moisture, but the daily heartwood water loss was not correlated with tree water use. Water is stored in and released from the heartwood of *Q. alba*, but heartwood water loss seems driven by environmental factors more than tree water use.

INDEX WORDS: *Quercus alba*, TDR, water relations, heartwood, sap flux

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B. A., The Colorado College, 2002

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2005

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December 2005

ACKNOWLEDGEMENTS

I thank my family and friends for their support over the past few years as I worked toward this degree. My labmates Chelcy Ford, Jason Nedlo and Luke Pangle helped with ideas, field work and teatime, and lab coordinators Mary Anne McGuire and Mike Murphy assisted me in many ways. Finally, I thank Bob Teskey for letting me do a unique research project and my committee members, Rod Will and Larry Morris, for helpful comments.

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INTRODUCTION

Trees take up water from the soil through their roots and transport this water up the stem through sapwood xylem elements. When water reaches the leaf it evaporates into the atmosphere through open stomata while carbon dioxide diffuses into the leaf. In order to take in carbon through the stomata for tree growth or maintenance of tissues, there must be an adequate supply of water.

One unique aspect of tree water relations is the storage of water in the stem. Trees store water in sapwood during times of lower water demand and use this water when evaporative demand for water at the leaf surface is more than the water supplied by the roots. Many tree species have been shown to store 2-20% of water used on a daily basis in their sapwood, and this water allows the tree to take in more carbon than if extra water was not stored in the sapwood (Waring and Running 1978; Tyree and Yang 1990; Goldstein et al. 1998; McLaughlin et al. 2003; Phillips et al. 2003).

This study explores the use of stored water in stems of white oak trees (*Quercus alba*, L.) in both sapwood and heartwood. As white oak sapwood ages, tyloses form in the vessel elements that clog the vessels and prevent water from being conducted up the stem. These blocked vessels undergo further chemical changes and become heartwood, which has not been considered to be active in tree water relations. Since white oak trees have relatively shallow sapwood compared to other tree species, they have a relatively small sapwood volume to use for water storage, and a relatively large heartwood volume. This project investigated the hypothesis that heartwood is used as an extra storage area

for water in white oak. If water could move laterally between the sapwood and heartwood, the heartwood could act as a passive, sponge-like reservoir, soaking in water at times when there is extra water available in the sapwood and releasing this water into the sapwood during times of water stress. This could improve tree water status and allow greater carbon uptake than if the trees only depended on water stored in their small sapwood volume.

The objective of this research project was to quantify water movement through the sapwood and heartwood of white oak trees and to determine what, if any, contribution heartwood water storage made to the daily water budget of these trees. It was hypothesized that the heartwood water content of white oak would vary daily and seasonally, water would be absorbed by the heartwood at night and released into the sapwood xylem during the day, and water stored in heartwood would be used for transpiration to reduce water stress. It was also hypothesized that heartwood water fluxes would be related to sap flux and soil moisture availability. We used a variety of sensors to measure water movement in white oak sapwood and heartwood on daily and seasonal timescales.

LITERATURE REVIEW

Tree moisture measurement techniques and temporal variation in stem moisture content

Water content measurement techniques

The simplest technique of measuring stem water content is to harvest the trees and directly measure the water content by weighing tissue samples before and after drying (Clark and Gibbs, 1957). After harvest, it is possible to separate the sapwood from the heartwood and estimate the water content of different parts of the stem by such gravimetric measurement, but the measurements are not repeatable since the tree is destroyed in the process. Removing increment cores from trees allows direct, repeated measurement of the water content of living tree stems, but it is unknown whether the coring process pushes water out of the core, causing underestimates of water content (Tyree and Yang 1990).

Nuclear scientists discovered that gamma radiation could be used to estimate the density of material, and this became the first non-destructive method for determining water content in tree stems. Using Gamma attenuation probes have been used for measuring the density of material and have been used to measure water content in soil and wood, and for defects in harvested tree stems for almost 50 years (Parrish 1961; Woods et al. 1965; Ryhiner and Pankow 1969). A probe with an americium-241 or cesium-137 radiation source and a fixed scintillation detector was used to measure moisture content in tree stems (Edwards and Jarvis 1983; Brough et al. 1986). Edwards

and Jarvis (1983) adapted this method for use in living tree stems in the field. They measured attenuation of a radioactive signal caused by living stems and dry stems, and calculated a correction factor that yielded the gravimetric water content of the stem. Although a gamma probe is capable of measuring water content by weight to within 1% (Brough et al. 1986), it is currently not used because of the risk of exposure to radiation.

Time-domain reflectometry (TDR) was first used to determine the distance to breaks in coaxial cable lines. To measure this distance, a pulsed signal is sent down a coaxial cable of known dialectric constant. Part of the signal is reflected at the break, and the time for signal return is measured (Jones et al. 2002). Topp et al. (1980) adapted this technique for measuring soil water content, creating a large coaxial tube with an inner rod and outer tube connecting to a coaxial cable and TDR meter, and placed soil between the two conductors. In this setup, the cable length (including the coaxial tube) remained the same, but the water content and soil type were adjusted (Topp et al. 1980).

There are many factors that can affect TDR readings. Increasing the water content of the material slows down the electrical signal. Also, different mineral compositions can affect the propagation of the electrical signal, so material-specific calibrations for TDR are sometimes necessary (Campbell Scientific 2003). TDR readings give the apparent distance of the TDR conductors, which is converted to the apparent dielectric constant (K_a) of the soil, a measure of how fast an electromagnetic wave travels through the material. Because the dielectric constant of air=1, soil=5 and water=80, most of the variation in the dielectric constant reading is due to the presence of water, therefore changes in the dielectric constant are directly related to the volumetric water content (VWC, or θ) (Jones et al. 2002; Campbell Scientific 2003). Topp et al. (1980) created a

general model for seven soil types that predicts soil volumetric water content from a TDR reading, although there was variation in the relationship between dielectric constant and water content in each soil texture studied. In later studies, two steel rods or probes with 2 or 3 rods installed in the soil were used as conductors, and were read using a TDR meter (Topp et al. 1982; Jones et al. 2002). Advantages of TDR for measuring water content are that the rods or probes are cheap and easy to install, it is relatively non-invasive or destructive, readings can be made quickly and are repeatable, and the equipment is not radioactive.

Constantz and Murphy (1990) developed the use of TDR in trees, where it has many of the same advantages over radiation methods. They calculated a calibration equation that converted the dielectric constant to volumetric water content in tree stems. This model accurately predicted the water content of trees, but differed from the Topp equation because there is a larger change in water content per unit change in dielectric constant in tree tissues than in soils (Constantz and Murphy 1990). The presence of ice in a stem also affects the TDR reading because ice has a low dielectric constant, similar to dry xylem or air. A partly frozen stem resembles a dry stem using TDR (Constantz and Murphy 1990; Sparks et al. 2000; Sparks et al. 2001).

Initial manual methods using TDR rods with a TDR meter were labor-intensive and difficult to automate, requiring a special wave generator and coaxial multiplexer for use with dataloggers. Water content reflectometers have overcome these limitations. They are TDR probes with a circuit that sends out a wave pulse and measure the wave propagation time, which can be recorded by a datalogger. A calibration equation converts voltage to the volumetric water content of the material (Campbell Scientific

2003). Because these probes were designed for use in soil, a separate calibration equation is needed for tree xylem (Constantz and Murphy 1990; Sparks et al. 2001). There are not many studies using TDR to measure tree stem moisture, and fewer that compare moisture contents estimated by different methods (for example, TDR readings confirmed with tree core moisture contents) (Sparks et al. 2001).

Daily and seasonal patterns of stem moisture

Using increment cores, Waring and Running (1978) found that the relative water content of *Pseudotsuga menziesii* ((Mirb.) Franco) sapwood ranged from 50-80% (60% average) during summer to near 100% in winter. Clark and Gibbs (1957) used gravimetric measurement of stem sections to determine seasonal changes in the water content of bark, sapwood and heartwood at different heights in several Canadian tree species with diffuse-porous and tracheid xylem anatomy. They found high levels of moisture in spring (90-155% of dry weight), declining stem moisture over the growing season (70-130% by weight), and stem recharge to high moisture levels the following winter (110-150%) (Clark and Gibbs 1957). Spring moisture decline came earlier for evergreen species (*Thuja occidentalis* (L.), *Abies balsamea* ((L.) Mill), and *Picea rubens* (Sarg.)) than deciduous species (*Betula lutea* (*alleghaniensis*) (F. Michx.), *Betula papyrifera* (Marsh.) and *Betula populifolia* (Marsh.)), and there was more annual variation in stem moisture in *Betula spp*. than in *T. occidentalis*, *A. balsamea*, or *P. rubens*. In general, *T. occidentalis* and *A. balsamea* had higher moisture contents than *Betula* spp. or *P. rubens.* (Clark and Gibbs 1957).

By measuring the Edwards and Jarvis (1983) measured gamma radiation attenuation of a *Pinus contorta* (Douglas ex Loudon) tree stem in chords from the outer stem to the inner stem, and were able to determine that the sapwood water content is high (above 90% by weight) and declines sharply at the sapwood-heartwood boundary to below 40% by weight. Diurnal variation in stem water content followed different patterns on two different sampling days (Edwards and Jarvis 1983). In an irrigated *Malus pumila* (P. Miller) stand, stem percent water content by weight gradually decreased between 10 and 14% on a July day from 6:00 until 14:00, and increased through the afternoon to 4% below the morning high value, with no difference between the mist irrigated and non-irrigated treatments at 6:00 and 20:00, and a 6% difference at 12:00 (Brough et al. 1986).

Using TDR, it was found that in winter the sapwood moisture level of the ring-porous species *Robinia pseudoacacia* (L.) declined to half of the summer moisture level (a reduction of 15%), while a diffuse-porous and two conifer species had much smaller (6% VWC average) seasonal declines in stem moisture (Sparks et al., 2000). Two ring-porous *Quercus* species had nearly identical seasonal water content variations, while red maple and black gum, diffuse-porous species, had similar changes in water content but differed from the *Quercus* trees (Wullschleger et al. 1996). The water contents of *Quercus alba* (L.) and *Quercus prinus* (L.) varied 15-20% annually, with average values of 0.47 and 0.49 VWC in a wet year and 0.50 and 0.53 VWC in a dry year. The stems studied had similar water contents during the summer, with dramatically lower moisture levels in the winter (Wullschleger et al. 1996). Two diffuse-porous species at the same site had similar annual moisture fluxes (15-20%) in a wet year, but much larger fluxes

(37%) in a dry year, suggesting that diffuse-porous species can withdraw more water from storage than ring-porous species when necessary (Wullschleger et al. 1996). Annual variation was higher for *Quercus lobata* (Nee) and *Quercus agrifolia* (Nee), which ranged from 0.39-0.71 and 0.36-0.66 VWC, and had a spring maximum and late summer minimum water content (Constantz and Murphy 1990).

Winter stem moisture levels in cold climates can vary due to the ice content of the stem, although in *P. contorta* there was no correlation between stem temperature (below 0°C) and ice content (Sparks et al. 2001). The TDR probes always measured at least 0.25 VWC, even when ambient temperature reached -20°C (Sparks et al. 2000). Contrary to other studies (Constantz and Murphy 1990; Wullschleger et al. 1996; Sparks et al. 2000), winter water contents in *P. contorta* were always higher than summer water contents, with a winter range of 0.49 to 0.72 and a summer range of 0.44 to 0.48 VWC (Sparks et al. 2001). This may be due to the site location in Idaho, with relatively dry summers and snowy winters, while other studies were in wetter locations. After one rainstorm, stem water increased 0.058 in 12 hours (Sparks et al. 2001). Variations in water content of sapwood and heartwood were not directly related; heartwood moisture changes lagged behind sapwood moisture changes and they varied different amounts; however, they showed similar trends. Daily fluctuations in stem water content ranged from 2-5% in May 1997 (Sparks et al. 2001).

Volumetric water content changes with irrigation

In irrigation studies using TDR, stem moisture increased after irrigation, usually reaching maximum water content a few days later, and then decreased until the next

irrigation event. In *Juglans regia* (L.), stem water content decreased from 0.44 to 0.42 in two weeks without rain or irrigation, and increased to 0.47 within 4 days after irrigation (Constantz and Murphy 1990). Potted *Sabal palmetto* ((Walter) Schultes & Schultes f.) declined from 0.56 to 0.24 VWC over an 8-day drought, and recovered to 0.54 within 2 days of watering (Holbrook and Sinclair 1992b). The moisture content in *Citrus limon* ((L.) Burman f) in Israel corresponded to the soil moisture, which increased after irrigation and decreased until the next irrigation event (Nadler et al. 2003). Irrigated *C. limon* trees had larger variations in water content than non-irrigated *C. limon* with increasing water stress, from ±0.03 (relative to pre-treatment values) in a fully watered treatment to -0.12 in a dry treatment. Diurnal fluctuations in stem water content varied from 0.01 to 0.03 (Nadler et al. 2003). Tropical dry forest trees lost 8-20% of their moisture over the dry season, but rehydrated within 7-10 days of rainfall (Borchert 1994).

Stem water storage and contribution to transpiration

3 kinds of water storage, and where they occur

Stem water storage takes three forms: elastic storage, capillary storage, and water released by cavitating vessels and tracheids (Tyree and Yang 1990). Water moves into or out of elastic storage with changes in cell volume that result from cell walls shrinking or expanding due to changes in water potential (Tyree and Yang 1990). Elastic water storage can occur in any flexible tissue, such as cambium and possibly developing sapwood, or the pith of young or non-woody plants (Holbrook 1995), although Tyree and Yang (1990) argue that woody tissue, including sapwood, is inelastic since it is dead. Water is held in capillary storage in intercellular cracks and narrow spaces in woody

tissue (Tyree and Yang 1990; Holbrook 1995). The majority of this water may be released from storage at relatively high water potentials, ≥-0.6 MPa (Tyree and Yang 1990). Xylem elements normally contain water but can cavitate when stem water potential gets too low, releasing the water for use elsewhere (Tyree and Yang 1990). Stem wood density has an inverse relationship to water holding capacity; wood with larger xylem elements and is less dense can contain more water and has a higher specific conductivity than denser tissue (Borchert 1994; Holbrook 1995; Stratton et al. 2000). However, less dense wood is more susceptible to embolism and cavitation.

Stem water storage characteristics can vary within a tree stem. For instance, larger diameter *Pseudotsuga menziesii* earlywood tracheids held more water than smaller, denser latewood tracheids, but the larger tracheids were more vulnerable to cavitation (Domec and Gartner 2002). Sapwood in the lower stem had more capacitance and vulnerability to cavitation than sapwood in the upper stem of *Pseudotsuga menziesii* (Domec and Gartner 2001).

When stem water potential drops and cavitation occurs, the water can be released from xylem elements into leaves, raising leaf water potential. After dehydration to -0.96 MPa, *Populus deltoides* (Bartr.) stems increased cavitation while the leaf water potential increased. Dehydrating *Thuja occidentalis* (L.) stems started cavitating at -2 MPa, increasing leaf water by 0.33 MPa in 4 hours (Dixon et al. 1984; LoGullo and Salleo 1992). Stratton *et al*. (2000) hypothesized that xylem vessels are the most important source of stored water in 6 evergreen, tropical dry forest trees, and Borchert (1994) found a greater range of stem density and water holding capacity in tropical than temperate trees. In wetter climates, capillary water may be the primary source of stored water used,

but in drier soils (below -2 MPa) cavitation-released water is probably the primary stored water source (Tyree and Yang 1990).

Stem capacitance

Capacitance is defined as the change in stem water content per change in xylem water potential (Edwards and Jarvis 1982). It is measured by water potential, and water potential moisture release qualities can be used to determine how much water is stored in sapwood (Meinzer et al. 2004). Capacitance also can be estimated using sap flow techniques that measure the quantity of water that enters and exits the stem. For example, at night, sap flow may recharge sapwood water stores and not be transpired (Caspari et al. 1993; Kobayashi and Tanaka 2001; Meinzer et al. 2004). Also, sap flux probes located at the base and crown of the stem can determine when water is being withdrawn or stored in sapwood (Loustau et al. 1996; Kobayashi and Tanaka 2001; Meinzer et al. 2004). A moisture release curve showing water content at different water potentials has 3 phases that vary somewhat by species (Waring and Running 1978; Tyree and Yang 1990; Meinzer et al. 2003). From 0 to -0.3 MPa capacitance is high, there is medium capacitance at typical daytime water potential values from -0.5 to -1.3 MPa, and below -2 MPa there is low capacitance evidenced by an increase in cavitations (Tyree and Yang 1990).

Trees with high capacitance had less diurnal variation in leaf water potential, suggesting that high xylem water content buffers leaves from diurnal water stress (Stratton et al. 2000; McLaughlin et al. 2003). In *Sabal palmetto*, which is an arborescent palm rather than a tree, stem tissue consists of elastic parenchyma cells and xylem

vessels, and can act as a large storage reservoir for water; a 4-m tall *S. palmetto* stem can hold 100 kg water under moderately saturated conditions (Holbrook and Sinclair 1992a). Such stems have been shown to hold enough water to keep some attached leaves green for >100 days after cutting (Holbrook and Sinclair 1992b; Holbrook and Sinclair 1992a).

Tropical dry forest trees shed their leaves during the dry season. This reduces water leaving the stem, and the tree uses this "saved" water for flowering and shoot growth before the next rainy season begins (Borchert 1994). In *T. occidentalis*, water stored in xylem contributes <6% to daily transpired water under normal conditions ($-0.5 \leq \psi \leq .1.5$ MPa) (Tyree and Yang 1990); however, 6 dry forest tree species in Panama stored 4-54 liters of water in sapwood daily, providing 9-15% of water used daily; there was a linear relationship between sapwood area and the volume of water withdrawn from storage (Goldstein et al. 1998). Similarly, water contributed by sapwood storage increased with tree size in *Pseudotsuga menziesii, Quercus garryana* (Dougl. ex Hook.) and *Pinus ponderosa* (Dougl. ex Laws.) in southern Washington and Oregon. The average stored water used daily in transpiration by 15 m tall *P. menziesii* was 7.2%, while 60-m trees used 23%. *Q. garryana* stored water use increased from 11% in 10-m trees to 17% in 25-m trees, and in *P. ponderosa*, stored water use ranged from 3% in 12-m trees to 10% in 36-m trees (Phillips et al. 2003). In many species, stored water contributes a small amount toward the water transpired on a daily basis, but over a growing season the contribution may significantly increase carbon gain for the tree.

Heartwood as a water storage reservoir

Since all plant tissues contain some amount of water, every part of a tree could be viewed as a potential water storage reservoir (Holbrook 1995). Few studies have investigated changes in the water status of heartwood; most have concentrated on water movement in the sapwood. The conducting xylem of the sapwood transports the majority of the water used (Jarvis 1975; Hinckley et al. 1978). It is unknown whether water can be stored in the heartwood for later use. Sapwood usually has a higher water content than heartwood (Hinckley et al. 1978; Holbrook 1995), but there is considerable variation in the heartwood water content between species. For example, *Picea abies* ((L.) Karst) was found to have a much drier heartwood than sapwood, but the heartwood and sapwood of *Quercus robur* (L.) had similar moisture contents (Fromm et al. 2001). A deuterium tracer experiment showed that water could move between the sapwood and heartwood of *Eucalyptus grandis* (W. Hill *ex* Maiden). At 0.5 days after deuterium was injected into sapwood, the deuterium concentration was much higher in the sapwood than the heartwood, but by 4 days after injection there were substantial amounts of deuterium in both the heartwood and sapwood (Kalma et al. 1998). There is evidence that although sapwood and heartwood are adjacent they are not hydrologically interconnected (Holbrook 1995). Using dye, Edwards and Jarvis (1982) found the heartwood of *Picea sitchensis* ((Bongard) Carriere) and *Pinus contorta* (Dougl. ex Loud) to be hydraulically disconnected from the sapwood xylem. Different species and wood types seem to vary in their hydraulic properties, with heartwood and sapwood being connected to different degrees.

Timing of water storage and use

The residence time of water in a tree varies greatly depending on species and climate conditions, but can generally be related to sapwood capacitance and water conducting properties within a region. Using deuterium water as a tracer, James et al. (2003) found that water inserted at the base of the stem was transpired from the leaves after 1-5 days, and was completely flushed from the xylem by 22 days after injection. Differences between species could be explained by sapwood water storage capacity, radial water transport and specific conductivity, but not always tree size. While the largest and smallest trees (*Anacardium excelsum* ((Bentero & Balb. *ex* Kunth) Skeels) and *Cordia alliodora* ((R. & P.) Oken.)) had the largest and smallest relative water storage capacities, the larger of the middle-sized trees, *Ficus insipida* (Willd.), had a smaller relative water storage capacity than the smaller of the middle-sized trees, *Schefflera morototoni* ((Aubl.) Maguire, Steyerm. & Frodin). However, all other factors in that study scaled by tree size (James et al. 2003). Similarly, a deuterium tracer showed that trees with more sapwood capacitance, determined with sapwood cores in a thermocouple psychrometer, were able to transport water deeper into the stem (*S. morototoni*, 16 cm deep) than in trees with little sapwood capacitance (*C. alliodora*, 2 cm) (Meinzer et al. 2003).

Several studies have quantified daily water content changes in the stem, yielding short-term water storage and release values. *P. menziesii* sapwood varied between 0.33 and 5% relative water content on a daily basis, but *Pinus sylvestris* (L.) water content varied by up to 20% in one day, with the relative water content increasing after rain storms in both species (Waring and Running 1978). Similarly, *Liriodendron tulipifera*

(L.) sapwood storage provided an average of 2 l d^{-1}, or 2-10% of daily water use (McLaughlin et al. 2003). Sap flux probes installed in the base and crown of tree stems indicate that water stored by sapwood capacitance in four tropical dry forest species supplied water for transpiration between 7 and 10 AM (Meinzer et al. 2003). When sap flux in the crown exceeds sap flux at the base, water is withdrawn from sapwood storage, and when basal sap flux is greater than crown sap flux, water is replaced in sapwood storage. In 5 tropical dry forest species, crown sap flux began 6 minutes to one hour before basal sap flow in the morning, and in the evening crown sap flux ended before basal sap flux while the stem was refilling. Crown sap flux exceeded basal sap flux from dawn until 11 AM, indicating that stored water from the xylem was used during the morning (Goldstein et al. 1998). *P. menziesii* withdrew water from storage from 10 AM to 2 PM and had a net increase in stem water flow during the other hours of the day, while Oregon white oak, *Q. garryana*, withdrew water from sapwood water storage from 8 AM to 12 PM, and recharged the stem at varying rates for the rest of the day (Phillips et al. 2003). In contrast, there was little difference in sap flow rates in the bole and crown of the Japanese *Quercus mongolica* (Fish), and little nighttime sap flow, suggesting that sapwood water storage and capacitance was not important to that tree during the very wet study period (Kobayashi and Tanaka 2001).

Tree water use

Measurement techniques

The amount of water used by trees can be measured by enclosing transpiring leaves in chambers as sap flow in xylem lower in the stem, or at the stand level using

eddy covariance. All these methods have benefits and disadvantages due to scaling, calibration, time lags and weather conditions.

An infra-red gas analyzer (IRGA) that measures water vapor or a porometer can measure the amount of water transpired by a leaf, branch, or tree enclosed in a cuvette or chamber. There are problems with scaling tree or water use from relatively small leaf surface area samples, and in larger branch and tree chambers the chamber alters the microclimate and affects transpiration levels (Pearcy et al. 1991). An advantage to measuring transpired water over sap flux is that there is less of a time lag between changes in atmospheric conditions and changes in leaf transpiration, and it is much easier and cheaper to use a portable IRGA than to set up an eddy covariance system.

Sap flux measurements measure tree-scale water use, and can yield the species contribution to stand or ecosystem water use. Several sap flux probe concepts exist, but they all measure heat movement in the xylem. In the heat pulse method, a heater in the xylem is heated for 1-2 seconds, and thermocouples downstream of the heater measure the sap and xylem temperature. A datalogger records the time it takes the two thermocouples to reach the same temperature after the heat has dissipated. Thermal dissipation probes, such as the Granier sap flux probes used in this study, have two probes containing thermocouples that are installed in the xylem. The upper probe is heated with a constant current, and as sap travels up the xylem it cools both probes. The temperature difference between the heated and unheated probes is related to the speed of sap ascent and can be scaled to calculate the volume of whole-stem water use. Sap flux collars use the heat balance method, where a heater is wrapped around a stem and

insulation is secured around the heater. Thermocouples located axially and radially from the heater determine how much heat is dispersed by axial sap flow (Jackson et al. 2000).

The eddy covariance technique of measuring stand or ecosystem transpiration and carbon fluxes is the least invasive technique, requiring equipment mounted on a tower above the canopy rather than enclosing tree parts or installing sap flux probes, but it requires specific topographic and atmospheric conditions for accurate measurements. A sonic anemometer and infra-red gas analyzer measure the direction and magnitude of carbon dioxide and water vapor fluxes over the canopy. Ideally, eddy covariance forest stands are at least 1 km^2 and flat, with a breeze to stir the canopy boundary layer. Problems with this technique include windless days and nights when atmospheric eddies are not formed and cannot be measured, and the measurement area (fetch) varies between readings, depending on the size of the eddy formed and measured. Except in monospecific stands, eddy covariance cannot estimate the contribution of water and carbon flux by species (Moncrieff et al. 2000).

Water-conducting tissue: sapwood depth

There is considerable diversity between sapwood depth of different species; however, diffuse-porous and tracheid species typically have more water-transporting sapwood than ring-porous species (Wullschleger et al. 2001). Only the current year ring of sapwood is generally considered to conduct water in ring-porous species; however, there is evidence that deeper sapwood is also hydroactive. Six years of sapwood rings conducted water in *Q. rubra* and *Q. alba*, but all earlywood more than one-year-old and more than 50% of latewood up to 6 years old was blocked by tyloses, so the remaining

latewood vessels conducted water (Cochard and Tyree 1990). In contrast, Fromm et al. (2001) found the outer 7 sapwood rings of *Q. robur* to be free of tyloses, and assumed they could transport water. Using a cut *Q. robur* stem, Cermak et al (1992) determined that 10 sapwood rings conducted water, but the outer rings transported a larger portion of water, with flow decreasing to 5% in the inner sapwood rings. Staining revealed that 4-5 growth rings also transported water in the Mediterranean-climate shrub *Quercus durata* (Jepson) and tree *Quercus agrifolia* (Nee) (Goulden and Field 1994), and despite differences in diameter and species, sapwood depth was similar (2.4 cm average) in *Q. robur*, *Q. alba*, and *Q. prinus*, (Wullschleger et al. 2001).

Diffuse-porous and tracheid species are known to have deeper sapwood with more conducting rings than ring-porous species. *Lithocarpus edulis*, a "radial-porous" evergreen, monsoon-forest oak, conducted water with at least 20 growth rings and a high density of ray cells (Hirose et al. 2005). Sapwood depth increased with stem diameter in diffuse-porous *Liriodendron tulipifera*, up to 15 cm in 69 and 78 cm diameter trees (Wullschleger and King 2000; Wullschleger et al. 2001), while understory *Acer rubrum* L. stems consisted solely of sapwood for 12-18 years (up to 4 cm dbh) (Wullschleger et al. 1998). Sapwood depth in *Pinus palustris* (Mill.), *Pinus echinata* (Mill.), *Pinus elliottii* (Engelm.), and *Pinus taeda* (L.) ranged from 9.4 to 20.5 cm (average=14.6 cm), in trees ranging from 31.6-53.7 cm diameter (average 44.3 cm) (Ford et al. 2004b).

Sapwood conductance radial profiles

In all trees, more water is transported in the outer sapwood rings than the inner rings, but there are variations in the difference between sap flow in the different rings

between species. In a severed *Q. robur* stem, sap flux velocity was 40 m h^{-1} in the outer ring, and dropped to 10 m/hr in the third ring. The radial profile was much more symmetrical around the stem in *Q. robur* than *Picea abies* (Cermak et al. 1992). Intact stems of *P. palustris*, *P. echinata*, *P. elliottii* and *P. taeda* also had Gaussian-shaped radial profiles, with highest sap flux in the outer 2-4 cm of sapwood (Ford et al. 2004a; Ford et al. 2004b). In *Anacardium excelsum*, *Ficus insipida*, *Cordia alliodora* and *Schefflera morototoni*, tropical dry forest species, sap flux also decreased from outer to inner xylem (James et al. 2003).

Water use in oaks and other species

Whole-tree and stand-scale water use varies by species and depends on factors such as sapwood area, atmospheric conditions and soil moisture availability. Environmental variables such as vapor pressure deficit (VPD) in the air, photosynthetically active radiation (PAR) from the sun, or soil moisture control tree water use by driving water gradients, photosynthesis, or providing water to roots. Trees with different xylem anatomies use different amounts of water. Since this study is on *Q. alba*, the focus of this section is on ring-porous *Quercus* spp. and co-occurring species.

Quercus spp. have faster sap flow rates than many other tree species. Wide, long earlywood vessels provide less resistance to flow than shorter or narrower vessels or tracheids, and allow water to travel up the stem at a higher rate than in species with other xylem anatomies (Sperry 2003). However, oak vessels develop tyloses and clog within a few years of development and, as a result, oak sapwood is relatively shallow, with less

sapwood area in oaks than in diffuse-porous or tracheid tree species with similar diameters (Cochard and Tyree 1990).

Spicer and Holbrook (2005) measured tree water use in four Massachusetts species using sap flow probes. Results of sap flux density in the outer cm of sapwood were shown for several days in 2002 (Spicer and Holbrook 2005). The daily high sap flux density of *Q. rubra* was 23 g m^{-2} s^{-1} on 6 days in September, and one *Fraxinus americana* (L.) had a maximum daily sap flux density of approximately 40 g m^{-2} s^{-1}, while another *F. americana* tree had a maximum daily sap flux density of about 22 g m^{-2} s^{-1} during 8 days in August. *A. rubrum* reached a daily maximum rate of around 50 g m^{-2} s^{-1} on 6 days in August, and *T. canadensis* reached a daily maximum of about 25 g m^{-2} s^{-1} on 3 days in June and 4 days in October (Spicer and Holbrook 2005). (Spicer and Holbrook 2005). The four species studied had similar diameters (33-39 cm), and daily tree water use from least to greatest was *Q. rubra*, *T. canadensis*, *F. americana* and *A. rubrum* (Spicer and Holbrook 2005). Maximum sap flux rates of *Q. rubra* were higher in upland and lowland stands within a watershed in a forest in southeast New York (Engel et al. 2002). *Q. rubra* dominated the forest and was the focus of the study (Engel et al. 2002). *Q. rubra* in the uphill study plot had lower sap flux density and lower stomatal conductance rates than trees in the lower elevation plot (Engel et al. 2002). Over several days in August and September 2000, the maximum sap flux rate of *Q. rubra* was 70 g m^{-2} s^{-1} in the upper plot and 95 g m^{-2} s^{-1} in the lower plot (Engel et al. 2002). However, in upland trees, which receive solar radiation for longer every day, sap flow occurred near maximum rates for longer each day then in the lowland trees (Engel et al. 2002).

Stomatal conductance was negatively correlated with VPD in both upper and lower trees (Engel et al. 2002).

Wullschleger et al (2001) measured stand transpiration in an East Tennessee upland oak forest. Growing season stand transpiration was 267 mm, with a maximum daily transpiration of 2.2 mm d^{-1} (Wullschleger et al. 2001). The major contributors to the overstory portion of stand transpiration were *A. rubrum* (59 mm) and *N. sylvatica* (19 mm) (Wullschleger et al. 2001). *Q. prinus*, which had the largest sapwood area of the three oak species studied, transpired 35 mm (Wullschleger et al. 2001). Stand sap flow was related more closely to solar radiation (PAR) than to VPD, and maximum sap flow rates for *Q. alba*, *A. rubrum* and *L. tulipifera* were between 42 and 59 g m^{-2} s^{-1}, which is within the range of sap flow rates found for *Q. rubra* in Massachusetts and New York (Spicer and Gartner 2001; Wullschleger et al. 2001; Engel et al. 2002). Oren and Pataki (2001) measured water use of a southeastern deciduous forest where *A. rubrum* and *Q. alba, Quercus velutina* (Lam.) and *Q. falcata* (Michx.) were common, and determined the response of transpiration to changes in soil moisture, VPD and PAR. This study found similar canopy transpiration rates to Wullschleger et al. (2001); annual canopy transpiration was 278 mm, with a daily maximum transpiration of 2 mm, and most of the transpiration occurred during the 6-month growing season (Oren and Pataki 2001). Soil drying decreased daily transpiration in most of the six species studied, and decreased transpiration more dramatically in *A. rubrum* than the other species. When soil moisture was not limiting, there was a linear relationship between canopy transpiration and PAR; however, *Quercus* spp. water use leveled off at a relatively low VPD, while water use continued to increase with increasing VPD in *A. rubrum, C. tomentosa* and *L. styraciflua*

(Oren and Pataki 2001). Although they did not report sap flux rates, Pataki et al (1998) measured canopy conductance of 3-year-old *P. taeda*, *L. styraciflua* and *Q. phellos* in closed chambers in North Carolina. They found that *L. styraciflua* had the highest rate of stomatal conductance, at 91.3 mmol m^{-2} s^{-1}, *P. taeda* had a stomatal conductance of 87.4 mmol m^{-2} s^{-1}, and *Q. phellos* conducted the least amount of water, 47.6 mmol m^{-2} s^{-1} (Pataki et al. 1998). Daily sap flux increased curvilinearly with VPD in all species, leveling off when daily average VPD exceeded 0.6 kPa (Pataki et al. 1998). Stomatal conductance was higher on days with more solar radiation, and declined with declining soil moisture (Pataki et al. 1998).

Studies of oaks in other regions of the world tend to support the relatively low transpiration rates of this genus when compared to other genera. For instance, water use of *Q. agrifolia* and *Q. durata* in California was measured using ventilated chambers (Goulden and Field 1994). Chamber transpiration in *Q. agrifolia* reached a maximum level of 3.5 mmol m-2 s-1, and *Q. durata* had a maximum transpiration of 2.0 mmol m-2 s-1 on 16 April 1991; both of these transpiration rates were much lower than the eastern *Qurecus* spp. (Pataki et al. 1998) and may result from the drier conditions in California (Goulden and Field 1994).

A 16-m tall *Quercus mongolica* (Fish) in Japan reached a maximum rate of sap ascent of about 15 cm h^{-1} on 24-25 August, 1996 (Kobayashi and Tanaka 2001). From 7-11 August, 1997 the maximum sap ascent rate was higher, at 23 cm h^{-1} (Kobayashi and Tanaka 2001). Tree water use over these and two additional days (total of 9 days) averaged 8 kg d^{-1}, and like in the Eastern US oaks, diurnal water use patterns were more closely related to solar radiation levels than VPD (Kobayashi and Tanaka 2001). This

tree had a lower daily water use on the days measured than *Q. garryana* in Oregon. Phillips et al (2003) studied water use of small and large individuals of three tree species receiving different amounts of precipitation in eastern Oregon and southwestern Washington: *Q. garryana* (1085 mm annual rainfall), *P. menziesii* (2400 mm) and *P. ponderosa* (360 mm). They examined water use by small and large individuals of each tree species to find out the amount of stored water the trees used (Phillips et al. 2003). Fifteen and 60-m tall *P. menziesii* trees used 14.3 and 205 kg d^{-1} water, 10 and 25 m tall *Q. garryana* used 14.2 and 38.0 kg d^{-1} water, and 12 and 36 m Ponderosa pine used 84 and 167 kg d^{-1} water (Phillips et al. 2003). As the growing season progressed and a drought occurred, all trees except the small Douglas-fir trees used a larger percent of water stored in the sapwood on a daily basis (Phillips et al. 2003).

CHAPTER 1

WHOLE-STEM WATER RELATIONS IN WHITE OAK (*QUERCUS ALBA L.*)[1]

[1] Goranson, C.E., Will, R.E., Morris, L.A. and Teskey, R.O. To be submitted to Tree Physiology.

ABSTRACT

Transpiration can draw water out of a tree faster than absorption by the roots can replace it. In many tree species, sapwood serves as a storage area that absorbs and releases water at different times of day and allows more transpiration and carbon gain than if water moved from the roots to the stomata at a constant rate. This study investigated whether *Quercus alba* (L.) also uses heartwood as a water storage organ. Sap flux probes were installed in the sapwood of 5 trees and monitored from June to November, 2004, and heartwood water variation was measured using automated TDR probes installed directly in the heartwood of each tree from June 2004 to May 2005.

Average tree water use ranged from 31.5 to 119.1 L d^{-1}. Daily sap flux was well correlated with daily total PAR (r^2=0.75). On average, only 4.5% of transpired water was attributable to sapwood water storage. There were small changes in the volumetric water content (g cm^{-3}) of the heartwood on a daily basis, and larger changes in water content seasonally. Average heartwood water contents ranged from 0.54 from 0.62 g cm^{-3} and daily heartwood water losses ranged from 0.012 to 0.034 g cm^{-3}. The volume of water lost from the heartwood depended on tree size and ranged from 7.8 to 25.9 L d^{-1}. Daily, weekly and monthly heartwood water contents were best predicted by air temperature + soil moisture (r^2=0.31, 0.3 and 0.17), and heartwood water losses were predicted by the change in stem temperature (weekly, r^2=0.3; monthly, r^2=0.38) and soil moisture + VPD (monthly, r^2=0.47).

During the growing season heartwood water content generally declined in the morning as sap flux increased, and then increased in the afternoon as sap flux declined; however, similar heartwood water content patterns were found all year, including when the tree lacked leaves. Water leaving the heartwood probably improves water relations for *Q. alba*, but seems to be more closely related to temperature and soil moisture availability than to the atmospheric demand for water on the tree.

Key words: *Quercus alba*, TDR, water relations, heartwood

INTRODUCTION

At times, transpiration causes water to be lost from the stem faster than it is replaced by the roots, causing diurnal and seasonal changes in the water status of sapwood xylem. Sapwood capacitance allows water to be stored in the xylem that can be used during times of water stress. Stored water can prolong stomatal conductance and carbon uptake when water is limiting (Dixon et al. 1984; LoGullo and Salleo 1992).

Many tree species store water in their stems, and this stored water provides a small but important part of the water transpired daily. Several studies have shown that, on weekly timescales, stem water content increases after rain or decreases during drought (Waring and Running 1978; Constantz and Murphy 1990; Holbrook and Sinclair 1992b; Borchert 1994; Nadler et al. 2003), but there are few diurnal or longer-term studies of the phenomenon. In *Thuja occidentalis* (L.), stored water contributed less than 6% of water

transpired daily (Tyree and Yang 1990), while *Liriodendron tulipifera* (L.) stored and withdrew 2-10% of daily water used from sapwood (McLaughlin et al. 2003). Stored water accounted for 9-15% of transpired water for six tropical dry forest species on a daily basis, and there was a linear relationship between the amount of sapwood and volume of stored water used daily (Goldstein et al. 1998).

There is considerable variation in the moisture content of tree stems throughout the year. Some tree species have higher stem water contents in the growing season, while others have higher water contents in the dormant season. This suggests that in some tree species environmental factors may have a greater effect on stem moisture content than does the level of physiological activity, but previous studies have not focused on the environmental variables that could be related to changes in stem moisture. *Quercus prinus* L., *Quercus alba* (L.), *Acer rubrum* (L.) and *Nyssa sylvatica* (Marsh.) in Tennessee had higher moisture contents during the growing season, and lower water contents in the dormant season (Wullschleger et al. 1996). However, *Quercus agrifolia* (Nee) stems in central California contained more moisture from January-May, and lower moisture levels from June-December (Constantz and Murphy 1990). In Canada, the water contents of *T. occidentalis, Abies balsama* (L.), *Picea rubens* (Sarg.), *Betula lutea* (*alleghaniensis*) (F. Michx.), *Betula papyrifera* (Marsh.) and *Betula populifolia* (Marsh.) were highest in the spring, and declined over the growing season; *T. occidentalis, A. balsama* ((L.) Mill) and *P. rubens* (Sarg.) began their seasonal moisture decline earlier than the *Betula* species (Clark and Gibbs 1957). During winter thaws when water was liquid rather than ice in the stem, *Pinus contorta* (Dougl. ex Loudon) had a higher water content than in the growing season (Sparks et al. 2001).

Although heartwood represents the largest component of the stem of mature trees, its role in stem water storage is unknown. A deuterium tracer study indicated water flow between sapwood and heartwood in *Eucalyptus grandis* (W. Hill *ex* Maiden) (Kalma et al. 1998), but such studies are rare. While conifers such as *Picea abies* (L. (Karst)) and *Pinus contorta* (Douglas ex Loudon) have very dry heartwood compared to sapwood, the moisture content of *Quercus robur* (L.) heartwood and sapwood is much more similar (Edwards and Jarvis 1983; Fromm et al. 2001). Ring-porous species such as *Quercus spp.* rely on a few sapwood rings to conduct and store water, and have a large proportion of heartwood in their stems compared with diffuse-porous or tracheid xylem species (Hinckley et al. 1978).

Given that *Quercus* species have a small amount of water conducting tissue and large volume of heartwood, it seems reasonable that *Quercus* heartwood could serve as a passive water storage reservoir for the tree, supplying water to the sapwood for transpiration when water demand exceeds root system transport capacity. The adaptation of automated TDR probes for use in tree tissue has made it possible to continuously monitor the volumetric water content of woody stems (Sparks et al. 2001). We investigated diurnal and seasonal fluxes of water through *Q. alba* sapwood using sap flux probes, and changes in heartwood water content using TDR probes, to determine the volume and timing of water fluxes. We sought to determine the degree of hydraulic connectedness between the water supplies in the heartwood and sapwood, and whether heartwood contributed water to transpiration on a daily basis.

It was hypothesized that the heartwood water content of white oak would vary daily and seasonally, water would be absorbed by the heartwood at night and released

into the sapwood xylem during the day, and water stored in heartwood would be used for transpiration to reduce water stress. It was also hypothesized that heartwood water fluxes would be related to sap flux and soil moisture availability.

METHODS

Site and equipment setup

This study was conducted in an upland oak-hickory area of the Whitehall Forest (33.92°N, -83.30°W), an experimental forest of the University of Georgia, Athens, GA. The soil type at the study site was a Pacolet sandy clay loam, which is a rocky soil lacking a well-defined organic horizon that overlays bedrock (Anonymous 1968). Five white oak (*Quercus alba* L.) trees were chosen based on size (>30 cm dbh) to accommodate 25-cm TDR probe rods within the heartwood, and healthy appearance (Table 1). Trees were located within 30 m of a centrally-located data logger. Sap flow data were collected from day 149 to day 331 (28 May-26 November) of 2004, and TDR data were collected from day 155 (4 June), 2004 until day 159 (8 June), 2005. There were occasional failures in data collection due to rainstorms.

Two-cm long thermal dissipation sap flux probes were constructed as in Granier (1987) to measure water use by the trees. Sap flux probes were installed on the north and south sides of each tree, at 1.4 and 3.9 m height for a total of four probes per tree. In addition, one 10-cm Granier-style long probe with 5 thermocouples was constructed as in (Ford et al. 2004b) and installed at 2 m height on the east side of each tree. Bark was removed from each probe location with a rasp and a template was used to drill evenly-

spaced, parallel holes into the tree stem. The probes were coated in heat conducting silicone grease (Chemtronics, Kennesaw, GA), inserted in the tree, and insulated with Styrofoam blocks. The stems were wrapped with Reflectix insulation (Markleville, IN) to protect the probes and minimize thermal gradients. The sap flux probes were connected differentially to multiplexers (AM 32 or AM 16/32, Campbell Scientific, Logan UT) connected to a CR 23X datalogger (Campbell Scientific, Logan UT) and logged every 5 minutes, with 15 minute averages recorded (Appendix 1).

Sap flux density and daily tree water use were calculated for each probe using the following equation (Granier 1987):

$$v=119[(dT_{max}-dT)/dT]^{1.231} \text{ g } H_2O \text{ m}^{-2} \text{ sapwood second}^{-1} \quad (1)$$

Where v is sap flux density, dT is the temperature difference between the heated and unheated probe, and dT_{max} is the highest temperature difference between 5 and 6 AM each day.

The sapwood area of each tree was calculated from measurement of sapwood depth in increment cores, tree dbh and bark depth. Total water use by the study trees was calculated by multiplying the sap flux volumes by the area of sapwood over time.

A CS616 volumetric water content reflectometer (VWR) probe (Campbell Scientific, Logan UT) was installed in each tree to measure the water content of the heartwood (Figure 1). The VWR probes were cut to 25 cm in length. To avoid measuring sapwood water content, the sapwood was removed from the area adjacent to the probe with a drill, chisel and hammer before installing the VWR probe. A template was used to drill parallel holes in the trees before installing the probe. Each VWR probe was sealed to a tree stem with silicone sealer, and the probes were covered with foam

insulation and Reflectix insulation to minimize thermal gradients. A thermocouple was installed 6cm deep in each tree stem to measure the heartwood temperature, since measurement temperature affects the VWR probe reading. The VWR and thermocouple from each tree were connected to the panel of a CR23X datalogger and were logged every 5 minutes, with 15 minute averages recorded.

A Theta probe (Delta-T Devices, Cambridge, UK) was installed 30 cm deep in the soil 1.5 m from the north side of each study tree to record soil moisture. Theta probes were connected to an AM 32 multiplexer wired to a CR23X datalogger. The Theta probes were read hourly, with 4-hour averages recorded.

A weather station in an open field 200 m from the study site recorded photosynthetically active radiation (PAR), air temperature and vapor pressure deficit (VPD) every 15 minutes. Rain data for Athens were obtained from the Georgia Forestry Commission rain gauge, located at the entrance of Whitehall Forest. These data were accessed on the Georgia Forestry Commission website, http://weather.gfc.state.ga.us/.

Stem TDR probe calibrations

A section of white oak stem harvested from the Whitehall Forest, 1 km from the study site, was used to create a calibration for the volumetric water content reflectometer probes used to detect changes in water content of the heartwood. A new calibration was needed because the original calibration curves provided by the instrument manufacturer, Campbell Scientific, were based on organic and mineral soils. In addition, 5 cm of the original probe length was cut off before installation, and temperature affects the probe reading.

A 15 cm long, 32 cm diameter (with bark removed) stem section was soaked in water between harvest and calibration. The bark, cambium and sapwood were removed with a chisel, and the initial stem volume was measured with a ruler. The heartwood was reinforced with hose clamps to prevent the stem from cracking. Two 3.6 mm holes were drilled in the heartwood using a template, and the probe was inserted in the holes.

A thermocouple was installed in a hole drilled 6 cm into the stem section to monitor the internal temperature. The VWR probe and thermocouple were connected to a CR23X datalogger, the sensors were read every 5 minutes, and 15 minute averages were recorded. The calibration experiment was carried out at relatively constant tempereature (24-27°C) on a lab bench. The stem section and VWR probe were left out to dry each day and were wrapped in plastic and placed in a tightly fitting plastic bag each night during calibration to allow the moisture level to re-equilibrate throughout the stem. In the morning, the stem was removed from the plastic and weighed. The last VWR probe reading before removal from the plastic bag each day was used for calibrating the probe because we assumed a moisture gradient would form in the stem section soon after exposure to air.

At the end of the water content calibration, the stem sections were dried in an oven to obtain the dry weight, and the volumetric water content during the experiment was calculated. A calibration equation was determined using PROC REG (SAS V 8e, Cary, NC) to convert the temperature-corrected readings to volumetric water contents (Figure 2):

$$\theta_{stem}=0.0461*P - 0.7047 \quad (2)$$

Where θ_{stem} is the volumetric water content of the stem, and P is the reading of the volumetric water content reflectometer probe in microseconds (μs). This calibration equation was applied to data collected from the 5 study trees.

In addition, a temperature calibration was conducted with a white oak stem section in a growth chamber (Environmental Growth Chamber, model C3). A TDR probe and several thermocouples were installed, and the stem was wrapped in several layers of plastic to inhibit evaporation. The growth chamber was set at six different air temperatures, from 5 to 30° C at 5° increments, and after the stem had equilibrated for 24 hr, the CS616 reading was recorded. There was a small but clear increase in probe reading with temperature increases, and the data were adjusted to a standard temperature, 25° C, before conversion to VWC to remove variation caused by stem temperature. The effect of temperature on probe reading was (Figure 3):

$$P=0.0006*T_s^2 + 0.02T_s + 24.311 \quad (3)$$

Where P is the CS616 TDR probe reading in μs, and T_s is the stem temperature (°C). It was assumed that the effect of stem temperature on probe reading would be similar at different moisture contents. The slope of this equation was used to remove the effect of temperature on probe reading. 25°C was chosen as the standard temperature, and the average slope of the line at the measurement temperature and standard temperature was used to correct the probe reading:

$$C= [(0.0012*T_s +0.032)/2]*(25-T_s) + P \quad (4)$$

Where C is the corrected probe reading, T_s is the stem temperature (°C) and P is the CS616 probe reading in μs. When converted to water content, the temperature effect increased the TDR reading by about 3% over a 25°C range. Since a typical diurnal

temperature change in the study trees was only a few degrees, temperature did not have a large effect on probe reading, but this correction factor removed the small variation due to temperature.

Heartwood volume and water content estimates

The heartwood volume for estimating total volume of water absorbed by and withdrawn from the heartwood was estimated based on allometric equations from white oak trees in North Carolina, 160 km from this study site and at a higher elevation (Martin et al. 1998). The heartwood volume was calculated by estimating the total volume of the tree (calculated using the diameter outside the bark), and subtracting the sapwood volume.

The volume of water withdrawn (or stored) daily from the heartwood was calculated by multiplying the heartwood volume by the volumetric water content (at 15-minute intervals) and summing the water losses (or gains) over each day.

Increment cores were used to check the accuracy of the VWR probes. The volumetric water content of the heartwood of those cores was determined by measuring the initial volume and wet weight of the cores, drying the cores to determine the amount of water in the wet cores, and dividing the water volume by the original core volume. Dry wood density was also calculated. A paired t-test indicated no significant difference between the sensor readings or the manual calculations ($p=0.66$).

Heartwood moisture release curves

Moisture release curves were generated using water potential readings measured with a WP-4 dewpoint potentiometer (Decagon Devices, Pullman WA). Two heartwood cores were removed from each study tree with an increment borer and placed in glass vials in a cooler, and their length and initial weight were recorded. One core from each tree was placed in deionized water overnight to saturate the tissue. The saturated cores were drained and blotted before water potential measurement. The water potential of the heartwood cores was measured, and the cores were allowed to dry 0.5-1 hour before being wrapped in Parafilm and stored in glass vials in a refrigerator overnight to allow the moisture level to re-equilibrate throughout the heartwood tissue. The water potential of each core was measured 11-18 times as it dried, and the cores were dried at 65° to determine the dry weight and calculate the volumetric water content of the cores at each reading.

Statistical analysis

Statistical analyses (t tests, regressions and standard error calculations) were performed using SAS 8 (SAS Institute, Cary NC), Excel and Sigmaplot.

RESULTS

Climate

Climate data are shown in Figure 4. Average daily temperature peaked in July 2004 at 25.4ºC and declined to a minimum of 5.6ºC in December 2004. The average

daily temperature stayed low in January 2005 and increased for the remainder of the study period until June 2005 (Figure 4A). Daytime average VPD peaked at 0.75 kPa during June, a period of high temperature and low rainfall (Figure 4E) and decreased over the summer. VPD stayed relatively low from September 2004 until March 2005, ranging from 0.12 to 0.33 kPa, and increased to 0.46 kPa in April 2005. VPD changed relatively little from April (0.46 kPa) to May (0.48 kPa) 2005. Error bars show the standard error of the mean of the 5 TDR probe readings. Soil moisture was relatively high during the entire study period, and average soil moisture ranged from 0.22 g cm^{-3} in July 2004 to 0.38 g cm^{-3} in February 2005. Soil moisture was lower during June-August 2004 but increased from September to November 2004 and stayed above 0.30 g cm^{-3} from November 2004-April 2005 before decreasing in May 2005. PAR levels were highest in June 2004 (977 mols m^{-2} $month^{-1}$), decreased steadily until December (202 mols m^{-2} $month^{-1}$) and increased until May 2005 (868 mols m^{-2} $month^{-1}$). Monthly rainfall varied from month to month, ranging from 266 mm in September 2004 to 24 mm in October 2004.

Sapwood water transport

Daily water use

There was a strong diurnal pattern in daily tree water use, with sap flow beginning after dawn, peaking in early afternoon and declining in the evening in all trees. This is illustrated in Figure 5. This figure shows tree water use for August 18-19 2004, which were sunny days in the middle of the growing season. The smaller trees (Trees 1-3) used less water than the larger trees (Trees 4 and 5), and the daily patterns were somewhat

different, with the largest tree maintaining peak sap flux for a shorter period of time than the smaller trees (Figure 5).

Mean daily sap flux averaged over time increased linearly with sapwood area (Figure 6). Tree 3 had the smallest amount of sapwood area (234 cm^2) and also had the smallest sap flux in daytime (30 L d^{-1}) and nighttime (1.4 L d^{-1}). Tree 5 had the largest sapwood area (510 cm^2) and had the highest daytime (113 L d^{-1}) and nighttime (5.8 L d^{-1}) sap flux of the 5 trees studied (Table 2). Smaller trees (1-3) had an average daily sap flux of 42.5 (SE=1.2) L d^{-1} and the larger trees (4-5) had an average daily sap flux of 112.3 (SE=2.9) L d^{-1} (Table 2) over the measurement period from day 149-331 (28 May to 26 November), 2004.

When sap flux was plotted on a sapwood area basis, i.e., sap flux density (g m^{-2} s^{-1}) for the two days shown in Figure 5, a similar pattern to that in Figure 5 was seen, but Trees 1-4 had similar sap flux densities throughout the day indicating that sap flux was correlated with sapwood area (Figure 7). However the largest tree (Tree 5), had a higher sap flux density than the other four trees. All 5 trees had similar sap flux densities when sap flux started and ended with dawn and dusk each day. There was some variation from day to day; for example, on day 231 the sap flux densities of Trees 1-4 were closer (ranging from 55-75 g m^{-2} s^{-1}) than on day 232 when Trees 1 and 4 had higher sap flux densities than Trees 2 and 3 (ranging from 50-80 g cm^{-2} s^{-1}) during late morning and early afternoon. Tree 5 had the highest sap flux density on both days (105 and 115 g m^{-2} s^{-1} on days 231 and 232) (Figure 7).

Figure 8 shows the daily sapwood water flux for each tree in g cm^{-2} d^{-1}. The larger trees, tree numbers 4 and 5, usually had the highest water fluxes. Daily sap flow

was generally similar from day to day over the growing season until day 250 and then gradually decreased until the end of the measurement period (Figure 8).

Sap flow sensors installed at 1.3 and 4 m height in each tree were intended to show times and quantities of water withdrawal and recharge in the sapwood. Lags in the onset of lower sap flow were expected in the mornings and it was expected that upper sap flow would end before lower sap flow in the evenings. However, Figure 9 shows that there was not a consistent difference in sap flow rates in upper and lower sensors in the small (Tree 1) and large (Tree 5) trees. Because the upper and lower sap flow rates were so similar, especially with the onset of sap flow in the morning, these data did not yield sapwood water storage amounts.

Daily sap flux was regressed against environmental variables to find the best predictor of water use. Figure 10 shows the relationship between the 5-tree average total sap flux (g m^{-2} d^{-1}) and daily total PAR (mol m^{-2} d^{-1}), daytime average VPD (kPa) or daily average temperature (ºC) (Figures 10 A, B and C). All three environmental variables were linearly related to water use, but daily total PAR was the best predictor of daily sap flux (r^2=0.75) (Figure 10A). Daytime VPD was also a reasonable predictor of sap flux (r^2=0.62) (Figure 10B), and temperature was the worst predictor (r^2=0.47) (Figure 10 C).

Long (10 cm) sap flow probes were installed to measure the radial profile of sap flow in the trees. Because the heated probe extended into the heartwood where little water turnover occurred, the heat conducted along the sensor and accurate sap flow rates were not recorded. Even so, the data recorded by the outer two thermocouples (at 1 and 3 cm deep in the sapwood) can be used to show relative rates of sap flow in outer and inner

sapwood. Relative sap flow rates of outer and inner sapwood in a small tree (Tree 1, with 3.3 cm sapwood) and a large tree (Tree 5, with 3.1 cm sapwood) are shown for 3 days in August 2004 in Figure 11. Sap flow was detected in all visible sapwood rings, and sap flow in the inner sapwood was less than sap flow in the outer sapwood. In the smaller tree (Tree 1), inner sapwood sap flow reached about 50% of the outer sapwood sap flow rate, and in the larger tree (Tree 5) inner sap flow was typically around 20% of the outer sap flow rate (Figure 11).

Nightly water use

Nighttime sap flow is an estimate of the water withdrawn from sapwood water storage during the day and replaced at night. Figure 12 shows the relationship between daytime sap flow (from 6:00 to 19:45) and sap flow the following night (20:00 until 5:45 the next morning). There was a weak positive correlation (r^2=0.40) between daytime and nighttime sap flow; with increasing daytime sap flow more water was replaced in the sapwood the following night. Sapwood capacitance, or the amount of nighttime sapwood recharge, increased linearly with increasing tree water use. Larger trees used more water than the smaller trees and had higher capacitances, but the percent of daytime water use replaced at night was not higher in the large trees than the small trees. Table 2 lists daytime and nighttime sap flow for each tree, and the percent of daytime water use that was replaced at night. Nighttime sapwood recharge average values ranged from 1.4 L night^{-1} in Tree 2 to 5.82 L night^{-1} in Tree 5 (Table 2). The percent of daytime sap flow replaced at night ranged from 3.7% in Tree 4 to 5.1% in Trees 2 and 5, and the 5-tree

average amount of nighttime sapwood recharge was 4.5% of the daytime water use (Table 2).

Heartwood water relations

Moisture release curves

Figure 13 shows moisture releases for heartwood, made by progressively drying heartwood increment cores from each tree and measuring their water potential in a dewpoint potentiometer. This graph illustrates the relationship between the water potential (MPa) and volumetric water content (g cm^{-3}) of the heartwood. The resulting curve has two sections: a region above ψ=-2 MPa, where there is no clear relationship between water potential and water content, and below ψ=-2 MPa, where water potential declines sharply (Figure 13). The highest water content measured in the cores was 0.66 g cm^{-3}, with a water potential of -1.41 MPa, and the lowest water content was 0.25 g cm^{-3} with a water potential of -14.7 MPa. The water content in the region above ψ=-2 MPa where of Figure 13 is about the same as the actual range of water content measured in the heartwood of the study trees, 0.43-0.69 g cm^{-3} (Table 4). This suggests that the water potential in the heartwood always stays above -2 MPa and may not fluctuate much with changing heartwood water contents.

Variation in heartwood volumetric water content

Heartwood water content was measured for 354 out of 362 days from 3 June 2004 to 31 May 2005. Missing data were due to operator error (accidentally tripping the circuit breaker) or temporary datalogger removal. Table 3 lists the heartwood volume (L)

of each tree, which ranged from 4764 L in Tree 3 to 21674 L in Tree 5. The range of volumetric water content measured over the study period was similar for each tree, but the smaller trees (Trees 1-3) had a slightly higher and wider range of water content than the larger trees (Trees 4-5). For example, compare the water content range of Tree 2 (0.47-0.67 g cm^{-3}) with that of Tree 4 (0.46-0.60 g cm^{-3}) (Table 3). The average heartwood water content for individual trees over the study period ranged from 0.50 g cm^{-3} in Tree 5 to 0.62 g cm^{-3} in Tree 1 (Table 3). Daily changes in heartwood water content and daily heartwood water loss were slightly smaller on average when only growing season data were averaged; however, results varied somewhat between trees (Table 3).

On some days more water was absorbed by the heartwood of each tree than was released, but on other days more water was released by the heartwood than was gained. When averaged on longer timescales (week to month) there was little difference between the average amount of water gained and lost by heartwood. Table 3 presents the average amount of water loss and gain by individual trees on a daily basis. Due to variation in the timing of high and low water content values on different days and in different trees, changes in water content were calculated by summing all gains and all losses in water content over each day. For example, on some days the heartwood gained water from midnight to early morning, lost water in the morning and afternoon and then gained water in the evening. Water gained in the early morning and evening was summed for water gained, and the water lost during the day was summed to calculate water lost. Average daily increases and decreases in the volumetric water content of individual trees ranged from 0.0072 g cm^{-3} in Tree 4 to 0.034 g cm^{-3} in Tree 1. When these changes in water

content were multiplied by the heartwood volume in each tree, daily heartwood water exchange volumes (the volume of water gained and lost in the heartwood on a daily basis) were obtained. Tree 2 (a small tree) had the lowest average daily heartwood water exchange (7.8 L d^{-1}), because of its low daily change in water content (0.015 g cm^{-3}) despite having the highest heartwood volume of the small trees (Trees 1-3). Tree 5 (a large tree) had the highest daily water exchange (25.9 L d^{-1}) even though it had a low daily change in water content (0.012 g cm-3), because of its large volume of heartwood (Table 3). The large trees may have had lower daily water turnover rates than the smaller trees because the inner, older heartwood may be less permeable to water than the outer heartwood, or there may be more resistance to water movement through the heartwood tissue as heartwood depth increases.

Seasonal patterns

Figure 14 shows the 5-tree average heartwood water content plotted by month from June 2004 to May 2005; error bars are the standard error of the monthly average water contents. The average heartwood water content increased over the growing season from 0.53 g cm^{-3} in June 2004 to 0.61 g cm^{-3} in October 2004. Then, the heartwood water content decreased in November, and reached 0.54 g cm^{-3} in December 2004. The average water content stayed low over the winter through February 2005, and then the water content increased throughout the spring to 0.62 g cm^{-3} in May 2005 (Figure 14). This cyclical pattern may be related to tree water use, since the heartwood gained water during the summer growing season and in the spring when the trees were becoming

physiologically active, and the heartwood dried out in the winter when sap flow and physiological activity were minimal.

It is possible that temperature affects the heartwood water content. Figure 15 shows the monthly air temperature plotted with the monthly average stem temperature. From October 2004 to May 2005 the temperature and water content curves follow a similar pattern (Figure 15). From June to September 2004 the temperature line generally decreased while the water content line increased (Figure 15). This could mean that temperature does not affect the heartwood water content as much as physiological processes in the tree during the most active part of the growing season (through September). Or, it could be a coincidence that the temperature and water content curves were related from October to May. Temperature may be a useful predictor of water content even if it does not cause changes in heartwood water content.

Table 4 lists environmental variables that were analyzed as predictors of heartwood water content at daily, weekly and monthly timescales. Rain, soil moisture, air temperature, VPD, and PAR were the single-variable predictors, and the best 2-variable predictors of the variable combinations were temperature + soil moisture and VPD + soil moisture (Table 4). On a daily timescale, air temperature was the best individual predictor for the small trees (Trees 1-3, r^2 ranging from 0.33 to 0.36) and VPD was the best individual predictor of heartwood water content in the large trees (Trees 4-5, r^2 0.11 and 0.13), although soil moisture had a slightly higher r^2 value for Tree 5 (r^2=0.16). The 5-tree average heartwood water content was best predicted by temperature (r^2=0.21), but this increased to r^2=0.31 for both the two-variable analyses (Table 4). The combination of air temperature + soil moisture increased the r^2 value of all trees except

Tree 4, with individual tree water content r^2 values ranging from 0.07 in Tree 4 to 0.45 in Tree 1. Using VPD + soil moisture as predictors, the individual tree r^2 values were considerably lower in the smaller trees (r^2=0.05 in Trees 1 and 3, and 0.12 in Tree 2) and somewhat higher in the larger trees (r^2=0.12 in Tree 4 and 0.19 in Tree 5), but the 5-tree average r^2 value was the same (r^2=0.31) for both 2-variable analyses.

When weekly heartwood VWC averages were considered the r^2 values improved, but not substantially (Table 4). Air temperature and VPD were still the best predictors of water content in the small and large trees, with air temperature r^2 values ranging from 0.35 in Trees 1 and 3 to 0.39 in Tree 2 and VPD r^2 values of 0.13 in Tree 4 and 0.19 in Tree 5. When air temperature and VPD were combined to predict heartwood water content the r^2 value of the smaller trees improved (to r^2=0.43-0.49), while VPD + soil moisture slightly improved the r^2 in the larger trees (to r^2=0.14 and 0.20) (Table 4). The 5-tree average water contents were best predicted by air temperature (r^2=0.2) and air temperature + soil moisture (r^2=0.3), but 5-tree average heartwood water contents were not predicted by VPD + soil moisture at the weekly timescale (r^2=0.07) (Table 4).

None of the environmental variables measured were good predictors of heartwood water content of individual trees (Table 4). Soil moisture and VPD were the predictors with the most consistent r^2 values across all individual trees, with the soil moisture r^2 ranging from 0.12 in Tree 4 to 0.27 in Tree 2 and the VPD r^2 value ranging from 0.11 in Tree 1 to 0.21 in Tree 5. Air temperature and PAR, which are autocorrelated, were similar predictors- they predicted the heartwood water content moderately for the smaller trees (r^2=0.3 to 0.39 for temperature and r^2=0.31 to 0.46 for PAR) and did not predict the heartwood water content of the larger trees well ($r^2 \leq 0.08$). The combination of air

temperature + soil moisture was the best predictor of water content in individual trees and the 5-tree average water content with individual r^2 values ranging from 0.13 in Tree 4 to 0.42 in Tree 2 (Table 4). The 5-tree average was predicted almost equally well by PAR (r^2=0.18) and air temperature + soil moisture (r^2=0.17). However, air temperature + soil moisture could predict the heartwood water content in each individual tree moderately well ($r^2 \geq 0.13$) but PAR only predicted the water content of the smaller trees (r^2 ranging from 0.31 to 0.46), and did not predict the water content of the larger trees ($r^2 \leq 0.04$) (Table 4).

Monthly averages of the amount of water lost (or exchanged) daily by the heartwood of each tree is shown in Figure 16. These data are expressed as heartwood water loss in L per cm^2 of sapwood per day (Figure 16 A, L cm^{-2} d^{-1}) to compare large and small tree heartwood water loss in a biologically meaningful way from month to month. When expressed by heartwood volume (Figure 16 B, L m^{-3} d^{-1}) the water losses varied more from tree to tree. Trees 1 and 3 usually had higher heartwood water losses than the other trees, but by sapwood area, Trees 1, 3 and 5 usually had higher heartwood water losses (Figure 16 A). Heartwood water loss varied seasonally and between trees, but all water losses stayed within the range of 0.016-0.087 L cm^{-2} d^{-1} over the study period (Figure 16 A). There was considerable variation in the heartwood water losses between trees and from month to month. The smaller trees (Trees 1-3) exchanged more water in winter than in summer, while Tree 4 had a smaller annual range and Tree 5 had a larger annual range, but neither large tree had a strong annual pattern. The small tree with the widest range of daily heartwood water flux was Tree 1, with a summer minimum heartwood water turnover of 0.032 L cm^{-2} d^{-1} in August 2004, and a winter maximum

daily heartwood water flux of 0.087 L cm^{-2} d^{-1} in January 2005. The large tree with the most variation in monthly heartwood water flux was Tree 5, which had a summer low of 0.031 L cm^{-2} d^{-1} and three almost equally high months, July September and March, with heartwood water loss of between 0.68 and 0.70 L cm^{-2} d^{-1} (Figure 16).

Five-tree averages of heartwood water loss were plotted in Figure 17, with the standard error of individual tree monthly averages shown as error bars. The average heartwood water loss declined from 20.4 L m^{-3} d^{-1} in June 2004 to 14.6 L m^{-3} d^{-1} in August and remained around 15 L m^{-3} d^{-1} through November 2004 (Figure 17).
In December 2004 the daily heartwood water loss increased and stayed between 21.6 and 28.2 L m^{-3} d^{-1} over the winter until April 2005. In May 2005 the daily heartwood water loss decreased to 15.3 L m^{-3} d^{-1}, which is within the range of the previous growing season heartwood water loss rate (Figure 17). This pattern of increased heartwood water loss in the dormant season is counterintuitive, and suggests that physiological activity is not the main driver of heartwood water fluxes. It is especially odd that the largest daily heartwood water fluxes occur in winter when the heartwood water content is low (Figure 14); apparently low availability of heartwood water is not related to low daily heartwood water exchanges. One hypothesis is that soil moisture availability influences the amount of heartwood water flux. Figure 18 shows monthly average soil moisture values plotted over heartwood water loss values. Both soil moisture and heartwood water loss followed similar patterns during the study period; lower in the hot summer when plants were drawing down soil water and higher in the winter when the weather was cool and plants weren't using much water.

Diurnal patterns

On most days, a diurnal pattern in heartwood volumetric water content was evident in the trees. Figure 19 shows diurnal variation in the water content of each tree under two different weather conditions, two hot days in early September 2004 with high VPD (Figure 19 A) and PAR and two cold January 2005 days with low VPD and PAR (Figure 19 B). A diurnal pattern of water content decline in the afternoon and increase at night was observed for Trees 1, 3 and 5, but was not seen for Trees 2 or 4 (Figure 19A). On both days, the heartwood water content of Tree 5 varied a similar amount, while there was a stronger diurnal trend in Trees 1 and 3 on day 248 and a weaker diurnal variation on day 249. In January (Figure 19B), the heartwood water content of the smaller trees (Trees 1-3) declined slightly and then increased on day 387, but on day 388 the heartwood of Trees 1-3 lost water all day. Trees 4 and 5 did not have strong diurnal heartwood water content patterns on days 387-388 (Figure 19B).

Figure 20 shows the heartwood water content of a small (Tree 1, Figure 20A) and large (Tree 5, Figure 20B) tree over 10 days in May and June, 2005. Plotted on the second dependent axis of Figure 20 is the temperature of each tree stem, measured with a thermocouple inserted into each tree. Figures 20 A and B are plotted on different scales to clearly show the changes in heartwood water content in Tree 5. Heartwood water content followed the same pattern as stem temperature, with changes in heartwood water content lagging changes in temperature. There were longer time lags between changes in temperature and water content in the larger tree (Figure 20B) than the smaller tree (Figure 20A), probably due to the larger thermal mass of the larger tree which would slow temperature changes in the stem. Before May 29 2005 the temperature and water content

followed each other closely, but on May 29 a shift occurred where water content and temperature followed the same shapes, but were not overlapping. This shift demonstrates that temperature is not the only factor that is related to changes in heartwood water content; a change in weather conditions or soil moisture may have influenced the water content, causing it to become uncoupled from stem temperature.

From these data we cannot tell whether or not changes in temperature cause changes in heartwood water content. However, if temperature is related to changes in heartwood water content on a daily timescale, the thermal mass of the trees may explain why small trees have more daily variation in water content than large trees. Since smaller trees have less thermal mass their stem temperature can change more quickly than in larger trees, which could cause greater changes in the heartwood water content in the smaller trees. Another possibility is that stem cooling caused by sap flow causes the release of water from the heartwood into the transpiration stream, but daily air temperature fluctuation also causes heartwood water loss in the winter when the trees are dormant.

To demonstrate that changes in volumetric water content were not the result of temperature affecting the TDR probe reading, Figure 21 shows the heartwood water content plotted against the stem temperature in each tree. Data are shown for two days that were also shown in Figure 20; Figure 21A (26 May 2005) shows a day with large diurnal variation in temperature and water content, and Figure 21B (31 May 2005) shows a day with less diurnal variation in temperature and water content. In Figure 21A there is a hysteresis pattern that is more obvious for the smaller trees (Trees 1-3) which had a greater percent change in heartwood water content during the day than the larger trees.

There was not a hysteresis pattern in any tree in Figure 21B on a day with little diurnal water content variation. Because Figure 21A reveals several water contents per temperature in each tree, this shows that changes in water content were not the result of temperature causing changes in the TDR reading.

Table 5 shows correlation coefficients for predicting the volume of heartwood water lost on a daily basis using daily, weekly and monthly averages with rainfall, soil moisture, air temperature, the daily change in temperature, VPD, PAR and soil moisture + VPD. The individual environmental variables correlated poorly with individual and average tree heartwood water losses, but the multiple regression using soil moisture + VPD yielded better r^2 values at weekly and monthly averages.

For daily water loss averages the change in stem temperature was the only individual environmental variable with an r^2 value above 0.09, and only for Trees 1 and 2 (r^2=0.20 and 0.21) (Table 5). The combination of soil moisture + VPD raised r^2 to 0.16 in Tree 1, but not in any other tree, and the 5-tree average water loss was not predicted well by any variable ($r^2 \leq 0.05$). When daily heartwood water losses were calculated by week the r^2 values for soil moisture increased for Tree 1 (r^2=0.23) and the 5-tree average (r^2=0.11), and the r^2 for temperature in Tree 1 also increased (r^2=0.29). The largest increase was seen in change in stem temperature in Tree 1 (r^2=0.45) and Tree 3 (r^2=0.18), with, although r^2 of Tree 2 did not improve over the daily average estimate. Soil moisture + VPD was a better predictor of heartwood water loss at a weekly scale than at a daily scale in small trees but not large trees. Using soil moisture + VPD to predict heartwood water loss, r^2 values increased for Tree 1 (r^2=0.42), Tree 2 (r^2=0.16), Tree 3 (r^2=0.1) and the 5-tree average (r^2=0.18) but not for Tree 4 (r^2=0) or Tree 5 (r^2=0.008)

(Table 5). On a monthly basis there was considerable improvement in the r^2 values of some environmental variables for Trees 1-3 and the 5-tree average, but no improvement in Trees 4 or 5 ($r^2 \leq 0.05$). The daily heartwood water loss of Tree 1 seems to correspond well to most of the environmental variables analyzed (soil moisture, $r^2=0.58$, temperature, $r^2=0.53$, change in temperature $r^2=0.60$, VPD $r^2=0.19$, PAR $r^2=0.11$, soil moisture + VPD $r^2=0.69$). Tree 2, Tree 3 and the 5-tree average were weakly to moderately correlated with soil moisture (Tree 2 $r^2=0.12$, Tree 3 $r^2=0.24$, 5-tree average $r^2=0.35$), change in stem temperature (Tree 2 $r^2=0.31$, Tree 3 $r^2=0.23$, 5-tree average $r^2=0.38$), and soil moisture + VPD (Tree 2 $r^2=0.54$, Tree 3 $r^2=0.26$, 5-tree average $r^2=0.47$) (Table 5). Tree 3 was also weakly correlated with VPD ($r^2=0.12$) (Table 5). Soil moisture + VPD was the best monthly predictor of average heartwood water loss, but it only related to the smaller tree water losses.

Sap flux and heartwood water loss

Figure 22 shows the diurnal pattern of sap flux and heartwood water content in a large tree (Tree 5) and a small tree (Tree 1). The sap flux and heartwood water content diurnal patterns are generally opposite each other, with sap flux occurring during the day and stopping at night, and the heartwood water content increasing at night and declining during the day (Figure 22). In the larger tree, sap flux started at the time when heartwood water content was highest, and the heartwood water content declined and stayed lower while sap flux was high. The heartwood water content increased as sap flux declined and stopped at night. In the smaller tree, the heartwood water content started to decrease in the early morning before sap flux started for the day and started to increase as sap flux

decreased in the afternoon (Figure 22). This suggests that heartwood water loss occurs in response to sap flux, but the pattern of temperature change followed by heartwood water loss (Figure 19) is more closely coupled than the sap flux-heartwood water content pattern seen in Figure 22. The temperature-water content relationship is more consistent throughout the year, including the winter when sap flux does not occur.

Figure 23 shows the tree water use (L) measured by sap flux and the heartwood water loss (L) measured by TDR probes. If the heartwood was used as a storage reservoir to lessen daily water stress, a positive correlation between the volume of sap flux and heartwood water withdrawal would support this hypothesis. Figure 23 shows that this was not the case; in fact, there was almost no relationship between the amount of water used by the tree and the amount of heartwood water loss (r^2=0.05). The water withdrawn from the heartwood is probably used for transpiration, but it does not seem strongly, directly related to tree water demand.

DISCUSSION

Sap flux data

Quercus *sap flux density*

The sap flux density of the white oak trees during this study was as high as 80 g m^{-2} s^{-1} during the day in late August, and the 5-tree average daytime sap flux was 36 g m^{-2} s^{-1}. PAR was the best predictor of sap flux density (r^2=0.75), followed by VPD (r^2=0.62) and temperature (r^2=0.47) (Figure 10). On several days in August and September, the sap flux density of *Quercus rubra* (Michx.) in New York reached 80 g m^{-}

^{2} s^{-1} in the middle of the day (Engel et al. 2002), which is the same as the sap flux density of the trees from this study in late August. In that study, vapor pressure deficit was used to predict tree water use, but there was considerable variation in how well VPD predicted water use between sites and days. The r^2 values for VPD predicting daily sap flux ranged from 0.22 to 0.73 for the days shown (Engel et al. 2002). In a study of *Quercus phellos* (L.) in the Piedmont of North Carolina, trees used somewhat less water than in this study, with a maximum daily mean sap flux density of 54 g m^{-2} s^{-1} (Pataki et al. 1998). However, the *Q. phellos* trees were understory saplings in chambers, and had a different microclimate from the *Q. alba* studied here. PAR and VPD were found to be good predictors of tree water use (Pataki et al. 1998). Decreased VPD and PAR levels would be expected in the microclimate of small understory trees in chambers compared to the VPD and PAR levels that the large, dominant trees in this study were exposed to. This would cause lower demand for water on the trees in Pataki et al (1998) and may explain why the sap flux rates of *Q. phellos* were lower. Another explanation is that *Q. phellos* has inherently lower sap flux rates than *Q. alba*. In another southeastern Piedmont study, three *Quercus* species, *Q. alba*, *Quercus velutina* (Lam.) and *Quercus falcata* (Michx.) also had similar average daytime sap flux densities to the *Q. alba* in this study, with an average sap flux density of 30 g m^{-2} s^{-1} in each species (Oren and Pataki 2001). Oren and Pataki (2001) were able to predict stand water use better than in this study or in the Pataki et al. (1998) study. Total stand transpiration was best predicted with PAR (r^2=0.87) and was also well predicted by VPD (r^2=0.81), but the r^2 values for individual tree species were not listed (Oren and Pataki 2001). Dominant *Q. alba* and *Q. rubra* in Tennessee had much lower sap flux densities than this study found (Wullschleger et al. 2001). Both

Quercus species' typical summer daytime maximum sap flux was around 40 g m^{-2} s^{-1}, which is half the maximum August rate of sap flux found in this study (Wullschleger et al. 2001). Solar radiation (PAR) was the best predictor of tree water use in both the Tennessee and Georgia *Quercus* trees (Wullschleger et al. 2001). Sap flux density in *Q. rubra* in Massachusetts was also lower, reaching 20-30 g m^{-2} s^{-1} during the day in September (Spicer and Holbrook 2005). In addition to possible species differences between *Q. rubra* and *Q. alba*, the VPD in Massachusetts in September should be lower than in Georgia in the summer, when most of the data in this study were taken. Also, September is the end of the growing season in Massachusetts, and lower sap flux rates should occur at the end of the season. It is likely that summer sap flux densities were higher than the 20-30 g m^{-2} s^{-1} measured in September.

Most studies have found *Quercus* daytime sap flux rates lower than the 80 g m^{-2} s^{-1} daytime maximum and 36 g m^{-2} s^{-1} daytime average found in this study; the sap flux rates were probably somewhat overestimated because the sapwood removed to install the TDR probes diverted water to other parts of the stem, increasing the sap flux in other areas. The TDR probes were installed below the sap flow sensors and all sapwood was intact at the height of the sap flow sensors, but it is likely that sap flow was still distorted and not circumferentially even at the sap flow sensor height. Some differences in water use should be expected between studies, though, because of differences in site, microclimate, species and tree size. Studies may have been conducted in above- or below-average rainfall years, which would affect the availability of water and nutrients to trees, and the different microclimates of understory or overstory trees would affect the rate of transpiration and demand for water uptake on trees in different sites.

Some non-*Quercus*, broad-leaved species had similar or lower sap flux densities than the trees in this study. *Carya tomentosa* ((Poir.) Nutt) had an average daytime sap flux of 35 g m^{-2} s^{-1} that was almost identical to that of *Q. alba*, but the sap flux density of both *Liquadambar styraciflua* (L.) and *Acer rubrum* (L.) were somewhat lower (23 and 29 g m^{-2} s^{-1}) (Oren and Pataki 2001). The sap flux densities of these three species were similar to the two *Quercus* species in the same study, but because of their diffuse-porous xylem structure the non-*Quercus* trees conducted more water than the *Quercus* trees. In Wullschleger et al. (2001), *Liriodendron tulipifera* (L.) and *A. rubrum* had lower daily maximum sap flux density rates (approximately 40 and 55 g m^{-2} s^{-1} in the middle of the day) than the *Q. alba* trees in this study, but *Nyssa sylvatica* (Marsh.) had a much higher midday sap flux density (85 g m^{-2} s^{-1}) that was similar to the maximum daily value of *Q. alba* in this study. Although many tree species had more sapwood area than *Q. alba*, the trees in this study had higher maximum sap flux densities than the rates reported for *Q. alba* and co-occurring species in some other studies.

Conducting sapwood depth

This study contributes to the evidence that *Quercus spp.* use several growth rings (≥6) to transport water, not just the current year ring (Hinckley et al. 1978). All the sapwood rings in each *Q. alba* studied conducted some water (Figure 9), though the inner sapwood rings typically conducted 20-50% of the water conducted by the outer rings. This result is similar to Spicer and Holbrook (2005), where 7 sapwood rings of *Q. rubra* growing in Massachusetts conducted water, and the inner sapwood conducted between 20 and 50% of the outer sapwood sap flux density for several days in September. In a lab

experiment of dye taken up by a cut *Q. robur* tree, the outer growth ring conducted the most water, with sap flux decreasing to 5% of the outermost ring in the 9th sapwood ring (Cermak et al. 1992). In that tree there were 20 rings of visible sapwood, and only 9 appeared to conduct water (Cermak et al. 1992). Cochard and Tyree (1990) examined *Quercus alba* and *Q. rubra* xylem vessels for tylose blockages, and found that the percent xylem vessels with tyloses increased in older growth rings. However, tylose formation did not completely block the xylem and 6-year old rings were able to conduct some water (Cochard and Tyree 1990). Water content across the sapwood was examined using CT-scan technology in *Quercus robur* (L.) from Germany (Fromm et al. 2001). That study found similar amounts of water in each sapwood ring (7 rings total). Fromm (2001) hypothesized that because all of the sapwood rings had similar water contents, they may all be important for water storage, but did not investigate water conductance in the stem.

Sapwood capacitance and water storage

Sap flux probes were installed at 1.3 and 3.9 m height to measure sapwood water storage. There was no apparent time lag or large differences in rates of sap flux between the upper and lower probes, so the probes did not yield sapwood storage data. This may be because these *Q. alba* trees had high sap flux rates and only 2.6 m vertical distance between the two sensors. Pataki et al. (1998) also had this problem with *Q. phellos* saplings (2.3 cm^2 basal area); the trees were too small to have detectable patterns of storage and withdrawal of water in their stems. In a study of 20 cm dbh *Quercus mongolica* (Fish) trees, on some days there was no difference between upper and lower sap flux rates, but after a rain storm more water was taken up than was used, and this

extra water was assumed to be stored in the sapwood for future use (Kobayashi and Tanaka 2001). In contrast, sapwood water storage in large (55 cm dbh) *Quercus garryana* (Dougl. ex Hook.) was observed using sap flow probes placed in the crown and at the base of the tree (Phillips et al. 2003). Upper and lower sap flux densities were more similar in small (23 cm dbh) *Q. garryana* than in the large *Q. garryana*, but some sapwood water storage and withdrawal was seen (Phillips et al. 2003). This suggests that *Q. garryana* is able to store more water in its stem than *Q. alba*, but it is more likely that the greater distance between upper and lower sensors used by Pataki et al. (1998) and Kobayashi and Tanaka (2001) made temporal differences discernable, where they were not in this study of *Q. alba*.

Nighttime water uptake was used to estimate sapwood water storage because upper and lower sap flux probes did not provide a good estimate. Nighttime water uptake supplied 0-18% of the water used daily, with an average of 4.5%. Nighttime water uptake in this study increased linearly with daily water use, with larger trees storing and using a larger volume of water than smaller trees, but still only recovering 4.5% of water use at night. Few studies have been done on water storage in *Quercus* spp., but in two studies oak species stored 10-25% of daily water used in their stems, somewhat higher than in *Q. alba* in this study (Kobayashi and Tanaka 2001; Phillips et al. 2003). *Q. mongolica* stored 0-10% of water used daily, depending on soil moisture (Kobayashi and Tanaka 2001), and *Q. garryana* used 9-23% of its daily water from storage (Phillips et al. 2003). Larger *Q. garryana* trees used a larger amount of water from storage (10-23%) than smaller *Q. garryana* (9-13%) (Phillips et al. 2003), which is contrary to the findings

of this study, where smaller and larger *Q. alba* trees used similar percent water from storage (Table 2).

Studies on stem water storage in conifers and tropical hardwoods have also generally found larger percent water stored than in this study. Four diffuse-porous tropical tree species also used 2-3 times (9-15%) the water from storage as was found in this study, with stem capacitance increasing with tree size (Goldstein et al. 1998). While *Thuja occidentalis* (L.) stored a similar amount of water (5-6%) to *Q. alba* (Tyree and Yang 1990), *Pinus ponderosa* (Dougl.) stored more water with increasing stem size; small trees stored 1.5-4.4% and large trees stored 4-20% (Phillips et al. 2003). Both small and large *Pseudotsuga menziesii* (Mirb. Franco) stored more water than *Q. alba*, with daily storage estimates of 7.2% for small trees and 20-25% for large trees (Phillips et al. 2003). Using a similar range of stored water were *Pinus densiflora* (Siebold & Zucc.) (10-29%) (Kobayashi and Tanaka 2001) and *Pinus pinaster* (Ait.), which used an average 12% water from storage, but at the end of a drought the percent stored water use increased to 25% (Loustau et al. 1996). Conifers may have a larger capacity for sapwood water storage compared to ring-porous species because of their large sapwood area and sapwood volume. Lower sap flux rates in conifers may also contribute to the need for water storage in conifers.

While nighttime sap flow can be used as an estimate of tree water storage, studies that use the difference in basal and canopy sap flux found larger percent water withdrawn from storage than in this study. These other studies also report stem recharge at different times during the day (Loustau et al. 1996; Goldstein et al. 1998; Kobayashi and Tanaka 2001; Phillips et al. 2003), where this study was only able to measure nighttime recharge.

If sap flow probes had been installed higher in the stem or in the canopy in this study, it is possible that there may have been detectable differences between lower and upper stem sap flux, which may have revealed afternoon or morning stem recharge and increased the average percent water stored in *Q. alba*.

Water loss from heartwood and whole tree stems

This study found diurnal and seasonal variation in the volumetric water content of the heartwood. Studies reporting stem water content over time are rare, and almost all have focused on water content variation in the sapwood. Some studies have installed TDR probes in the trees, being careful to insert the TDR probe in sapwood only, while other studies have inserted TDR probes perpendicular to the stem, so the probes measured sapwood and heartwood water content together. Because of the paucity of studies on this subject, studies investigating sapwood will be discussed as well as studies measuring whole-stem water content, or only heartwood water content.

Several studies have measured the water content of non-*Quercus* species, finding different patterns of water content variation. Sparks et al. (2001) installed TDR probes in the sapwood of *Pinus contorta* (Dougl. ex Loud) in Idaho and found both diurnal and seasonal variations in sapwood water content. On a daily basis, the sapwood gained and lost 2-5% of the sapwood volumetric water content, within the range of 0.42 and 0.49 g cm^{-3}, between days 135 and 150, 1997 (Sparks et al. 2001). The sapwood in Sparks et al. (2001) had slightly lower average water contents than the *Q. alba* heartwood in this study, and slightly larger diurnal variation in water content. The larger percent diurnal variation in *P. contorta* may be because sapwood transports water more effectively than

heartwood, or it could be due to the greater water stress expected in a dry climate. The diurnal pattern of sapwood water content found in *P. contorta* is almost identical to the diurnal pattern found in *Q. alba* in this study, with water content increasing at night to an early morning high water content, and decreasing during the day before refilling in late afternoon (Sparks et al. 2001). Over the growing season from April to October 1997, the sapwood water content of *P. contorta* ranged from 0.42 to 0.54 g cm^{-3} (Sparks et al. 2001), which is similar to the annual range of *Q. alba* heartwood (0.10 to 0.20 g cm^{-3} annual range, depending on the study tree).

The sapwood of each tree species measured gravimetrically by Clark and Gibbs (1957) had a different annual moisture content pattern, and they all varied from the annual heartwood water content pattern in *Q. alba*. In *Thuja occidentalis*, *A. balsamea* and *Picea rubens* (Sarg.), the sapwood water content increased and decreased dramatically several times during the measurement period without a clear annual pattern (Clark and Gibbs 1957).

Constantz and Murphy (1990) used 13-cm TDR probes inserted through the bark, sapwood and into the heartwood of *Quercus agrifolia* (Nee) and *Quercus lobata* (Nee) in California to measure the stem water content for 1-2 year periods. Depending on bark depth, the probes probably measured 2-3 cm bark, 2-3 cm sapwood and 7-9 cm heartwood, so the TDR readings were strongly affected by the water content of the heartwood. Diurnal patterns were not described in these trees, but the annual range of these *Quercus* spp. were similar but slightly larger than the range found in *Q. alba*; 0.36 to 0.66 g cm^{-3} in *Q. agrifolia* and 0.37 to 0.71 g cm^{-3} in *Q. lobata* (Constantz and Murphy 1990). *Quercus* trees in Georgia would typically experience less drought than those in

California where the Constantz and Murphy (1990) study took place. This may be the explanation for the higher volumetric water contents and narrower range of heartwood water contents found in *Q. alba* in this study.

Using 15-cm TDR probes, Wullschleger et al. (1996) monitored the stem water content (sapwood and heartwood) of *Q. alba* and *Quercus prinus* (L.) monthly in 1994 and 1995. Both *Quercus* species had nearly identical patterns of water content in each year, suggesting that climate affected those two species similarly, but *Q. prinus* had a higher water content in both years. In 1994, a wet year, *Q. alba* had an average water content of 0.47 g cm^{-3}, with a monthly average range of 0.35 to 0.55 g cm^{-3}, and the average water content of *Q. prinus* was 0.49 g cm^{-3} with a monthly average range of 0.45 to 0.65 g cm^{-3} (Wullschleger et al. 1996). The following year, 1995, was a dry year and both species had slightly higher water contents; *Q. alba* had an average value of 0.50 with a monthly average range of 0.40 to 0.50 g cm^{-3}, and *Q. prinus* had an average value of 0.53 g cm^{-3} with a monthly average range of 0.45-0.65 g cm^{-3} (Wullschleger et al. 1996). In both species, the annual average water content and range of monthly averages were less than the annual average (0.57 g cm^{-3}) and range of monthly averages (0.53-0.62 g cm^{-3}) found in *Q. alba* in this study. The annual pattern (April-December) of stem water content measured by Wullschleger et al. (1996) had increasing water contents in the spring, higher water contents with little variation in the summer, and declining stem water contents in the winter. Since this pattern was found in both *Quercus* species over two years (Wullschleger et al. 1996) as well as in *Q. alba* in this study, it is possible that this pattern of stem water content occurs every year in Southeastern region *Quercus*, but

the magnitude of annual variation probably changes with the climate conditions each year and from location to location.

In a brief study using gamma radiation, Brough et al. (1986) found that irrigated and unirrigated *Malus pumilia* (P. Miller) whole tree stems (sapwood and heartwood) lost 0.9-0.16 g cm^{-3} xylem water content on two summer days in 1982, but regained most of the xylem water deficit by late afternoon of each day. Irrigated trees lost about 4% less water than unirrigated trees (Brough et al. 1986). Data for *M. pumilia* were given for the hours of 6:00-20:00, and the diurnal pattern of water loss within that time was similar to *Q. alba*; the highest water content was measured at 6:00, the stem water content declined to 14:00-16:00, and then the water content increased for the rest of the afternoon (Brough et al. 1986).

TDR probes (7 cm long) installed across the stem of unirrigated *Citrus limon* ((L.) Burman f.) trees in Israel were measured three times a day every few days from June 24 to September 7 2001 (Nadler et al. 2003). The beginning water content of *C. limon* was lower than any value recorded in *Q. alba* over the year of data collection, and the water content of *C. limon* continued to decline because the trees did not receive any irrigation or rain. During the experiment the water content in these trees declined 17% from 0.37 to 0.20 g cm^{-3}, and had diurnal water content changes of up to 5% daily (Nadler et al. 2003). The timing of diurnal stem water content changes were not described (Nadler et al. 2003).

The diurnal patterns of stem water content in the Asian tree *Quercus mongolica* were strikingly different from the North American *Quercus* species. *Q. mongolica* was measured at several heights using TDR probes inserted into the stem through the sapwood and heartwood, and had extremely low stem water content values. The stem

water content declined from the bottom (1-2 m high) to the top (7 m high) of the stem (0.26 to 0.12 g cm^{-3} in August 1996 and 0.30 to 0.15 g cm^{-3} in August 1997) (Kobayashi and Tanaka 2001); all values reported were drier than any water content value reported for *Q. alba* (Wullschleger et al., 1996, or this study), *Q. lobata* or *Q. agrifolia* (Constantz and Murphy 1990). They also reported was almost no diurnal variation (2%) in stem water content over a two day sampling period (24-25 August 1996) (Kobayashi and Tanaka 2001). In a repeat of the measurements in August 1997 there was more diurnal variation with diurnal changes from almost 0 to 5% (Kobayashi and Tanaka 2001). Although Kobayashi and Tanaka (2001) attributed the diurnal changes in water content to changes in sapwood water storage, their TDR probes extended into the heartwood and some of the variation may have been due to heartwood water content changes (Kobayashi and Tanaka 2001).

Monthly harvests of *Thuja occidentalis* and *Picea rubens* (Sarg.) showed relatively little variation in moisture content over the measurement period, but *Abies balsamea* (L. (Mill.)) heartwood had a springtime high water content with late summer and winter low water contents (Clark and Gibbs 1957). Sparks et al. (2001) measured *P. contorta* heartwood water contents ranging from 0.18 to 0.35 g cm^{-3} from April to October 1997. *P. contorta* water contents were higher in the spring and summer, except for a mid-May decline and recovery, and lower from July to October (Sparks et al. 2001). The trees in Clark and Gibbs (1957) had less annual variation than *Q. alba* in this study, but *P. contorta* had a similar seasonal range to *Q. alba*, but at a lower water content.

Environmental variables correlate poorly with heartwood water content at different timescales

Heartwood water content followed a similar pattern to temperature on a daily basis, and was related to temperature and soil moisture on a seasonal time scale. As stem water contents were averaged over longer timescales, the relationship between individual trees and some environmental variables became stronger, but variation between individual trees was large and 5-tree average r^2 values were low. None of the environmental variables monitored corresponded well to all 5 trees; the 5-tree average r^2 values seemed to be due to the disproportionate influence of either Trees 1-3 or Trees 4-5. Soil moisture was the variable with the most consistent relationship to each individual tree, but the 5-tree average was still very low (r^2=0.05). Soil moisture availability increased in winter when tree water use stops, and VPD was low in winter; the combination of these two factors created the best predictor of heartwood water loss on a monthly timescale. Air temperature had a stronger relationship to heartwood moisture content than soil moisture (but not soil moisture + VPD) except in Tree 4, which did not correlate well with any environmental variable. Incorporating the volume to surface area ratio of the heartwood may improve models by helping to predict water loss by trees of different sizes; trees with more heartwood had less water loss than trees with smaller heartwood volumes.

Questioning the diurnal TDR-temperature relationship

Because changes in the volumetric water content of the heartwood follow a similar shape (regardless of offset) to stem temperature (Figure 20), but more logical

biological drivers such as PAR or VPD are not closely coupled with water content, it would be reasonable to assume that temperature changes are affecting the TDR probe reading. However, there are several reasons to believe that diurnal changes in heartwood water content actually do occur and are not just an artifact of temperature changes. One way temperature could affect the probe reading is through the thermal expansion of water, where warmer water expands and has a larger volume, even though there is the same amount of water. Thermal expansion of water does not account for the magnitude of water content change seen in these trees; its effect on water volume over the daily temperature change found in the study trees is too small- usually between 0.1 and 0.5 L d^{-1} while 5-tree monthly average heartwood water losses ranged from 11.9 to 21.5 L d^{-1}.

When performing the temperature calibration of the TDR reading in the growth chamber, temperature affected the TDR reading in a predictable way and these data were used to correct the field data. The apparent change in volumetric water content that resulted from temperature changes in the growth chamber was a change of 3% VWC (from 0.41 to 0.44 g cm^{-3}) over a 25ºC change in temperature. However, in the field the average diurnal change was 1 to 3.5% VWC while the diurnal change in stem temperature was only 1-3.5ºC. Because the temperature effect on the TDR reading in the growth chamber was much smaller than the change in water content and stem temperature observed in the field, changes in heartwood volumetric water content recorded in the field cannot be attributed to the effect of temperature on the TDR probes.

The water content and stem temperature TDR probe calibrations were each done with a single stem section, and the volumetric water content calibration was done at one temperature, while the temperature calibration was done at a constant volumetric water

content. There may be a temperature-volumetric water content interaction that results in different slopes of the calibration curves at different temperatures or water contents that were not measured here. This possible interaction might slightly exaggerate or depress diurnal water content variation or water content values at all timescales.

The close daily relationship between stem temperature and variation in water content was not seen during the experimental manipulation of temperature during TDR calibration in the growth chamber, and is not likely an artifact of the TDR probe sensitivity, which suggests that temperature may partially drive increases and decreases in heartwood water content. Apparently, the heartwood must be connected to a water source (either the rest of the tree or to the soil) for changes in water content with temperature changes to occur.

Conclusions

Quercus alba had a relatively high sap flux rate with low sapwood capacitance. Daily tree sap flux densities were well-correlated with PAR, and inner sapwood conducted a portion of the outer sapwood sap flux. There were daily and seasonal cycles in the heartwood water content of the study trees. Heartwood volumetric water content increased over the 2004 growing season, decreased sharply with the onset of winter, and increased in the spring of 2005. Part of the annual cycle was similar to the monthly air temperature cycle, and diurnal variation in heartwood water content was related to changes in stem temperature and soil moisture.

The hypotheses that the heartwood water content would vary diurnally and seasonally, and that water loss would occur in the day while water gain would happen at

night were accepted. Heartwood water loss was not directly related to tree water use, so the hypotheses that heartwood water loss would be related to sap flux were rejected.

It was surprising to find that diurnal heartwood water gains and losses happened year round, even in winter when the tree was assumed to be physiologically inactive. Seasonal and diurnal heartwood water loss and water content did not seem to be related to sapwood water use during the growing season. When water leaves *Q. alba* heartwood it should go into adjacent sapwood and enter the transpiration stream, making the heartwood an area of stem capacitance contributing to the water relations of *Q. alba* on a daily basis. However, winter daily heartwood water fluxes and lack of correlation between sapwood and heartwood water flux make this logical relationship uncertain.

If stem temperature does affect heartwood water losses and gains, daily heartwood water losses could be triggered by sap flow in the sapwood. As water flows through the xylem it cools the stem, and may cause the heartwood to release water into the xylem stream. Faster sap flow rates, indicating higher water demand, would cool the stem more and cause more water to leave the stem. However, there was no relationship between the amount of water used by the tree (daily sap flux) and the amount of water lost by the heartwood; the relationship seems more related to temperature change than any physiological factor. Diurnal temperature variation in winter could cause the same effect, with daily warming and cooling of the stem causing heartwood water increases and decreases, despite the tree not needing water at that time of year. Soil moisture availability was also increased in winter, and may have allowed the increased daily water gains and losses that occurred in winter. Seasonal heartwood water content changes also

appear related to stem temperature. In warmer months the heartwood water content was higher, but dropped with declining temperature in the winter.

This study has uncovered a new pattern in *Quercus* water relations and opens many possibilities for future research on heartwood water loss and modeling water content and loss in small and large trees. *Q. alba* heartwood exchanges water on a daily basis that seems closely related to changes in stem temperature, and closely related to temperature changes and soil moisture availability on longer timescales. Water stored and released from the heartwood probably benefits *Q, alba* and allows more carbon uptake than if the heartwood was truly excluded from the tree water pathway.

Table 1. Characteristics of five *Q. alba* trees used in study of heartwood water content in the Piedmont of Georgia.

Tree#	1	2	3	4	5	average
diameter (cm)	36.4	34.9	35.2	52.7	57.8	
slope position	middle	middle	upper	middle	upper	
sapwood density (SE)	0.66	0.62	0.64	0.58	0.57	0.61 (0.02)
heartwood density (SE)	0.69	0.64	0.69	0.69	0.61	0.66 (0.02)

Table 2. Daily and nightly water use between days 149-331 (28 May-26 Nov.) 2004. Daytime data are from 6:00-19:45; nighttime data are from 20:00-5:45 for five *Q. alba* trees in the Piedmont of Georgia.

	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Average
Sapwood depth (cm)	3.3	3	2.4	3.4	3.1	3
Sapwood area (cm^2)	318	292	234	486	510	368
Avg daytime water use (L)	44.22	53.67	30.11	111.3	113.29	70.5
Avg nighttime sap flux (L)	1.9	2.73	1.36	4.1	5.82	3.2
% daily water used replaced at night	4.3	5.1	4.5	3.7	5.1	4.5

Table 3. Heartwood volumes, volumetric water content (VWC) and water dynamics from June 3 2004 to May 31 2005 for each tree. Trees 1-3 were smaller (35-36 cm dbh) and Trees 4-5 were larger (53-58 cm dbh).

	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Average
Heartwood volume (L^3)	5132	5164	4764	14358	21674	10218
Range of VWC (g cm^{-3})	0.53-0.66	0.47-0.67	0.47-0.63	0.46-0.60	0.44-0.54	0.47-0.62
Avg VWC (g cm^{-3})	0.62	0.6	0.59	0.54	0.5	0.57
Avg daily change in VWC (g cm^{-3})	0.034	0.015	0.026	0.0072	0.012	0.019
Avg daily water lost from heartwood (L d^{-1})	17.3	7.8	12.2	10.2	25.9	14.7
Avg daily change in VWC, growing season data only	0.024	0.013	0.023	0.0069	0.013	0.016
Avg daily water lost from heartwood, growing season data only	12.3	6.7	11	9.9	28.2	13.6

Table 4. Correlation coefficient values from single and multiple regressions indicating how well environmental variables correlated with heartwood volumetric water contents averaged over different lengths of time: daily, weekly and monthly. Data are shown for individual trees and the 5-tree average heartwood water content.

	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Average
Daily averages						
Rain	0.02	0.005	0.03	0.009	0.007	0.02
Soil Moisture	0.05	0.11	0.05	0.07	0.16	0.02
Air Temp	0.34	0.36	0.33	0.03	0.08	0.21
VPD	0.004	0.018	0.006	0.11	0.13	0.0002
PAR	0.02	0.1	0.04	0.05	0.06	0.02
Air Temp + Soil Moisture	0.45	0.39	0.42	0.07	0.16	0.31
VPD + Soil Moisture	0.05	0.12	0.05	0.12	0.19	0.31
Weekly averages						
Rain	0.05	0.01	0.05	0.02	0.02	0.04
Soil Moisture	0.08	0.16	0.1	0.05	0.15	0.04
Air Temp	0.35	0.39	0.35	0.02	0.08	0.2
VPD	0.009	0.04	0.03	0.13	0.19	0.0001
PAR	0.09	0.19	0.13	0.05	0.07	0.06
Air Temp + Soil Moisture	0.49	0.43	0.45	0.06	0.15	0.3
VPD + Soil Moisture	0.11	0.17	0.11	0.14	0.2	0.07
Monthly averages						
Rain	0.02	0.001	<.001	0.03	0.02	0.01
Soil Moisture	0.22	0.27	0.19	0.12	0.24	0.05
Air Temp	0.34	0.39	0.3	0.08	0.2	0.11
VPD	0.11	0.13	0.2	0.14	0.21	0.02
PAR	0.31	0.33	0.46	0.02	0.04	0.18
Air Temp + Soil Moisture	0.38	0.42	0.36	0.13	0.24	0.17
VPD + Soil Moisture	0.23	0.29	0.21	0.15	0.25	0.06

Table 5. Correlation coefficient values from single and multiple regressions indicating how well environmental variables correlated with heartwood water loss (L d^{-1}) in individual trees and the 5-tree average. Data are shown for daily heartwood water losses averaged daily, weekly and monthly. Soil moisture + VPD was the best predictor of 5-tree average water losses on a monthly basis.

	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Average
Daily Averages						
Rainfall	0.02	0.02	0.006	0.06	0.05	0.05
Soil Moisture	0.08	0.02	0.02	0.01	0.002	0.003
Temperature	0.09	0.003	0.009	0.0002	0.002	0.002
Change in stem temperature	0.2	0.21	0.009	0.1	0.001	0.0002
VPD	0.004	0.009	0.001	0.01	0.002	0.002
PAR	0.002	0.03	0.01	0.01	0.01	0.01
Soil Moisture + VPD	0.16	0.06	0.04	0.01	0.003	0.003
Weekly Averages						
Rainfall	0.01	0.02	0.0001	0.02	0.01	0.005
Soil Moisture	0.23	0.04	0.07	0	0.0008	0.11
Temperature	0.29	0.02	0.06	0.005	0.005	0.09
Change in stem temperature	0.45	0.21	0.18	0.01	0.02	0.3
VPD	0.02	0.007	0.006	0	0.002	0.003
PAR	0.04	0.02	0.002	0.005	0.004	0.02
Soil Moisture + VPD	0.42	0.16	0.1	0	0.008	0.18
Monthly Averages						
Rainfall	0.0009	0.05	0.05	0.05	0.05	0.03
Soil Moisture	0.58	0.12	0.24	0.005	0.004	0.35
Temperature	0.53	0.02	0.13	0.03	0.005	0.21
Change in stem temperature	0.6	0.31	0.23	0.009	0.02	0.38
VPD	0.19	0.007	0.12	0.0005	0.0007	0.08
PAR	0.11	0.08	0.03	0.002	0.0002	0.03
Soil Moisture + VPD	0.69	0.54	0.26	0.009	0.007	0.47

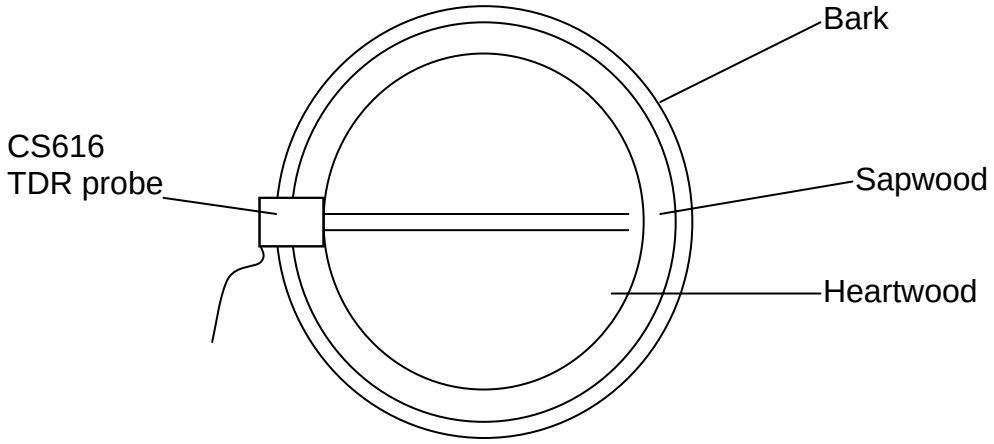


Figure 1. Diagram illustrating the placement of CS616 TDR probe in a tree stem.

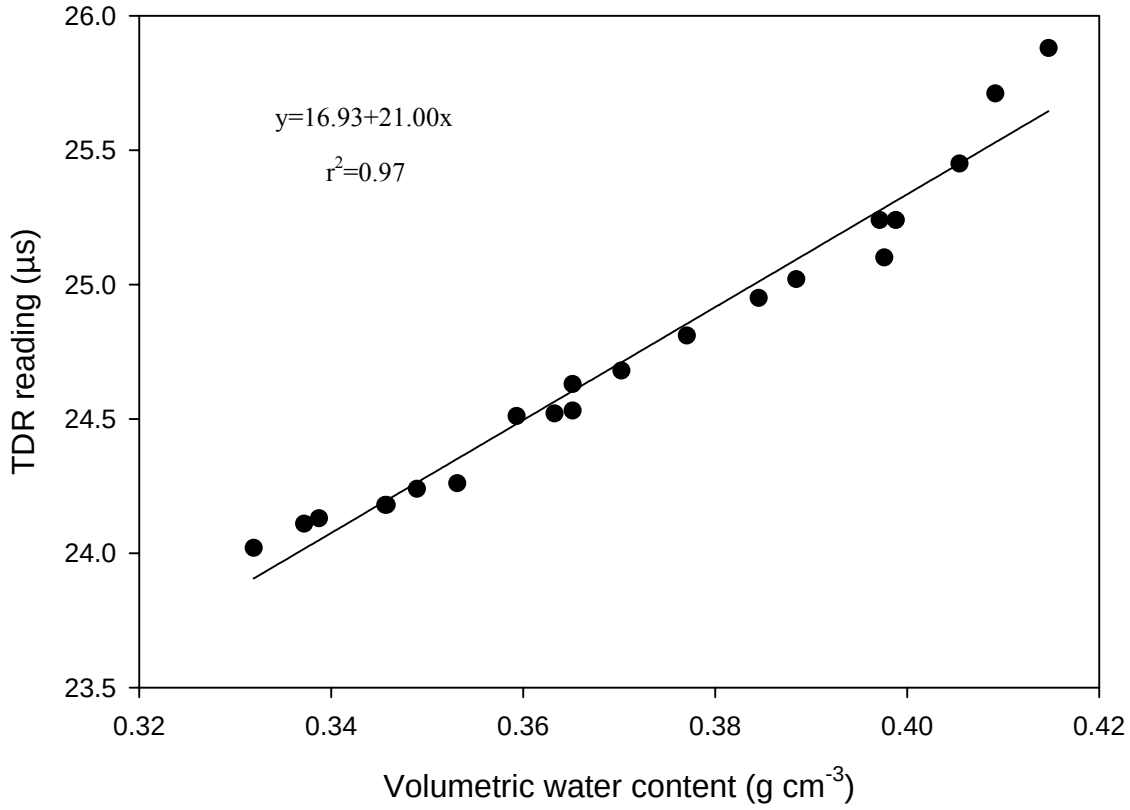


Figure 2. The relationship between TDR reading and volumetric water content of heartwood. Temperature was constant throughout readings.

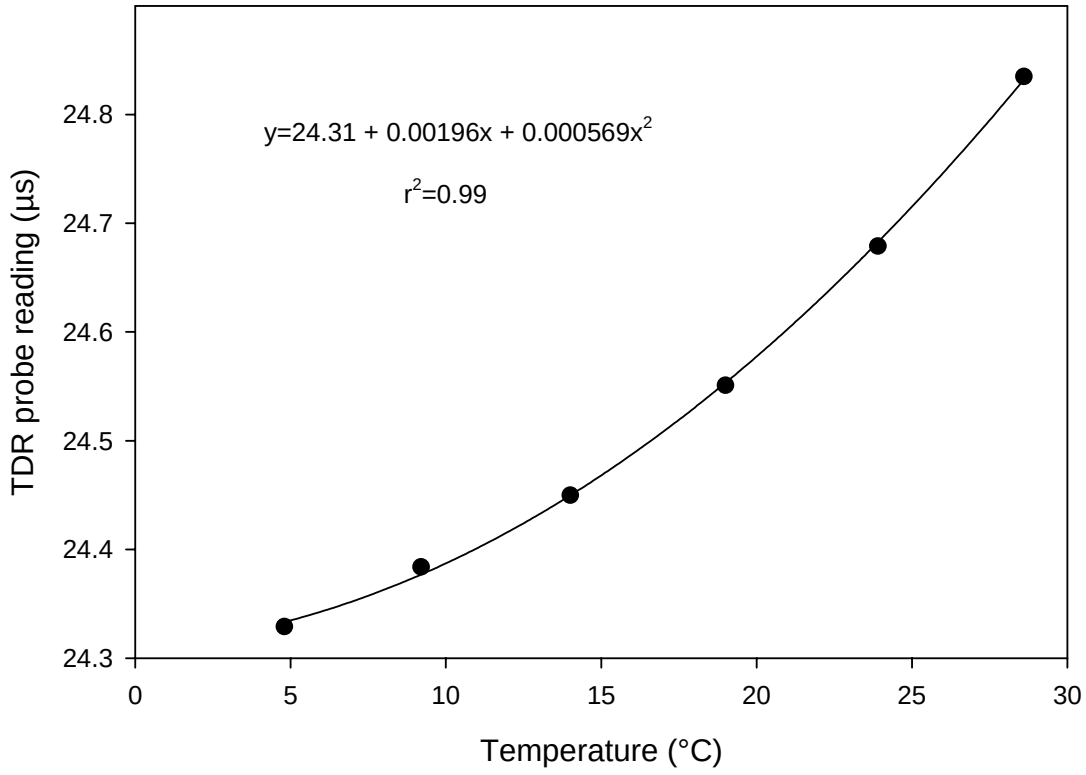
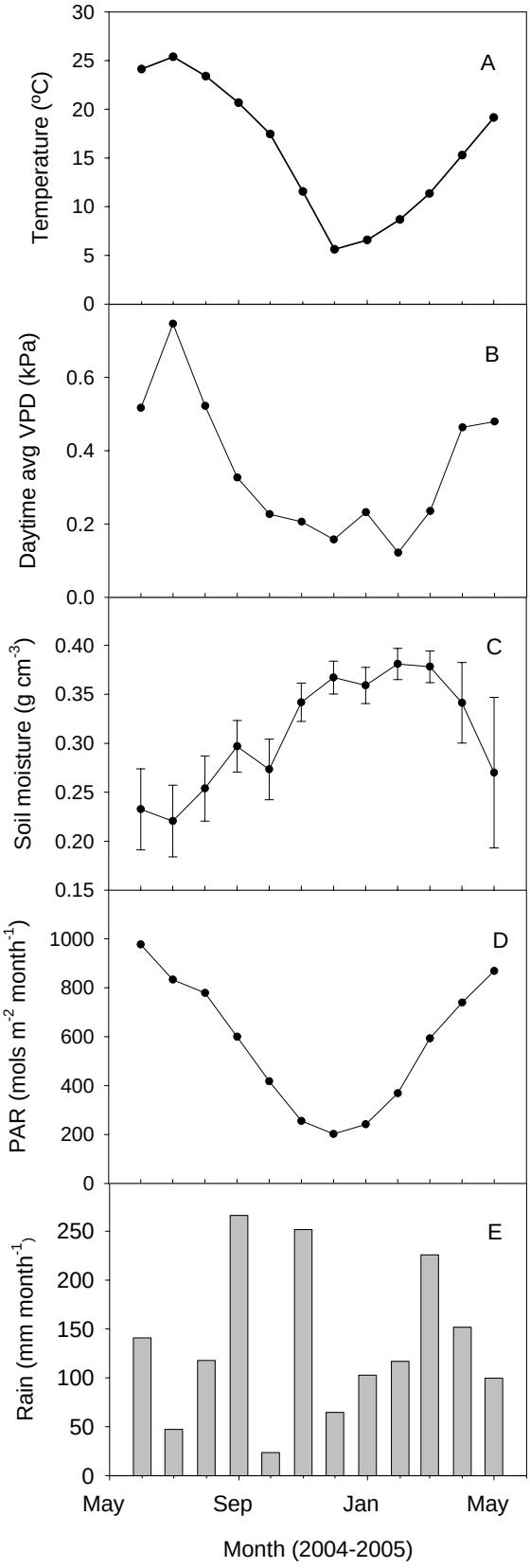


Figure 3. The effect of temperature on TDR probe reading. The water content of the heartwood stem was constant throughout all readings.

Figure 4. Climate data from June 2004 to May 2005. Data shown are mean monthly temperature (°C) (A), mean monthly daytime average VPD (kPa) (B), mean monthly daily average soil moisture (g cm^{-3}) with standard error (C), total monthly PAR (mols m^{-2}) (D) and total monthly rainfall (mm) (E).


A
B
C
D
E
Temperature (°C)
Daytime avg VPD (kPa)
Soil moisture (g cm-3)
PAR (mols m-2 month-1)
Rain (mm month-1)
May
Sep
Jan
May
Month (2004-2005)

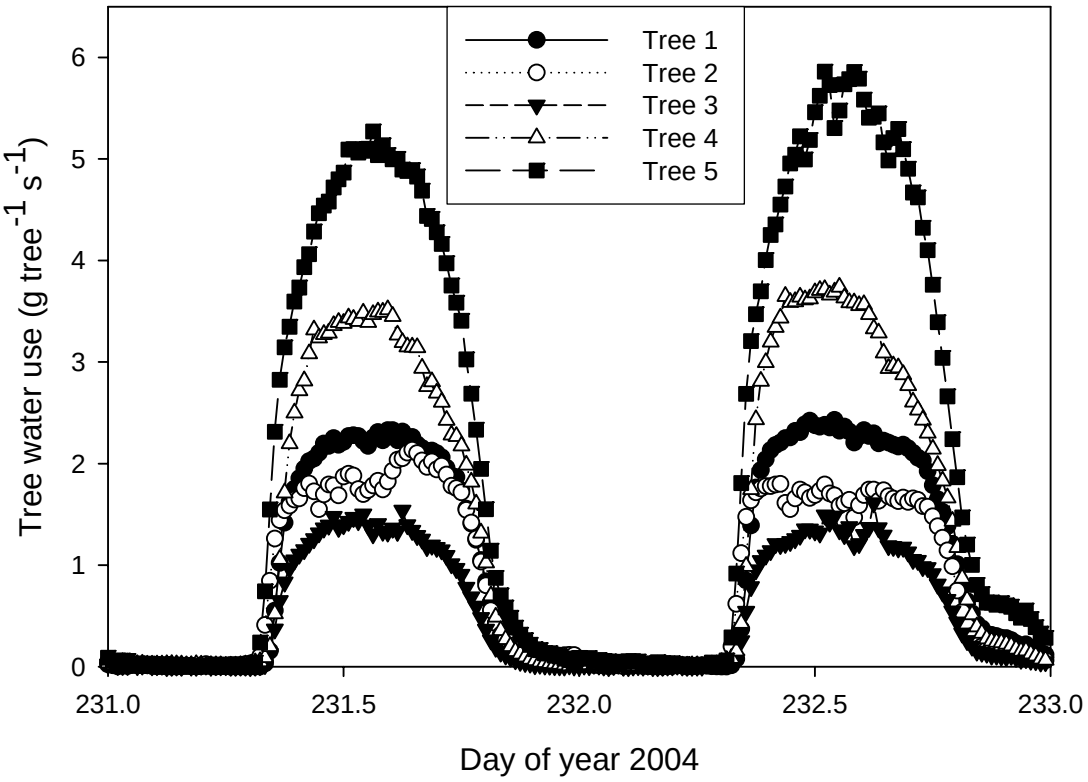


Figure 5. Diurnal pattern of sap flux in each tree on two hot, sunny days (August 18-19 2004).

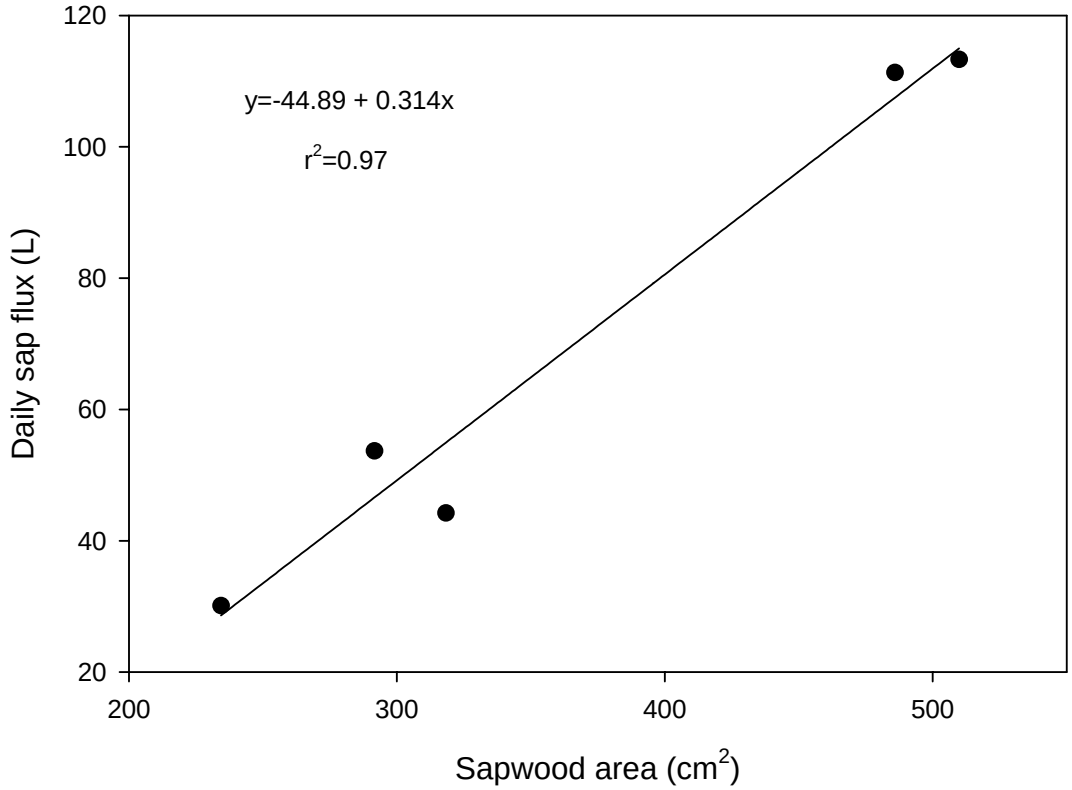


Figure 6. Average daily sap flux from June to November 2004 and the corresponding sapwood area of the five trees used in this study.

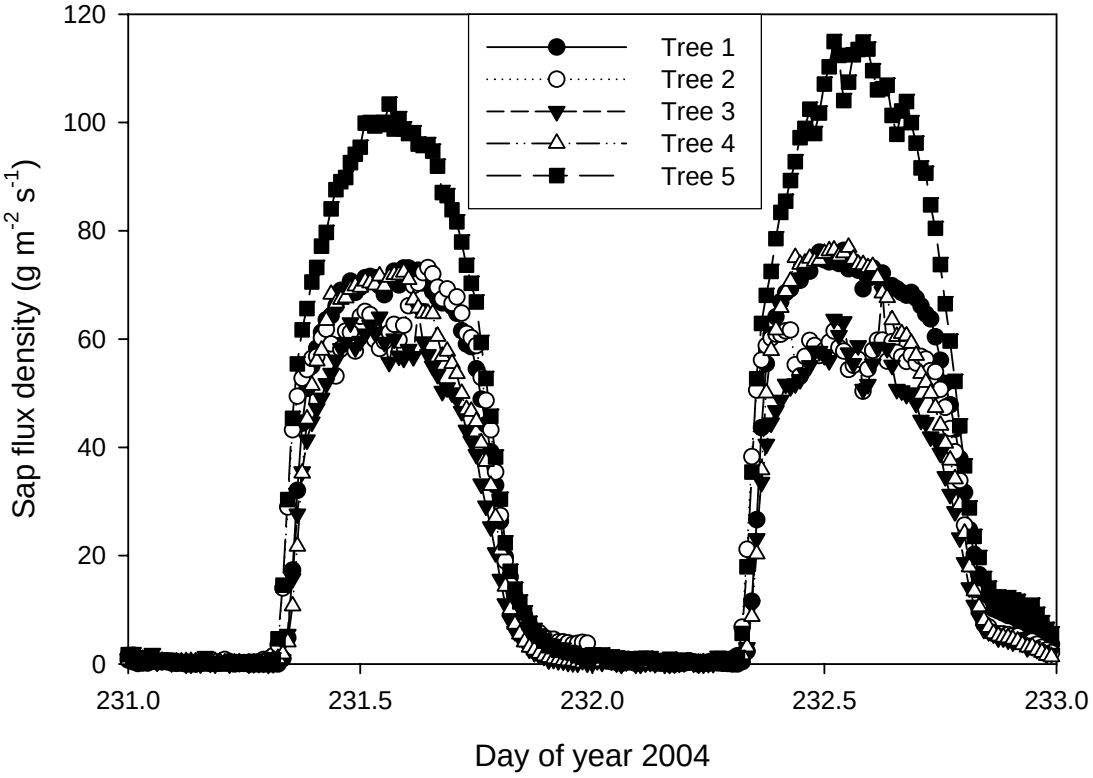


Figure 7. Diurnal pattern of sap flux density (g m^{-2} s^{-1}) in each tree on two hot, sunny days in August 2004.

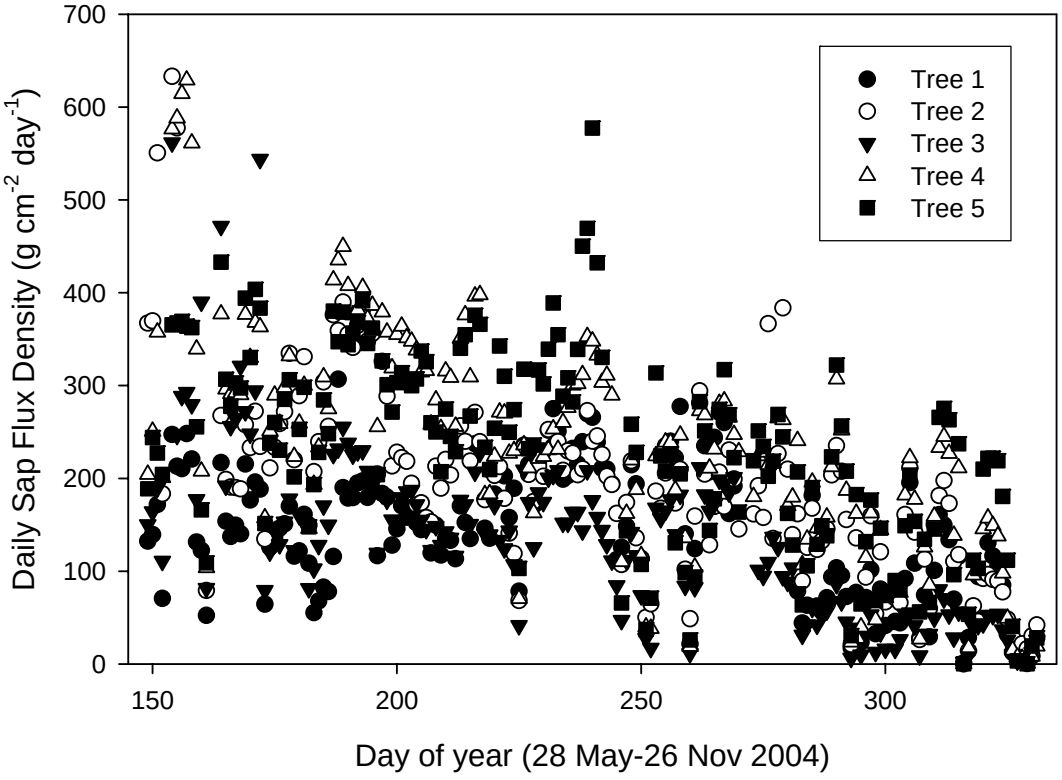


Figure 8. Daily sap flux density (g cm^{-2} d^{-1}) for all five trees over the growing season.

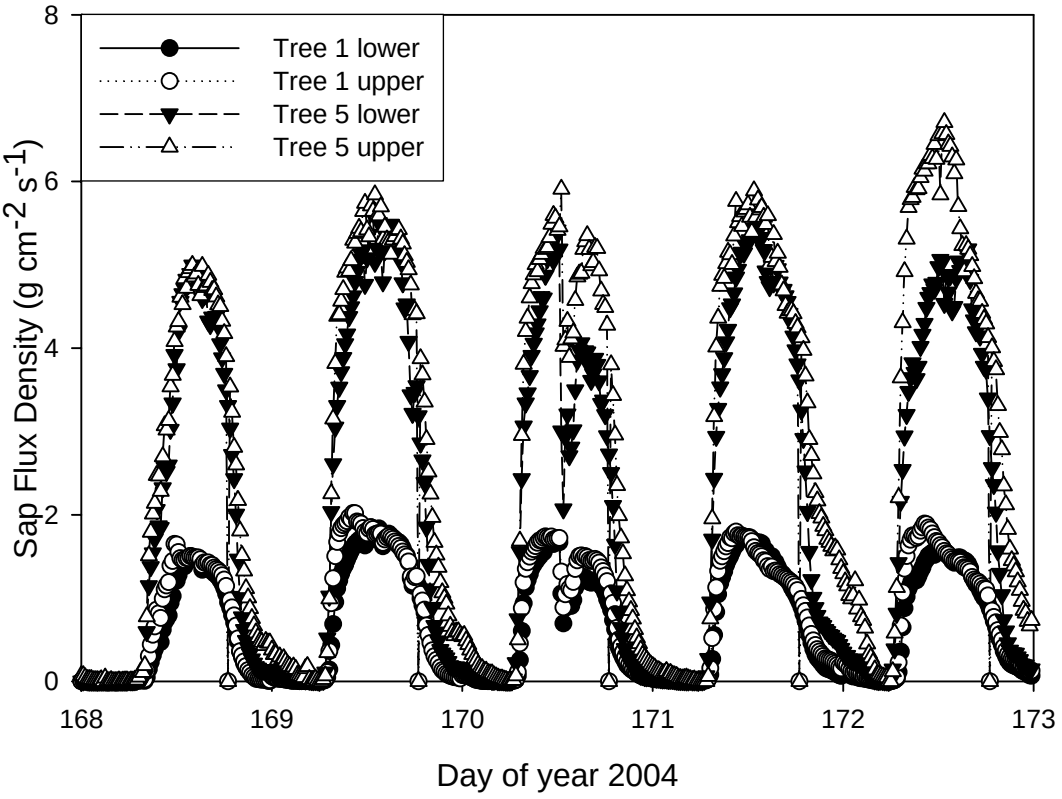
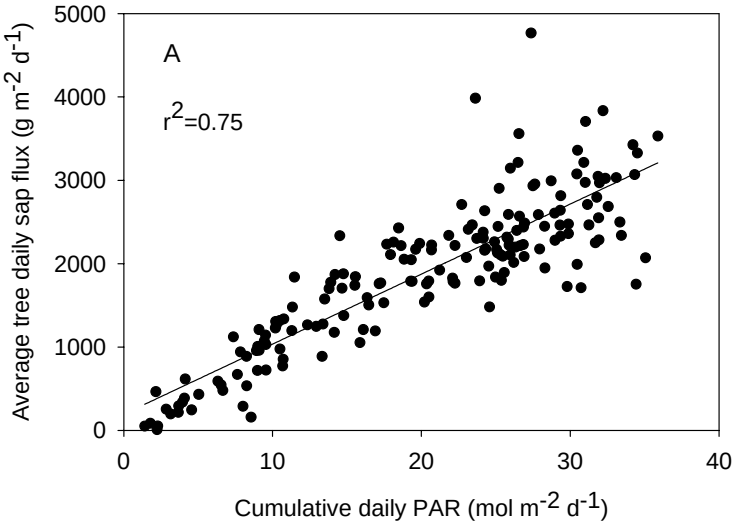
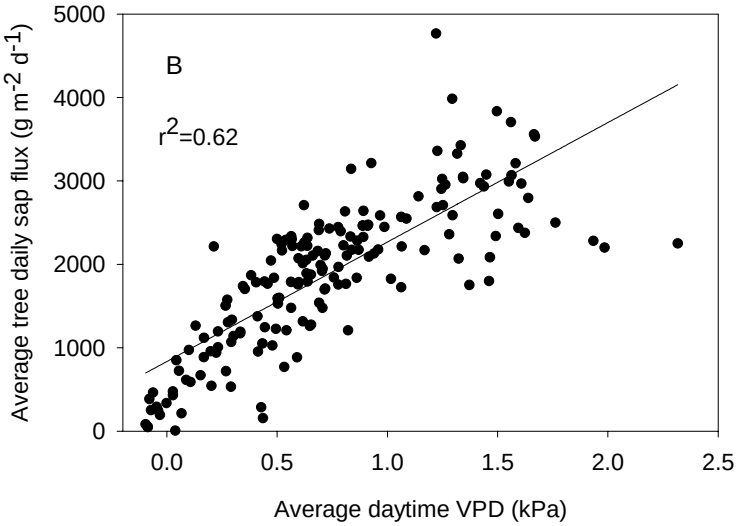
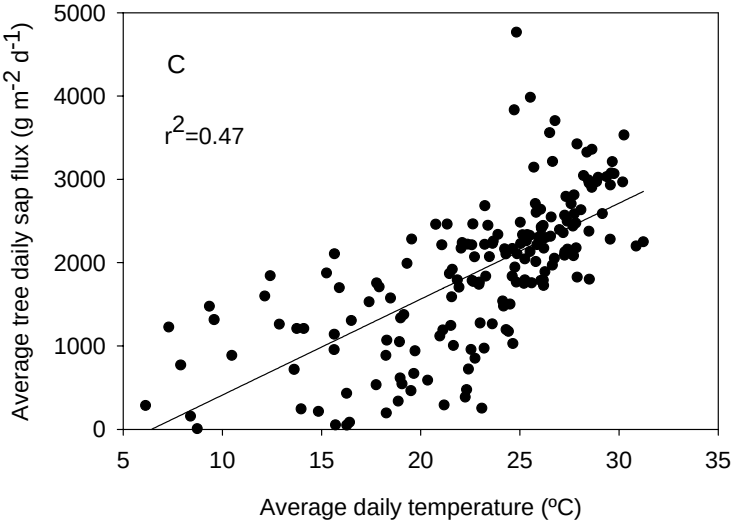


Figure 9. Sap flux (g tree^{-1} s^{-1}) data from sap flux sensors located at 1.3 and 4 m up the stem for the largest and smallest trees in the study. There was usually little difference in water use recorded by upper and lower sensors, especially at the onset of water use after dawn when the upper sensors were expected to record earlier, higher water use.

Figure 10. Daily sap flux (g m^{-2} d^{-1}) plotted against climate variables. Figure 9 shows the relationship between daily sap flux and total daily PAR (mol m^{-2} d^{-1}) (Figure 9A), average daytime VPD (kPa) (Figure 9B) and average daily temperature (ºC) (Figure 9C). PAR was the best predictor of daytime sap flux (r^2=0.75), followed by VPD (r^2=0.62) and temperature (r^2=0.47).


A
r^2=0.75
Average tree daily sap flux (g m^{-2} d^{-1})
Cumulative daily PAR (mol m^{-2} d^{-1})
0
1000
2000
3000
4000
5000
0
10
20
30
40


B
r^2=0.62
Average tree daily sap flux (g m^{-2} d^{-1})
Average daytime VPD (kPa)
0
1000
2000
3000
4000
5000
0.0
0.5
1.0
1.5
2.0
2.5


C
r^2=0.47
Average tree daily sap flux (g m^{-2} d^{-1})
Average daily temperature (ºC)
0
1000
2000
3000
4000
5000
5
10
15
20
25
30
35

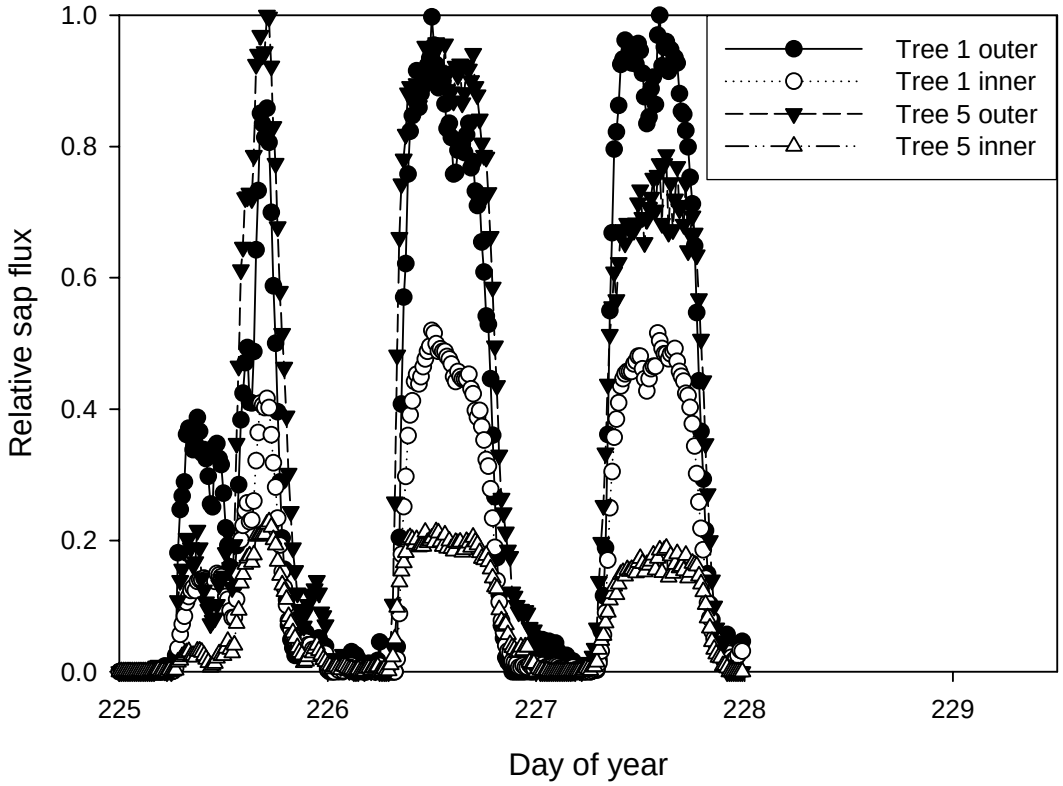


Figure 11. Relative sap flow rates of inner and outer sapwood in a large (Tree 5) and small (Tree 1) trees from August 12-15 2004. Inner sap flux reached about 20% (Tree 5) and 50% (Tree 1) of the outer sap flux rate during the day.

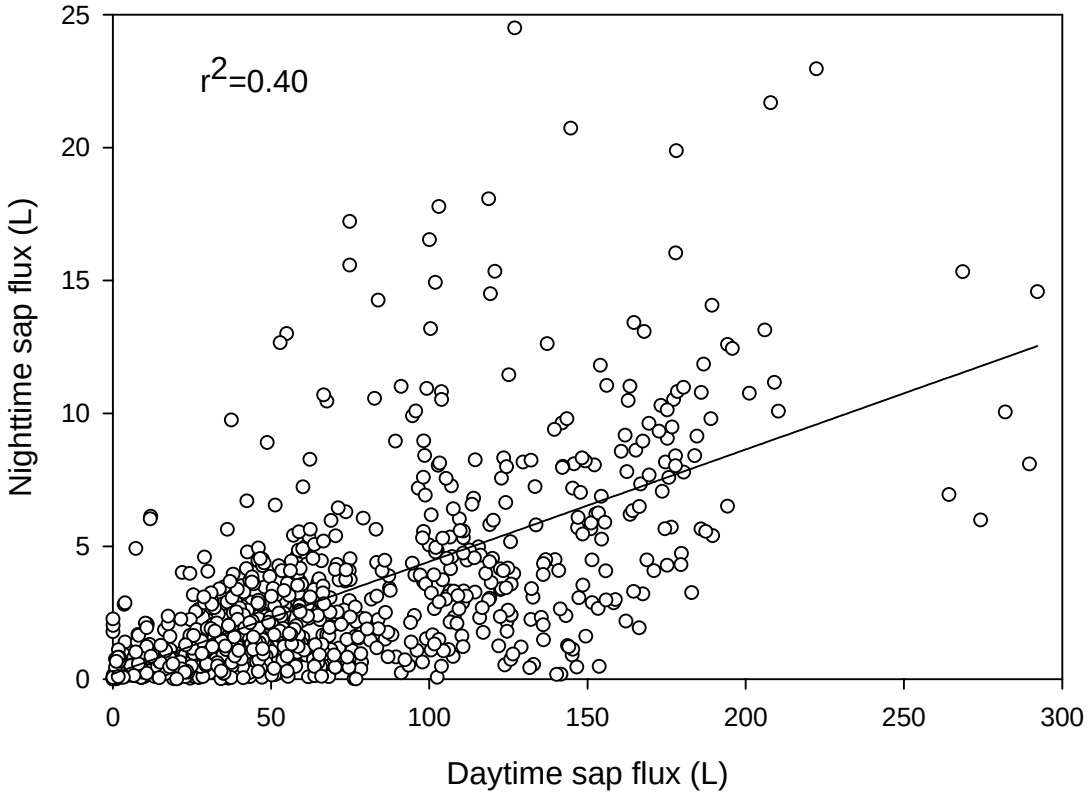


Figure 12. Relationship between daytime sap flux between 6:00 and 19:45, and nighttime sap flow the following night between 20:00 and 5:45. The average nighttime sap flow was 4.5 % of the daytime sap flow volume.

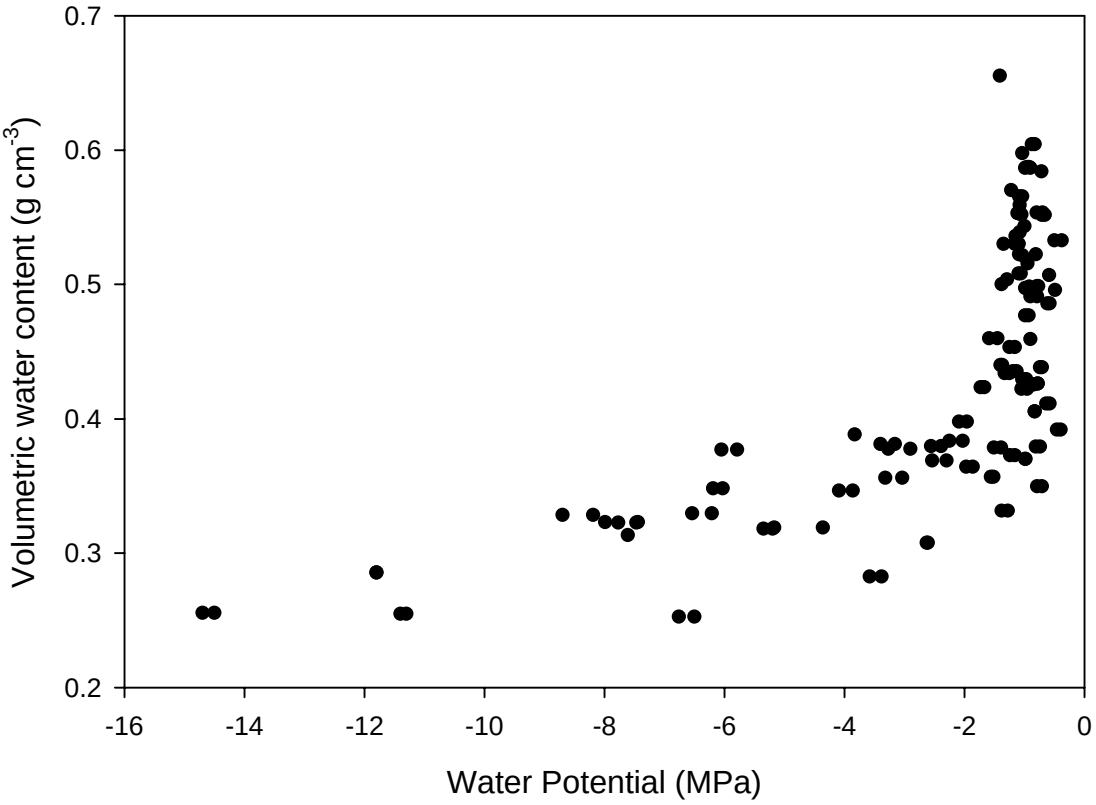


Figure 13. Heartwood moisture release curve. Although the water content declined, there was little change in water potential until the water content declined below 0.4 g cm^{-3}.

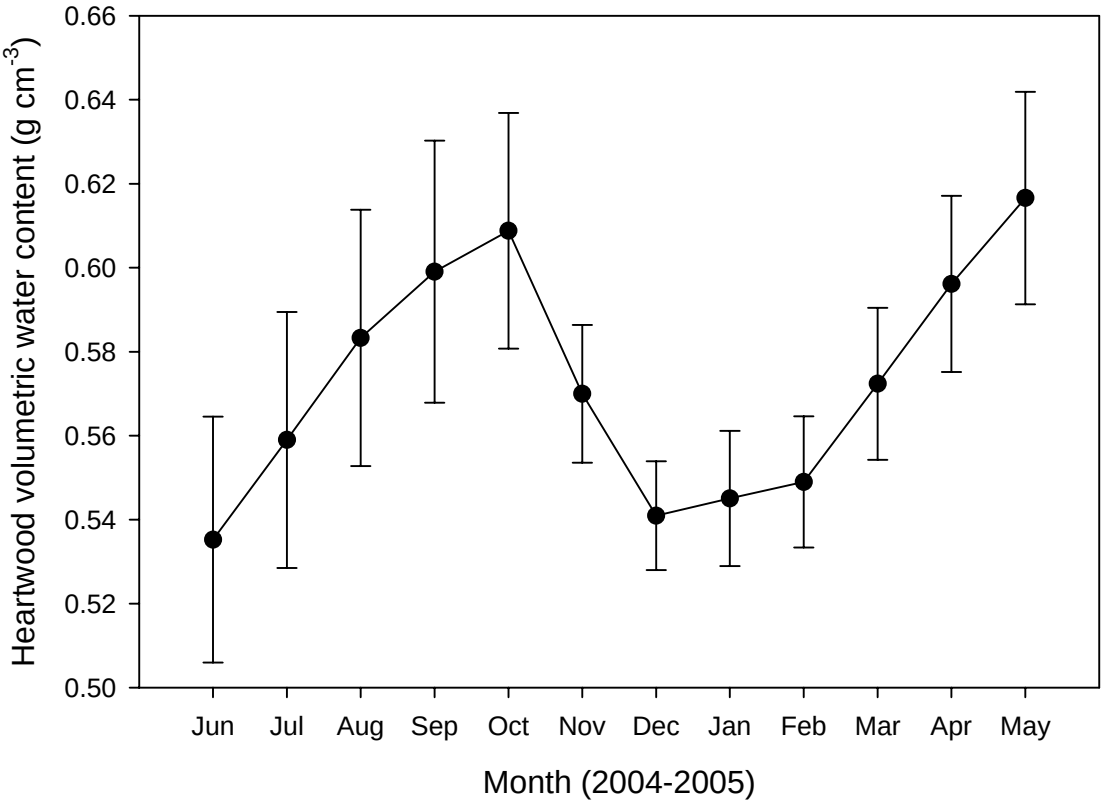


Figure 14. Monthly average heartwood water content (g cm^{-3}) from June 2004 to May 2005, with error bars showing the standard error of the individual tree average water contents.

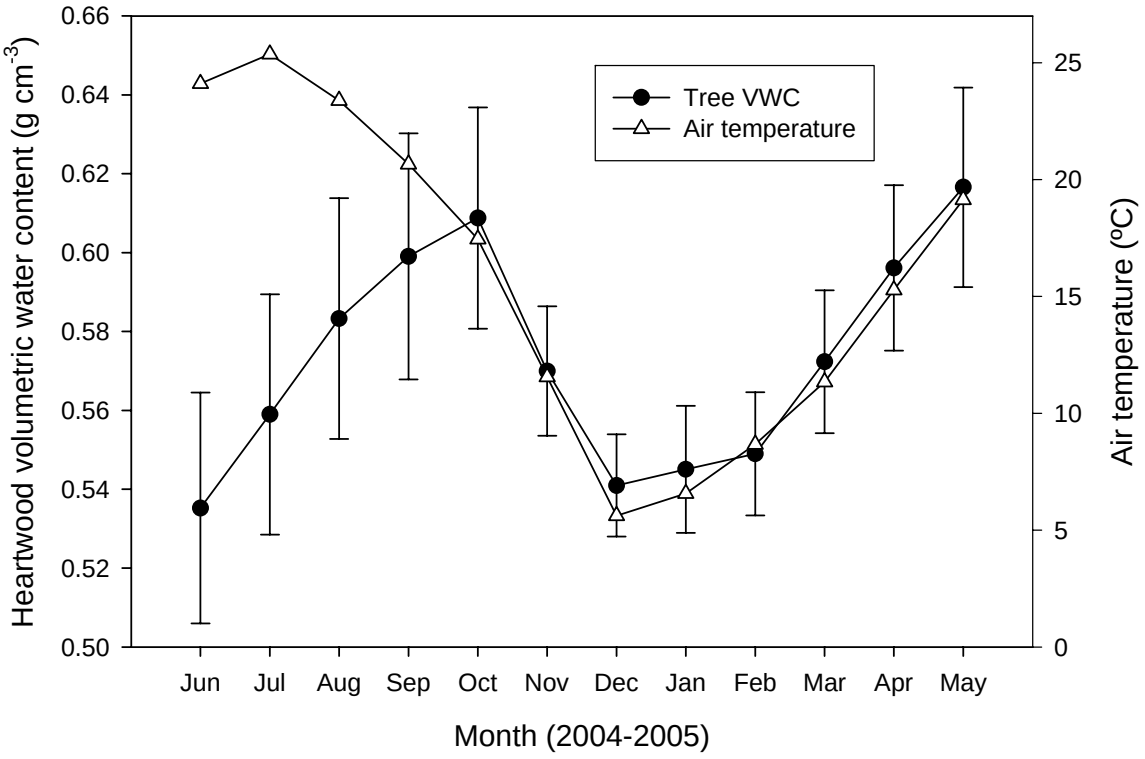


Figure 15. Monthly average heartwood water content from June 2004 to May 2005. Average air temperature is plotted on the second dependent axis, and error bars show the standard error of the individual tree average water content (g cm^{-3}) values.

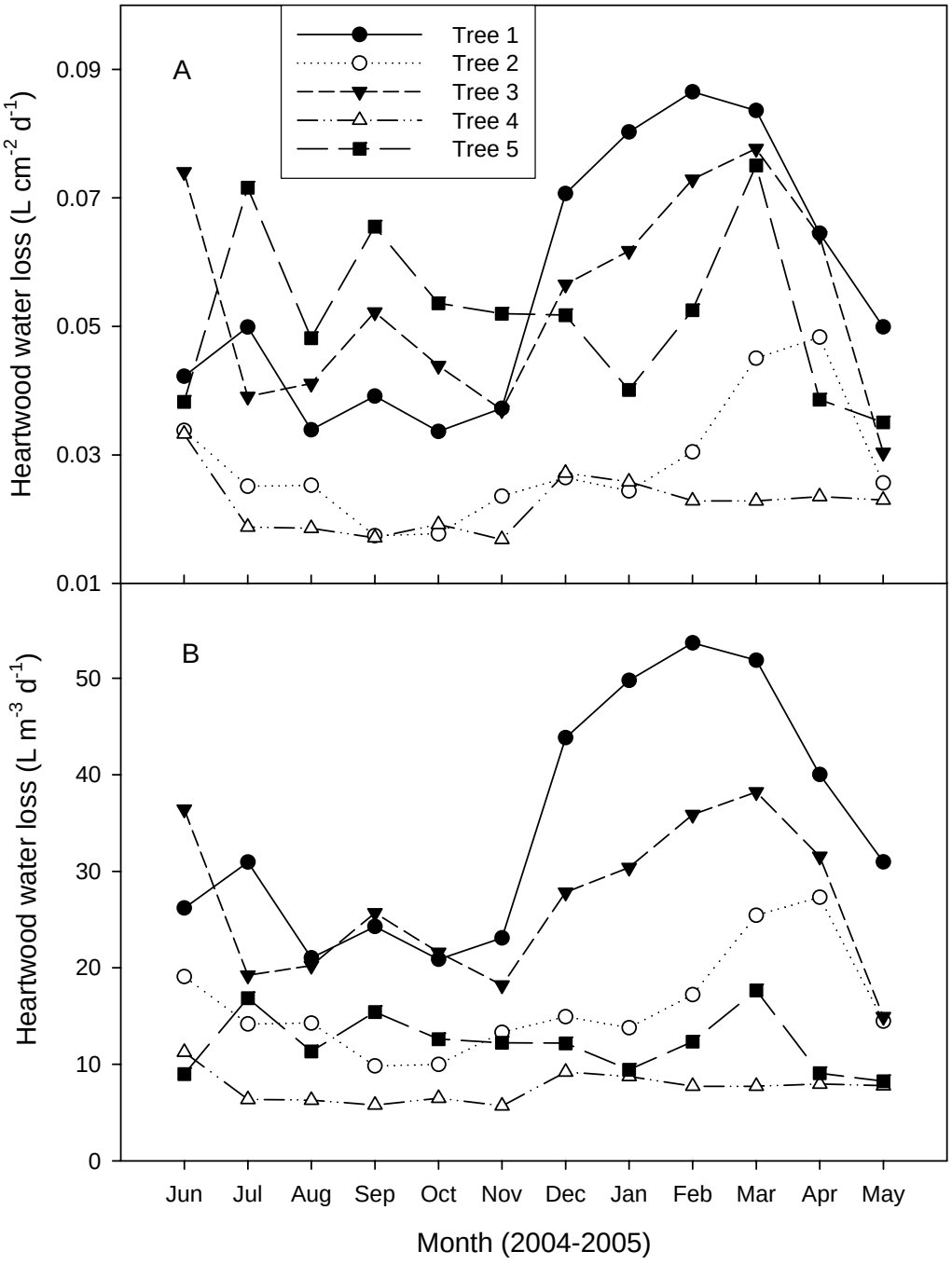


Figure 16. Individual tree daily heartwood water losses by month. There was considerable variation in the seasonal water loss patterns between trees. When heartwood water loss was plotted by sapwood area (A, L cm^{-2} d^{-1}) the data were more similar between trees than when heartwood water loss was plotted by heartwood volume (B, L m^{-3} d^{-1}).

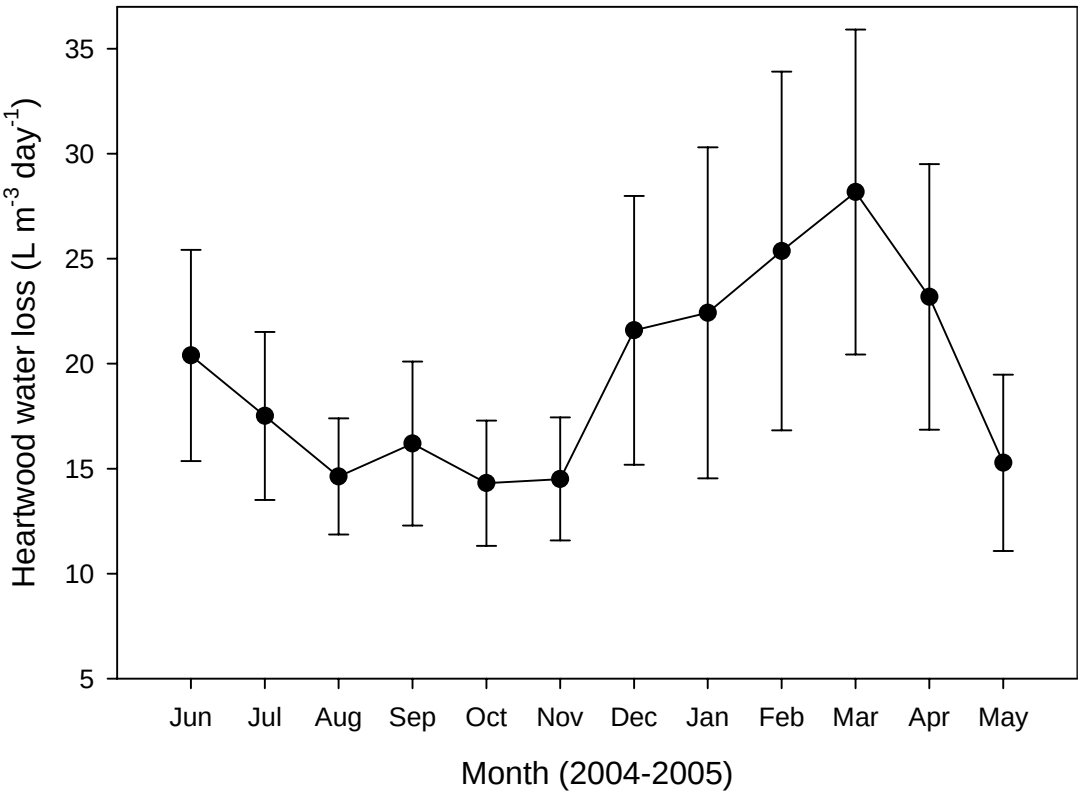


Figure 17. All-tree average daily heartwood water loss by month (L m^{-3} d^{-1}). Error bars are the standard error of the individual tree water losses.

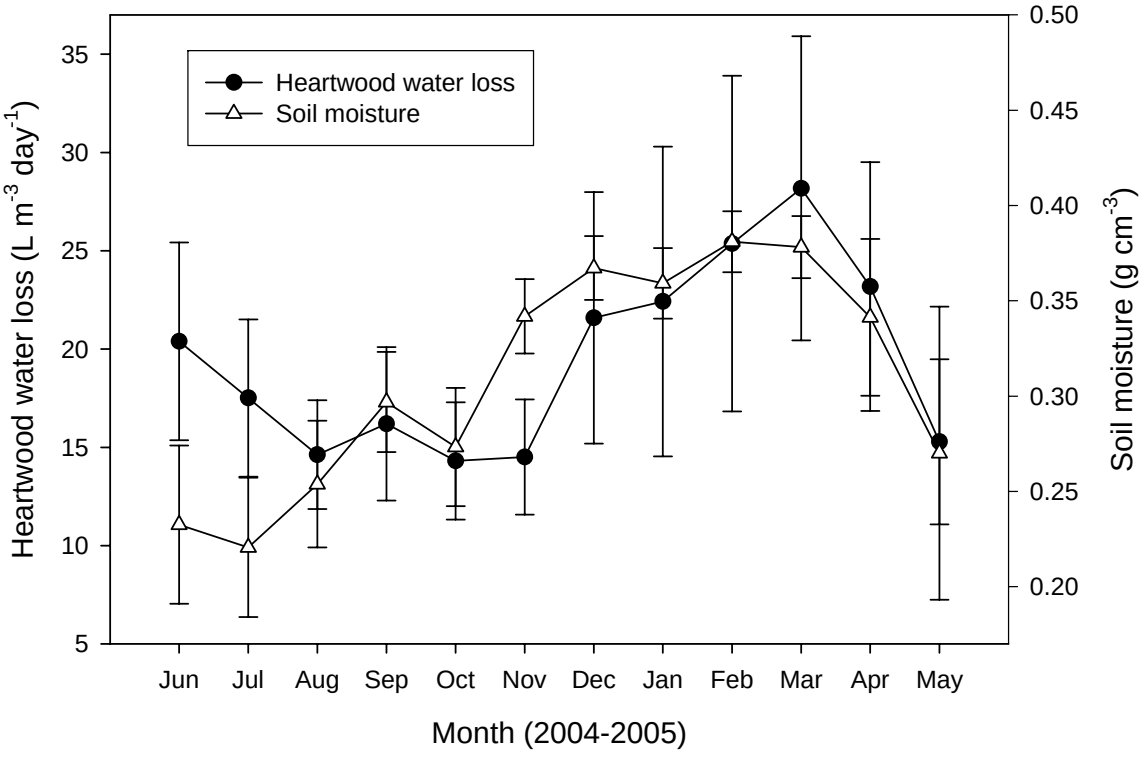
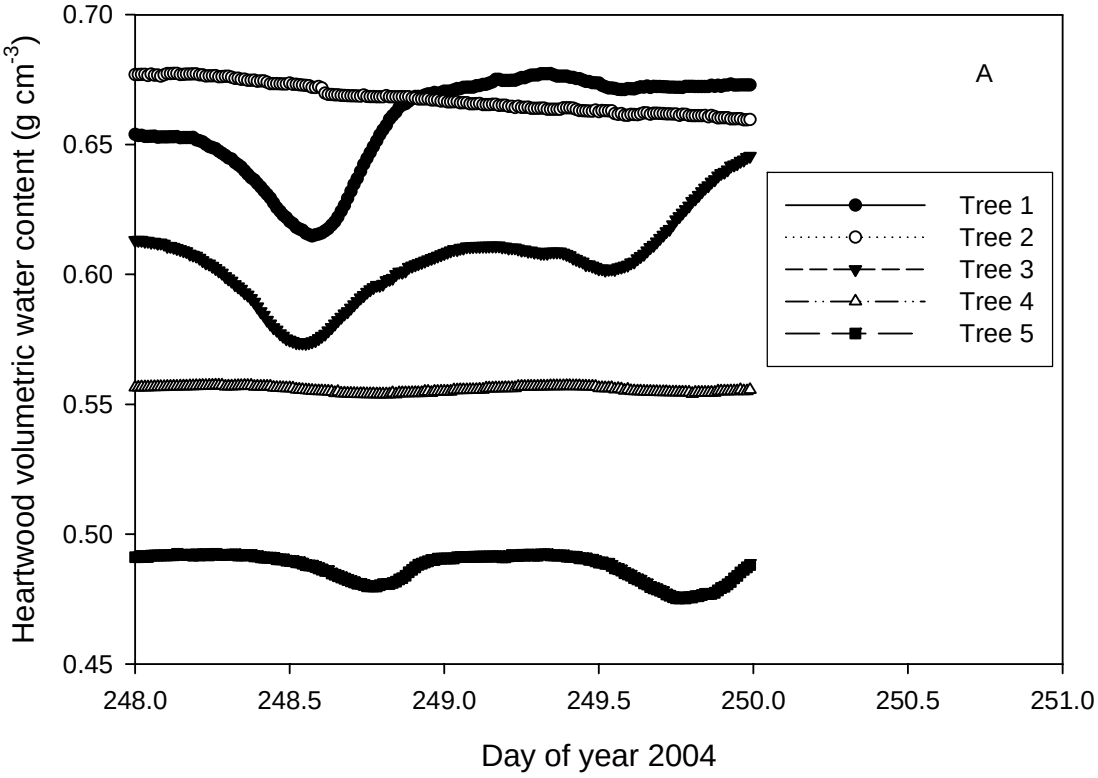
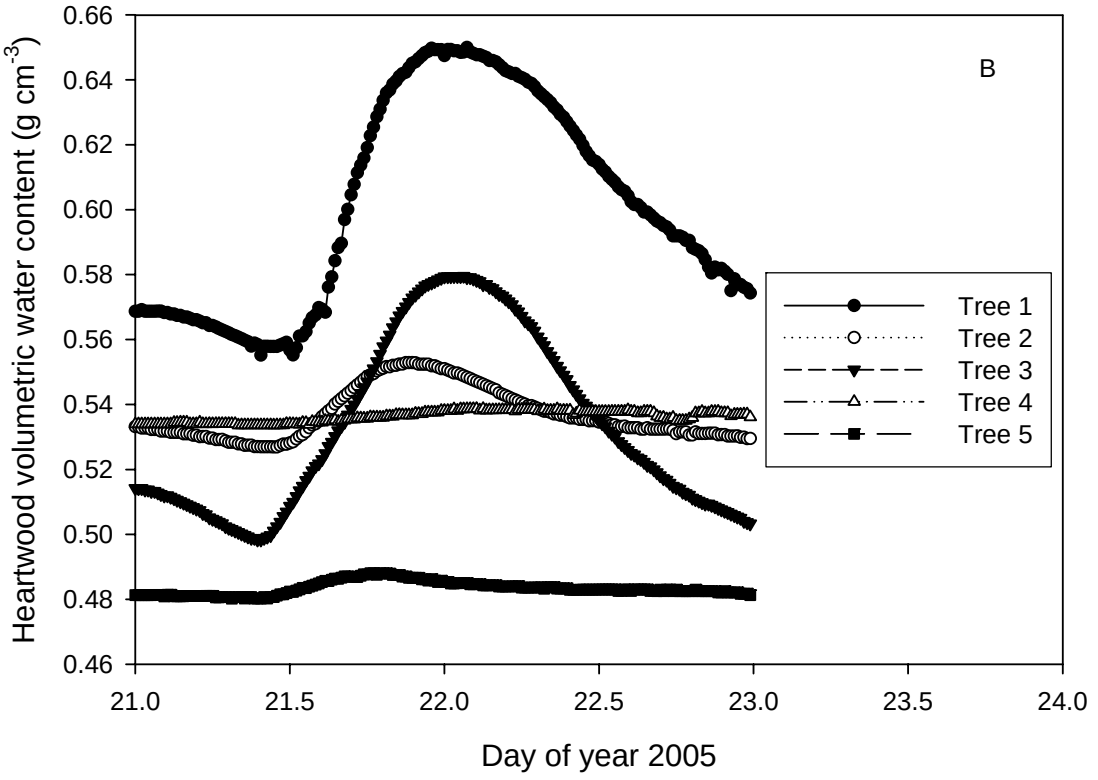


Figure 18. Heartwood water loss (L m^{-3} d^{-1}) is shown by month with the average soil moisture (g cm^{-3}) plotted on the second y-axis. Both heartwood water loss and soil moisture follow the same general shape, suggesting that heartwood water flux may be related to soil moisture availability. Error bars show the standard error of the individual values from each tree.

Figure 19. Diurnal pattern of heartwood water withdrawal and recharge on 2 hot days with high VPD and PAR (A) and 2 cold days with low VPD and PAR (B). There was considerable variation between the diurnal patterns from day to day and between trees on each day.


A
Heartwood volumetric water content (g cm-3)
0.70
0.65
0.60
0.55
0.50
0.45
248.0
248.5
249.0
249.5
250.0
250.5
251.0
Day of year 2004
Tree 1
Tree 2
Tree 3
Tree 4
Tree 5


B
Heartwood volumetric water content (g cm-3)
0.66
0.64
0.62
0.60
0.58
0.56
0.54
0.52
0.50
0.48
0.46
21.0
21.5
22.0
22.5
23.0
23.5
24.0
Day of year 2005
Tree 1
Tree 2
Tree 3
Tree 4
Tree 5

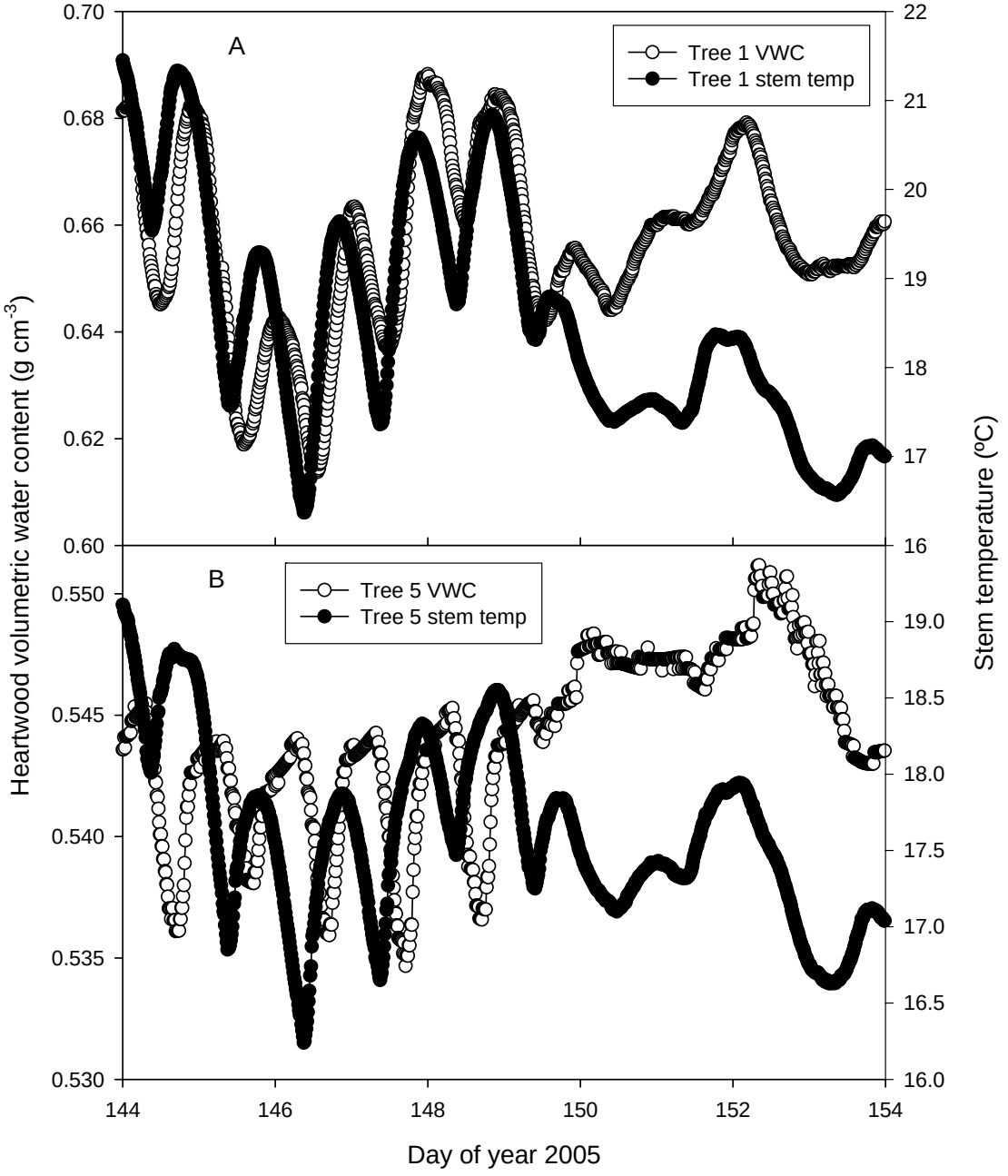
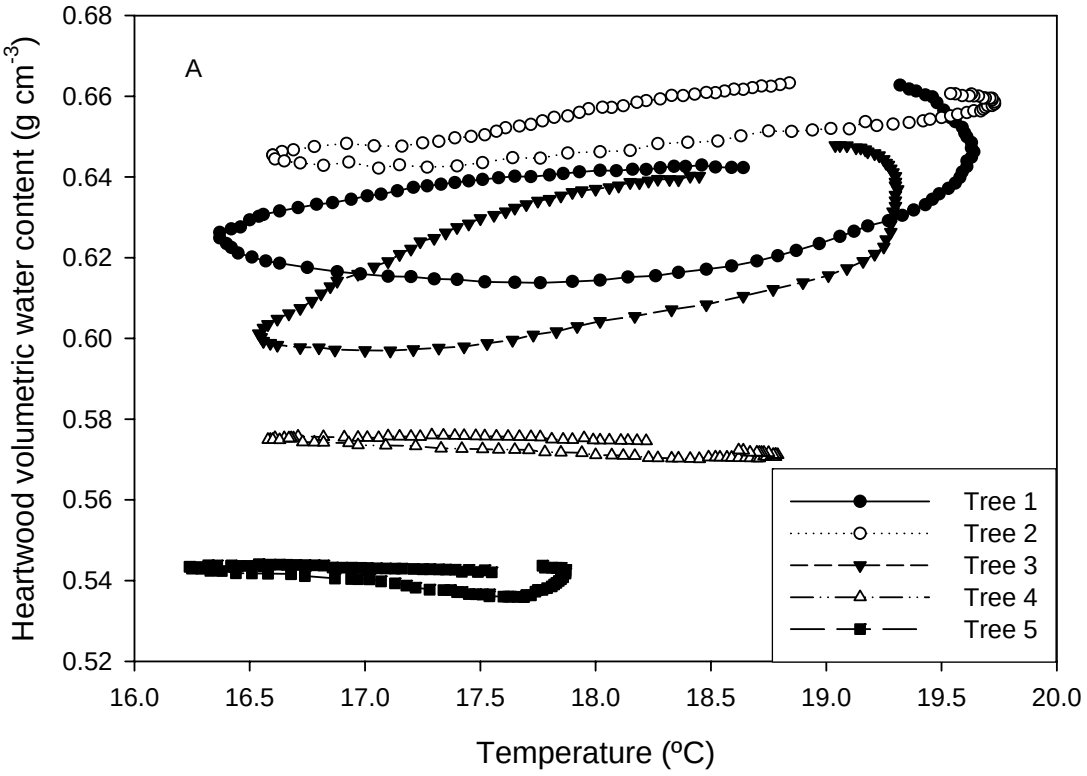
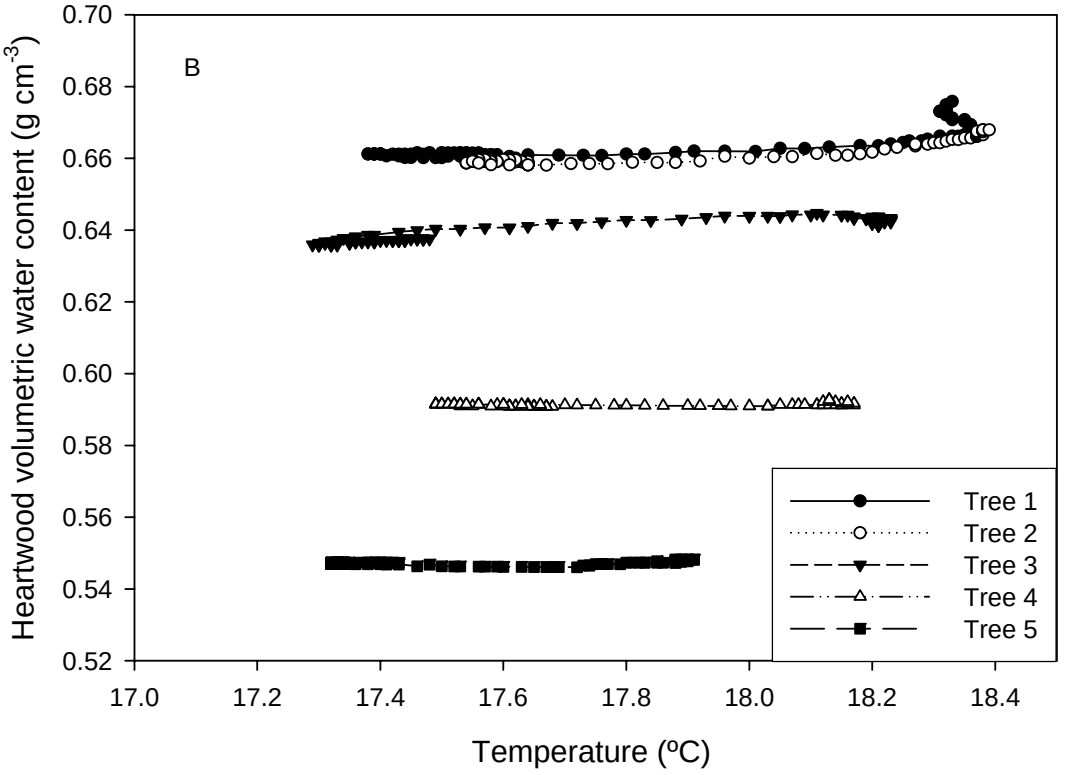


Figure 20. Heartwood water content and stem temperature in a small tree (Tree 1, Figure 18A) and a large tree (Tree 5, Figure 18B). On a daily timescale, heartwood water content followed a similar pattern to stem temperature.

Figure 21. Daily relationship between stem temperature and heartwood volumetric water content. On some days there was a more cyclical pattern (A, May 26 2005) and on other days the pattern was less cyclical (B, 31 May 2005).


A
Heartwood volumetric water content (g cm-3)
0.68
0.66
0.64
0.62
0.60
0.58
0.56
0.54
0.52
16.0
16.5
17.0
17.5
18.0
18.5
19.0
19.5
20.0
Temperature (ºC)
Tree 1
Tree 2
Tree 3
Tree 4
Tree 5


B
Heartwood volumetric water content (g cm-3)
0.70
0.68
0.66
0.64
0.62
0.60
0.58
0.56
0.54
0.52
17.0
17.2
17.4
17.6
17.8
18.0
18.2
18.4
Temperature (ºC)
Tree 1
Tree 2
Tree 3
Tree 4
Tree 5

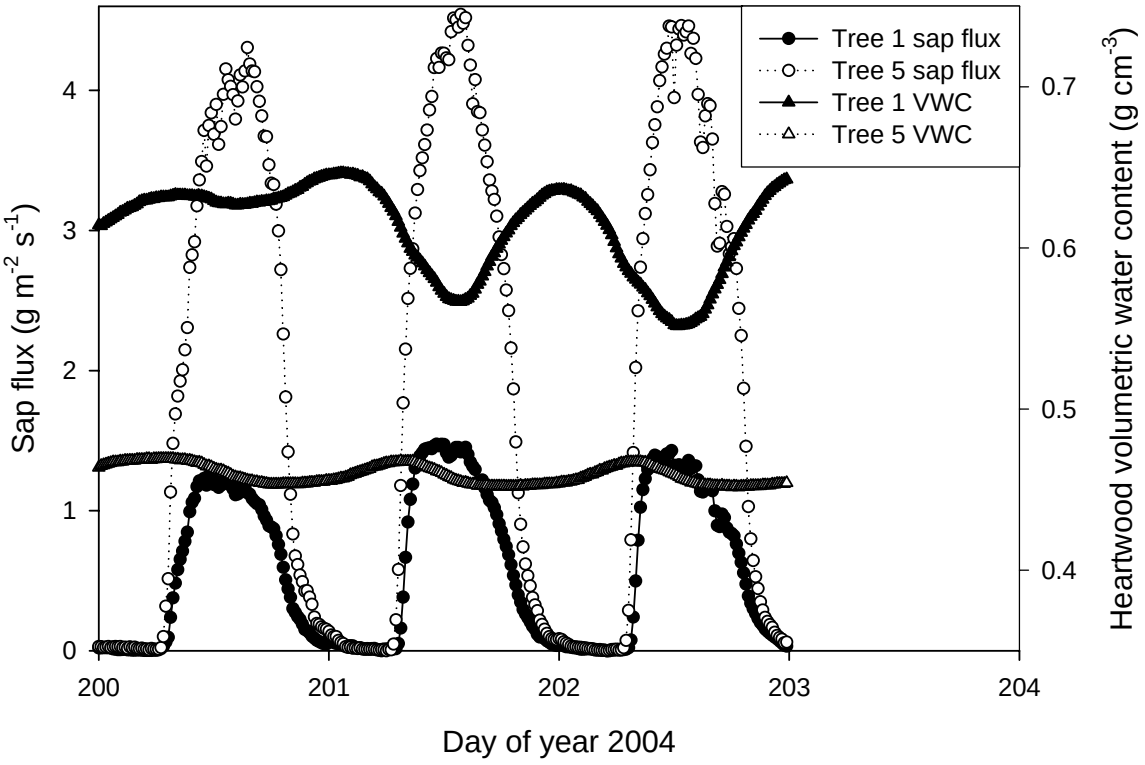


Figure 22. Diurnal pattern of sap flux (primary y-axis) and heartwood water content (second y-axis) in large (Tree 5) and small (Tree 1) trees. Heartwood water content decreased in the morning when sap flux was active, and recovered in the afternoon when sap flux declined.

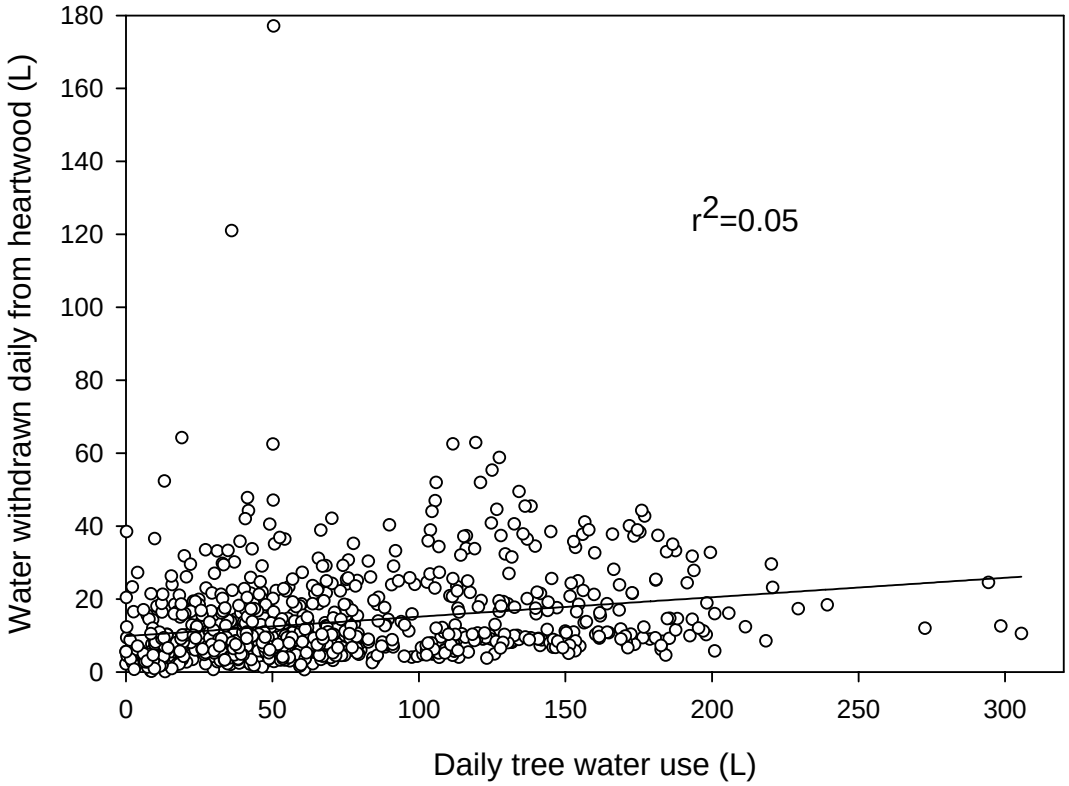


Figure 23. The daily tree water use (L) on days when sap flux data were collected, and the volume of water lost (L) daily from the heartwood. Although a positive correlation was expected, there was almost no relationship between the sapwood water use and heartwood water loss (r^2=0.05).

CONCLUSIONS

In this study, sap flux and TDR probes were used to measure water movement in the sapwood and heartwood of *Q. alba* trees. Sap flux was measured from June to November 2004, and TDR heartwood readings were made from June 2004 to May 2005. Sap flux was correlated with PAR levels, and there were diurnal and seasonal changes in the heartwood water content of each tree throughout the year. Heartwood water content was higher in the growing season and declined sharply in the dormant season, with monthly heartwood water contents correlating somewhat with air temperature + soil moisture. The diurnal changes in heartwood water content followed a similar pattern to daily stem temperature changes, and when averaged on a monthly basis the daily water losses were correlated with stem temperature changes and also soil moisture availability. Heartwood water content and changes in water content were easier to predict in the smaller trees than the larger trees, probably because temperature was the best predictor and the smaller trees had less thermal mass, allowing stem temperature to adjust faster than in the larger trees.

The hypotheses that the heartwood water content would vary diurnally and seasonally, and that water loss would occur in the day while water gain would happen at night were accepted. Heartwood water loss was not directly related to tree water use, so the hypotheses that heartwood water loss would be related to sap flux were rejected.

It was expected that sap flux probes installed in the upper and lower stem would record sapwood water storage and use. *Quercus alba* has relatively shallow sapwood (2-

3 cm deep in the study trees) and a fast sap flux rate ($\geq$3 g m^{-2} s^{-2}), and the probes were not spaced far enough apart to detect a difference in sap flux due to stem capacitance between the upper and lower probes. If it were possible to install sap flux probes in the canopy of the study trees, the probes might have measured instantaneous sapwood water storage and release. Since only nighttime sap flux was counted toward sapwood water storage, it is likely that some afternoon sapwood water storage was missed. Long sap flux probes may not have been in good contact with the sapwood and yielded relative rates of sap flux for inner and outer sapwood but not actual sap flux data. A better approach would have been to install two short sap flux probes at different depths to record deeper and shallower sapwood.

There was a very interesting relationship between stem temperature and heartwood water content and water loss. It had been expected that heartwood water loss would be related to tree water use, but there was no evidence that heartwood water loss was related to tree water stress or water demand. When water leaves the heartwood, it almost certainly enters the adjacent sapwood and is used for transpiration. White oak carbon uptake probably benefits from the extra water available in the heartwood, but heartwood water loss does not seem directly linked to tree water use. More research needs to be done on the topic of heartwood water storage, both to find out whether stem temperature causes some of the variation in heartwood water content and to compare white oak to the heartwood of other trees, particularly red oak species, which, compared to *Q. alba*, may have greater capacities to transport water in and out of heartwood.

REFERENCES

Anonymous. 1968. Soil Survey Clarke and Oconee Counties, Georgia Eds. USDA and U.o.G.C.o. Agriculture. U. S. Government Printing Office, Washington.

Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology. 74:1437-1449.

Brough, D.W., H.G. Jones and J. Grace 1986. Diurnal changes in water content of the stems of apple trees, as influenced by irrigation. Plant, Cell and Environment. 9:1-7.

Campbell Scientific, Inc. 2003. CS516 and CS625 water content reflectometers instruction manual, Logan UT.

Caspari, H.W., S.R. Green and W.R.N. Edwards 1993. Transpiration of well-watered and water-stressed Asian pear trees as determined by lysimetry, heat-pulse, and estimated by a Penman-Monteith model. Agricultural and forest meteorology. 67:13-27.

Cermak, J., E. Cienciala, J. Kucera and J.-E. Hallgren 1992. Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing. Tree Physiology. 10:367-380.

Clark, J. and R.D. Gibbs 1957. Studies in Tree Physiology IV: Further investigations of seasonal changes in moisture content of certain Canadian forest trees. Canadian Journal of Botany. 35:219-253.

Cochard, H. and M.T. Tyree 1990. Xylem disfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. Tree Physiology. 6:393-407.

Constantz, J. and F. Murphy 1990. Monitoring moisture storage in trees using time-domain reflectometry. Journal of Hydrology. 119:31-42.

Dixon, M.A., J. Grace and M.T. Tyree 1984. Concurrent measurements of stem density, leaf and stem water potential, stomatal conductance and cavitation on a sapling of *Thuja occidentalis* L. Plant, Cell and Environment. 7

Domec, J.-C. and B.L. Gartner 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. Trees. 15:204-214.

Domec, J.-C. and B.L. Gartner 2002. How do water transport and water storage differ in coniferous earlywood and latewood. Journal of Experimental Botany. 53:2369-2379.

Edwards, W.R.N. and P.G. Jarvis 1982. Relations between water content, potential and permeability in stems of conifers. Plant, Cell and Environment. 5:271-277.

Edwards, W.R.N. and P.G. Jarvis 1983. A method for measuring radial differences in water content of intact tree stems by attenuation of gamma radiation. Plant, Cell and Environment. 6:255-260.

Engel, V.C., M. Stieglitz, M. Williams and K.L. Griffin 2002. Forest canopy hydraulic properties and catchment water balance: observations and modeling. Ecological modelling. 154:263-288.

Ford, C.R., C.E. Goranson, R.J. Mitchell, R.E. Will and R.O. Teskey 2004a. Diurnal and seasonal variability in the radial distribution of sap flow: predicting total stem flow in *Pinus taeda* trees. Tree Physiology. 25:951-960.

Ford, C.R., M.A. McGuire, R.J. Mitchell and R.O. Teskey 2004b. Assessing variation in the radial profile of sap flux density in *Pinus* species and its effect on daily water use. Tree Physiology. 24:241-249.

Fromm, J.H., I. Sautter, D. Matthies, J. Kremer, P. Schumacher and C. Ganter 2001. Xylem water content and wood density in spruce and oak trees detected by high-resolution computed tomography. Plant Physiology. 127:416-425.

Goldstein, G., J.L. Andrade, F.C. Meinzer, N.M. Holbrook, J. Cavelier, P. Jackson and A. Celis 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant, Cell and Environment. 21:397-406.

Goulden, M.L. and C.B. Field 1994. Three methods for monitoring the gas exchange of individual tree canopies: ventilated-chamber, sap-flow and Penman-Monteith measurements on evergreen oaks. Functional Ecology. 8:125-135.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiology. 3:309-320.

Hinckley, T.M., J.P. Lassoie and S.W. Running 1978. Temporal and spatial variations in the water status of forest trees. Forest Science. 24 (Supplement):(Monograph 20).

Hirose, S., A. Kume, S. Takeuchi, Y. Utsumi, K. Otsuki and S. Ogawa 2005. Stem water transport of *Lithocarpus edulis*, an evergreen oak with radial-porous wood. Tree Physiology. 25:221-228.

Holbrook, N.M. 1995. Stem water storage. *In* Plant stems: physiology and functional morphology Ed. B.L. Gartner. Academic Press, San Diego, p. 440.

Holbrook, N.M. and T.R. Sinclair 1992a. Water balance in the arborescent palm, *Sabal palmetto*. I. Stem structure, tissue water release properties and leaf epidermal conductance. Plant, Cell and Environment. 15:393-399.

Holbrook, N.M. and T.R. Sinclair 1992b. Water balance in the arborescent palm, *Sabal palmetto*. II. Transpiration and stem water storage. Plant, Cell and Environment. 15:401-409.

Jackson, R.B., L.J. Anderson and W.T. Pockman 2000. Measuring water availability and uptake in ecosystem studies. *In* Methods in ecosystem science Eds. O.E. Sala, R.B. Jackson, H.A. Mooney and R.W. Howarth. Springer, New York, p. 421.

James, S.A., F.C. Meinzer, G. Goldstein, D. Woodruff, T. Jones, T. Restom, M. Mejia, M.J. Clearwater and P. Campanello 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. Oecologia. 134:37-45.

Jarvis, P.G. 1975. Water transfer in plants. *In* Heat and mass transfer in the biosphere: Part 1. Transfer processes in the plant environment Eds. D.A. deVries and N.H. Afgan. John Wiley & Sons, New York.

Jones, S.B., J.M. Wraith and D. Or 2002. Time domain reflectometry measurement principles and applications. Hydrological Processes. 16:141-153.

Kalma, S.J., P.J. Thorburn and G.M. Dunn 1998. A comparison of heat pulse and deuterium tracing techniques for estimating sap flow in *Eucalyptus gransis* trees. Tree Physiology. 18:697-705.

Kobayashi, Y. and T. Tanaka 2001. Water flow and hydraulic characteristics of Japanese red pine and oak trees. Hydrological Processes. 17:1731-1750.

LoGullo, M.A. and S. Salleo 1992. Water storage in the wood and xylem cavitation in 1-year-old twigs of *Populus deltoides* Bartr. Plant, Cell and Environment. 15:431-438.

Loustau, D., P. Berbigier, P. Roumagnac, C. Arruda-Pacheco, J.S. David, M.I. Ferreira, J.S. Pereira and R. Tavares 1996. Transpiration of a 64-year-old maritime pine stand in Portugal: 1. Seasonal course of water flux through maritime pine. Oecologia. 107

Martin, J.G., B.D. Kloeppel, T.L. Schaefer, D.L. Kimbler and S.G. McNulty 1998. Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. Canadian Journal of Forest Research. 28:1648-1659.

McLaughlin, S.B., S.D. Wullschleger and M. Nosal 2003. Diurnal and seasonal changes in stem increment and water use by yellow poplar trees in response to environmental stress. Tree Physiology. 23:1125-1136.

Meinzer, F.C., S.A. James and G. Goldstein 2004. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiology. 24:901-909.

Meinzer, F.C., S.A. James, G. Goldstein and D. Woodruff 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. Plant, Cell and Environment. 26:1147-1155.

Moncrieff, J.B., P.G. Jarvis and R. Valentini 2000. Canopy Fluxes. *In* Methods in ecosystem science Eds. O.E. Sala, P. Jackson, H.A. Mooney and R.W. Howarth. Springer, New York, p. 421.

Nadler, A., E. Raveh, U. Yermiyahu and S.R. Green 2003. Evaluation of TDR use to monitor water content in stem of Lemon Trees and Soil and their response to water stress. Soil Science Society of America Journal. 67:437-448.

Oren, R. and D.E. Pataki 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia. 127:549-559.

Parrish, W.B. 1961. Detecting defects in wood by the attenuation of gamma rays. Forest Science. 7:136-143.

Pataki, D.E., R. Oren, G. Katul and J. Sigmon 1998. Canopy conductance of *Pinus taeda, Liquidambar styraciflua* and *Quercus phellos* under varying atmospheric and soil water conditions. Tree Physiology. 18:307-315.

Pearcy, R.W., E.-D. Schulze and R. Zimmermann 1991. Measurement of transpiration and leaf conductance. *In* Plant Physiological Ecology Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, London, p. 457.

Phillips, N.G., M.G. Ryan, B.J. Bond, N.G. McDowell, T.M. Hinckley and J. Cermak 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest. Tree Physiology. 23:237-245.

Ryhiner, A.H. and J. Pankow 1969. Soil moisture measurement by the gamma transmission method. Journal of Hydrology. 9:194-205.

Sparks, J., G.S. Campbell and R.A. Black 2000. Liquid water content of wood tissue at temperatures below 0 C. Canadian Journal of Forest Research. 30:624-630.

Sparks, J., G.S. Campbell and R.A. Black 2001. Water content, hydraulic conductivity, and ice formation in winter stems of *Pinus contorta*: a TDR case study. Oecologia. 127:468-475.

Sperry, J.S. 2003. Evolution of water transport and xylem structure. International Journal of Plant Science. 164:S115-S127.

Spicer, R. and B.L. Gartner 2001. The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. Trees. 15:222-229.

Spicer, R. and N.M. Holbrook 2005. Within-stem oxygen concentration and sap flow in four temperate tree species: does long-lived xylem parenchyma experience hypoxia? Plant, Cell and Environment. 28:192-201.

Stratton, L., G. Goldstein and F.C. Meinzer 2000. Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. Plant, Cell and Environment. 23:99-106.

Topp, G.C., J.L. Davis and A.P. Annan 1980. Electromagnetic determination of soil water content: measurements in coaxial transmission lines. Water Resources Research. 16:574-582.

Topp, G.C., J.L. Davis and A.P. Annan 1982. Electromagnetic determination of soil water content using TDR: II. Evaluation of installation and configuration of parallel transmission lines. Soil Science Society of America Journal. 46:678-684.

Tyree, M.T. and S. Yang 1990. Water-storage capacity of *Thuja, Tsuga* and *Acer* stems measured by dehydration isotherms. Planta. 182:420-426.

Waring, R.H. and W. Running 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant, Cell and Environment. 1:131-140.

Woods, F.W., W.A. Hough, D. O'Neal and J. Barnett 1965. Gamma ray attenuation by loblolly pine wood: an investigation of integral counting. Forest Science. 11:341-345.

Wullschleger, S.D., P.J. Hanson and D.E. Todd 1996. Measuring stem water content in four deciduous hardwoods with a time-domain reflectometer. Tree Physiology. 16:809-815.

Wullschleger, S.D., P.J. Hanson and D.E. Todd 2001. Transpiration from a multi-species, deciduous forest as estimated by xylem sap flow techniques. Forest Ecology and Management. 143:205-213.

Wullschleger, S.D., P.J. Hanson and T.J. Tschaplinski 1998. Whole-plant water flux in understory red maple exposed to altered precipitation regimes. Tree Physiology. 18:71-79.

Wullschleger, S.D. and A.W. King 2000. Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. Tree Physiology. 20:511-518.

APPENDIX 1

DATALOGGER PROGRAMS

Campbell CR23x program for recording data from homemade Granier sap flux sensors (2 and 10 cm long), CS616 TDR probes, Theta TDR probes, and thermocouples using three AM32 multiplexers.

TABLE 1
00: SCAN INTERVAL
    01: 300 SECONDS (5 min)

Sap Flux 2 cm probe
01: P86: DO
    01: 41 SET PORT C1 HIGH
02: P87: BEGIN LOOP
    01: 0 DELAY
    02: 32 COUNT
03: P90: STEP LOOP INDEX
    01: 01 STEP
04: P86: DO
    01: 72 PULSE PORT C2
05: P02: VOLT (DIFF)
    01: 1 REPS
    02: 21 RANGE
    03: 1 DIFF CHANNEL
    04: 1CA LOC TO STORE
    05: 25 MULTIPLIER
    06: 0 OFFSET
06: P95: END LOOP
07: P86: DO
    01: 51 SET PORT C1 LOW

Sap Flux 10 cm probe
08: P86: DO
    01: 43 SET PORT C3 HIGH
09: P87: BEGIN LOOP
    01: 0 DELAY
    02: 15 COUNT
10: P90: STEP LOOP INDEX
    01: 01 STEP
11: P86: DO
    01: 74 PULSE PORT C4
12: P02: VOLT (DIFF)
    01: 1 REPS
    02: 21 RANGE
    03: 2 DIFF CHANNEL
    04: 33CA LOC TO STORE
    05: 25 MULTIPLIER
    06: 0 OFFSET
13: P95: END LOOP
14: P86: DO
    01: 53 SET PORT C3 LOW

CS TDR
15: P86: DO
    01: 45 SET PORT C5 HIGH
16: P138: CS616 PROBE
    01: 5 REPS
    02: 7 SE CHANNEL
    03: 5 CONTROL PORT
    04: 48 LOC TO STORE
    05: 1 MULTIPLIER
    06: 0 OFFSET
17: P55: POLYNOMIAL
    01: 5 REPS
    02: 48 LOC TO GET FROM
    03: 53 LOC TO STORE
    04: 0.0950
    05: -0.0211
    06: .0010
    07: 0
    08: 0
    09: 0

18: P86: DO
01: 55 SET PORT C5 LOW

19: P17: PANEL TEMP
01: 63 LOC TO STORE

Tree Thermocouples
20: P14: TC TEMP (DIFF)
01: 5 REPS
02: 21 RANGE
03: 7 CHANNEL LOC
04: 03 TC TYPE (K)
05: 63 REF LOC
06: 58 LOC
07: 1 MULT
08: 0 OFFSET

21: P92: IF TIME, THEN WRITE DATA
01: 0 MIN INTO A
02: 15 MIN INTERVAL, THEN
03: 10 SET OUTPUT FLAG HIGH
22: P80: SET ACTIVE STORAGE AREA
01: 1 STORAGE AREA
02: 100 ARRAY ID
23: P77: REAL TIME
01: 0110
24: P71: AVG
01: 63 REPS
02: 1 LOC TO GET FROM

TABLE 2
THETA TDR
00: SCAN INTERVAL
01: 3600 SECONDS (1 hr)

01: P86: DO
01: 46 SET PORT C6 HIGH
02: P87: BEGIN LOOP
01: 0 DELAY
02: 5 COUNT
03: P90: STEP LOOP INDEX
01: 01 STEP
04: P86: DO
01: 77 PULSE PORT C7

05: P02: VOLT (DIFF)
01: 1 REPS
02: 25 RANGE
03: 3 DIFF CHANNEL
04: 64CA LOC TO STORE
05: 0.001 MULTIPLIER
06: 0 OFFSET
06: P55: POLYNOMIAL
01: 1 REPS
02: 64CA LOC TO GET FROM
03: 69CA LOC TO STORE
04: 1
05: 6.25
06: -5.96
07: 4.39
08: 0
09: 0
07: P34: Z=X+F
01: 69CA LOC
02: -1.6 F
03: 74CA LOC TO STORE Z
08: P37: Z=X*F
01: 74 X LOC
02: 11.905 F
03: 79 LOC TO STORE Z
09: P95: END LOOP
10: P86: DO
01: 56 SET PORT C6 LOW

11: P17: PANEL TEMP
01: 84 LOC TO STORE
12: P92: IF TIME, THEN WRITE DATA
01: 0 MIN INTO A
02: 240 MIN INTERVAL, THEN
03: 10 SET OUTPUT FLAG HIGH
13: P80: SET ACTIVE STORAGE AREA
01: 2 STORAGE AREA
02: 200 ARRAY ID
14: P77: REAL TIME
01: 0110
15: P71: AVG
01: 21 REPS
02: 64 LOC TO GET FROM

CR10X Table 2 Program for Weather Station (Dynamax 1996)

```
00: SCAN INTERVAL
        01: 300         SECONDS
01: P10: BATTERY VOLTAGE
        01: 205 LOC TO STORE
[BATTV]
02: P17: PANEL TEMP
        01: 193 LOC TO STORE
[PTEMP]
03: P86: DO
        01: 48 SET PORT C8 HI
04: P22 EXCITATION W/ DELAY
        01: 3   EXCIT CH
        02: 0   DELAY W/ EXCITE
        03: 10  DELAY AFTER
EXCITE
        04: 0   mV EXCITATION
05: P01: SE VOLT
        01: 1   REPS
        02: 25  RANGE
        03: 5   SE CHANNEL
        04: 194  LOC TO STORE
[AIRT]
        05: 0.1 MULTIPLIER
        06: -40 OFFSET
06: P01: SE VOLT
        01: 1   REPS
        02: 25  RANGE
        03: 6   SE CHANNEL
        04: 195  LOC TO STORE [RHF]
        05: 0.001       MULTIPLIER
        06: 0   OFFSET
07: P86: DO
        01: 58 SET PORT C8 LOW
08: P56 eSAT
        01: 194 LOC [AIRT]
        02: 196 LOC TO STORE
[eSAT]
09: P36: Z=X*Y
        01: 196 X LOC [eSAT]
        02: 195 Y LOC [RHF]
        03: 197 LOC TO STORE Z [e]
10: P35: Z=X-Y CALCULATION OF
VPD
        01: 197 X LOC [e]
        02: 196 Y LOC [eSAT]
        03: 198 LOC TO STORE Z
[VPD]
11: P02: VOLT (DIFF)
        01: 1   REPS
        02: 3   RANGE
        03: 4   DIFF CHANNEL
        04: 199 LOC TO STORE [PAR]
        05: 263.635     MULTIPLIER
        06: 0   OFFSET
12: P03: PULSE
        01: 1   REPS
        02: 1   PULSE INPUT CHANNEL
        03: 21  LOW LEVEL AC, OUTPUT Hz
        04: 200  LOC TO STORE [WS]
        05: 0.75        MULTIPLIER
        06: 0.2         OFFSET
13: P89: IF (X>=<F)
        01: 200         X LOC [WS]
        02: 1   =
        03: 0.2 F
        04: 30  THEN DO
14: P30 Z=F
        01: 0   F
        02: 0   EXPONENT OF 10
        03: 201         Z LOC [WS]
15: P95: END LOOP
16: P04 EXCITE DELAY SE
        01: 1   REPS
        02: 5   RANGE
        03: 11  SE CHANNEL
        04: 2   EXCITE ALL REPS W/ EX CH 2
        05: 2   DELAY (UNITS 0.01S)
        06: 2500        mV EXCITATION
        07: 202  LOC TO STORE [WDIR]
        08: 0.142       MULTIPLIER
        09: 0   OFFSET
17:P34: Z=X+F
        01: 201         X LOC [WDIR]
        02: 90  F
        03: 202         LOC TO STORE Z
18: P89: IF (X<=>F)
```

```
        01: 202 X LOC [WDIR]
        02: 3 >=
        03: 360         F
        04: 30  THEN DO
19: P34: Z=X+F
        01: 202         X LOC [WDIR]
        02: -360        F
        03: 202  LOC TO STORE Z [WDIR]
20: P95: END
21: P03: PULSE
        01: 1   REPS
        02: 2   PULSE INPUT CHANNEL
        03: 2   SWITCH CLOSURE
        04: 203  LOC TO STORE [P]
        05: 0.254       MULTIPLIER
        06: 0           OFFSET
22: P11: SOIL TEMP 107
        01: 1   REPS
        02: 9   SE CHANNEL
        03: 1   EXCITE ALL REPS W/
EX CH 1
        04: 204  LOC TO STORE
[SOILT]
        05: 1   MULTIPLIER
        06: 0   OFFSET
23: P92: IF TIME, THEN WRITE DATA
        01: 0   MIN INTO A
        02: 15  MIN INTERVAL, THEN
        03: 10  SET OUTPUT FLAG
HIGH
24: P80: SET ACTIVE STORAGE AREA
        01: 1   STORAGE AREA
        02: 200         ARRAY ID
25: P77: REAL TIME
        01: 0110
26: P71: AVG
        01: 13  REPS
        02: 193 LOC TO GET FROM
27: P72: TOTALIZE
        01: 1 REPS
        02: 202 LOC TO GET FROM
[P]
```

Datalogger program for calibration of sap flux 10-cm probe

Calibrate long probes
TABLE 1
00: SCAN INTERVAL
    01: 15 SECONDS (.25 min)

Sap Flux 10 cm probe
01: P02: VOLT (DIFF)
    01: 11 REPS
    02: 21 RANGE
    03: 1   DIFF CHANNEL
    04: 1   LOC TO STORE
    05: 25   MULTIPLIER
    06: 0   OFFSET

02: P17: PANEL TEMP
    01: 12 LOC TO STORE
03: P92: IF TIME, THEN WRITE DATA
    01: 0   MIN INTO A
    02: 1   MIN INTERVAL, THEN
    03: 10 SET OUTPUT FLAG HIGH
04: P80: SET ACTIVE STORAGE AREA
    01: 1   STORAGE AREA
    02: 100 ARRAY ID
05: P77: REAL TIME
    01: 0110
06: P71: AVG
    01: 12 REPS
    02: 1 LOC TO GET FROM

Datalogger program for VWC calibration. Measures CS616 TDR probe and 2 thermocouples to record internal and external wood temperature in severed stump.

TABLE 1
CS TDR
00: SCAN INTERVAL
    01: 300 SECONDS (5 min)

01: P138: CS616 PROBE
    01: 1 REPS
    02: 1 SE CHANNEL
    03: 1 CONTROL PORT
    04: 1 LOC TO STORE
    05: 1 MULTIPLIER
    06: 0 OFFSET
02: P55: POLYNOMIAL
    01: 1 REPS
    02: 1 LOC TO GET FROM
    03: 2 LOC TO STORE
    04: 0.0950
    05: -0.0211
    06: .0010
    07: 0
    08: 0
    09: 0
03: P86: DO
    01: 51 SET PORT C1 LOW
04: P17: PANEL TEMP
    01: 5 LOC TO STORE
02: P14: TC TEMP (DIFF)
    01: 2 REPS
    02: 21 RANGE
    03: 2 CHANNEL LOC
    04: 01 TC TYPE (T)
    05: 5 REF LOC
    06: 3 LOC
    07: 1 MULT
    08: 0 OFFSET

05: P92: IF TIME, THEN WRITE DATA
    01: 0 MIN INTO A
    02: 15 MIN INTERVAL, THEN
    03: 10 SET OUTPUT FLAG HIGH
06: P80: SET ACTIVE STORAGE AREA
    01: 1 STORAGE AREA