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Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees

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Summary Trees of tropical semi-deciduous forests range from stem-succulent, "drought-avoiding" species with low-density wood (< 0.5 g cm^{-3}), which maintain high stem water potentials (Ψ_{STEM} > −0.7 MPa) throughout the year, to "drought-tolerant" deciduous hardwood species (wood density > 0.75 g cm^{-3}), which dehydrate strongly during seasonal drought (Ψ_{STEM} < −6 MPa). In stem-succulent and other drought-avoiding species, xylem vessels are surrounded by extensive parenchyma providing intracellular water storage, whereas in deciduous species, stem water storage is mainly extracellular. Thirteen tropical and two temperate tree species, representing different functional types, were studied. The contribution of stem water storage to these species' water use during water stress was determined by time-series analysis of dehydration and rehydration of excised leaf-bearing branches of these trees. During dehydration, stem water potential slowly declined 1–2 MPa in drought-avoiding species, but in deciduous species it rapidly fell 4–5 MPa, suggesting that water storage capacitance was related to xylem anatomy. After immersion of dehydrated, leafless branches in water, the decline in xylem tension and rate of water uptake during rehydration were linearly related, as predicted by application of Ohm's law to water flux. The decline of xylem tension during rehydration was biphasic, with a phase of rapid water uptake into extracellular spaces being followed by a prolonged phase of slow water uptake into living cells. The rate of water uptake during rehydration and the minima of leaf water potential observed in the field during the dry season were highly correlated with water storage capacitance, indicating that wood anatomy is a major determinant of drought adaptation.

Keywords: deciduous hardwood trees, drought avoidance, stem-succulent trees, stem water storage, tropical dry forest.

Introduction

Trees of tropical semi-deciduous forests exhibit considerable variation in leaf phenology and seasonal water relations. Leaf phenology ranges from shallow-rooted, deciduous hardwood species and stem-succulent species that are leafless during most of a severe dry season (lasting 5–6 months) to deep-rooted, leaf-exchanging and brevi-deciduous species that maintain leaves through much of the year and replace their foliage during the dry season (Borchert 1994*a*, Borchert et al. 2002). The degree of dry season water stress, measured by stem water potential (Ψ_{STEM}), varies widely among these functional types (Borchert 1994*a*, 1994*b*, Borchert et al. 2002). In deciduous species, Ψ_{STEM} may decline to less than −4 MPa), while stem-succulent trees remain well above −1 MPa, and leaf-exchanging and brevi-deciduous trees are intermediate (Figure 1). Across species, minimum Ψ_{STEM} declines with increasing wood density (Figure 1; Borchert 1994*a*, Borchert et al. 2002) and hence with declining stem water storage, which is inversely related to wood density (Borchert 1994*a*; Figure 2). Such a general relation is expected, because withdrawal of water from storage in tree stems will reduce the decline of Ψ_{STEM} during periods of water stress (Holbrook 1995). Generally, however, the causal relations between wood anatomy, stem water storage and xylem tension are not well understood (Meinzer et al. 2003). This paper addresses the relationships among these variables in branches of 15 tree species representing the major functional tree types (stem-succulent, leaf-exchanging, brevi-deciduous and deciduous) from tropical and temperate habitats.

In many deciduous, cold-temperate hardwood species, small-diameter (microporous) vessels are embedded in a ground tissue consisting mainly of tracheids connected to the vessels via numerous pits (Figure 2A). Water transport takes place throughout the sapwood (Figure 2D). Parenchyma cells are largely confined to the rays and constitute a relatively small fraction of the wood (Figure 2A; Braun 1970). Water storage occurs primarily in tracheids surrounding the vessels (Figures 2A and 2D), with parenchyma cells contributing as little as 6% of daily transpiration (Tyree and Yang 1990). Water storage in dead, lignified wood cells has been referred to as extracellular, capillary or inelastic water storage (Tyree and Yang 1990, Holbrook 1995). Because water storage capacitance of such tissues is low, small changes in water content re-

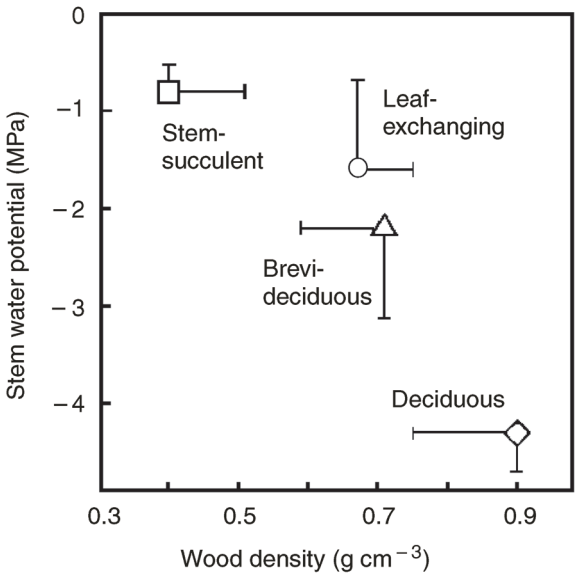

Figure 1. Relationship between minimum stem water potentials observed during the dry season and wood density in trees of four functional groups in the semideciduous forests of Guanacaste, Costa Rica. Data were calculated for the 36 species listed in Table 2 of Borchert 1994.

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sult in large changes of water potential (Holbrook 1995).

The anatomy of water-transporting tissues varies widely among tropical hardwood trees. In the leaf-exchanging and stem-succulent species included in this study (Table 1), water transport is confined to large-diameter (macroporous) vessels (Figure 2E), which are surrounded by a sheath of paratracheal parenchyma (Figure 2B; Braun 1970, Malavassi 1995). These vessels are often embedded in extensive strands or tangential bands of parenchyma (Figure 2F; Holbrook 1995), which are in contact with parenchymatic tissues in the bark and pith, and thus constitute a coherent system of living cells throughout the stem (Braun 1970). In stem-succulent species, parenchyma may constitute 40–80% of the low-density wood, and individual vessels are surrounded by this parenchymatic ground tissue (Figure 2C). These species have high water storage capacitance (intracellular or elastic water storage; Holbrook 1995), causing Ψ_{STEM} to change slowly during water loss or gain.

It is likely that interspecific differences in stem anatomy and tissue capacitance are responsible for the variation in minimum Ψ_{STEM} observed seasonally among tropical tree functional groups (Figure 1) and during dehydration of excised tree branches. Without water uptake from soil, dehydration of excised branches draws principally upon water stored in stem tissues. Thus, the goal of this study was to assess the linkage between wood anatomy, tissue capacitance and dehydration response of Ψ_{STEM} by testing the following predictions: first, that during dehydration, Ψ_{STEM} declines slowly in species with extensive intracellular water storage, but rapidly in species with mainly extracellular water storage; and second, that during rehydration, Ψ_{STEM} of leafless branches increases rapidly as extracellular water storage is replenished and slowly during intracellular water uptake. To evaluate these predictions, Ψ_{STEM} and stem water content were monitored simultaneously during controlled dehydration and subsequent rehydration of branches from a variety of cold-temperate and tropical tree species representing different functional types.

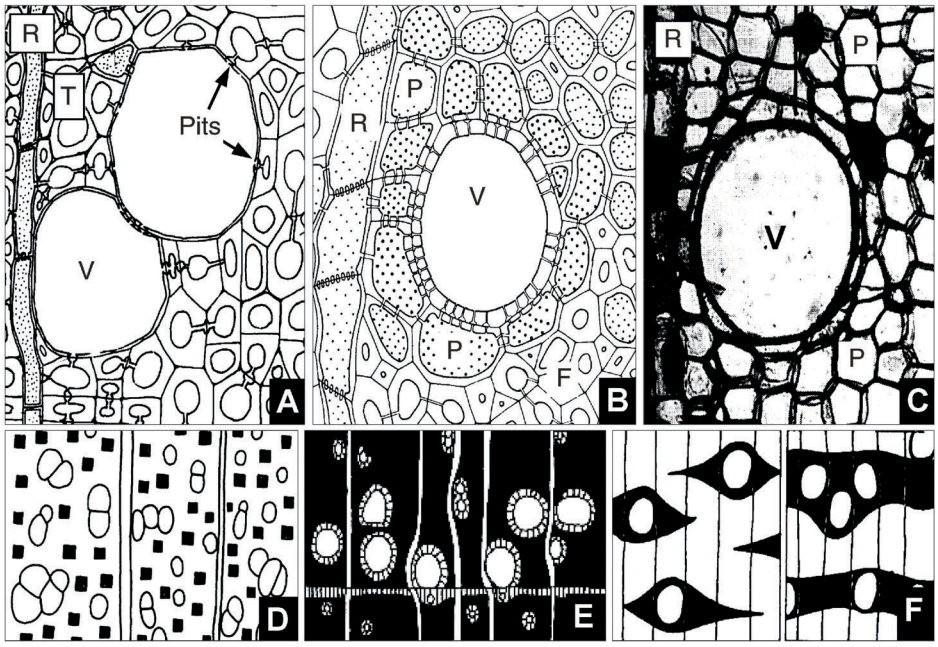

Figure 2. Functional anatomy of water conduction and storage in tree species of different functional types. (A) Cold-temperate hardwood species with vessels surrounded by tracheids (*Fagus sylvatica* L.). (B) Cold-temperate and tropical hardwood species with large vessels surrounded by a sheath of paratracheal parenchyma (*Fraxinus excelsior* L.). (C) Tropical stem-succulent tree with large vessels imbedded in parenchymatic ground tissue (*Bombax* sp.). (D and E) Water conduction (white) indicated by the distribution of fluorescent dye in the xylem. (D) Water conduction in the entire sapwood (vessels and tracheids of wood shown in A). (E) Water conduction restricted to macroporous vessels in wood shown in B. (F) Aliform or confluent complexes of interfibrillary parenchyma (black) surround vessels with a paratracheal parenchyma sheath in many tropical trees. Abbreviations: P = parenchyma; R = ray; T = tracheids; and V = vessel. (Modified from Braun 1970.)

Table 1. Capacitance during dehydration and rehydration of branches and minimum leaf water potential (Min Ψ_{LEAF}) observed in the field for 13 tropical tree species of three different functional types (deciduous hardwood (mesic leaves shed during the dry season); leaf-exchanging (coriaceous leaves exchanged during dry season) and stem-succulent (low-density wood, leafless during dry season)). Capacitance (in h MPa^{-1}) was calculated as the inverse of the rate of decline of water potential of exposed leaves ($\Delta\Psi_{LEX}/T$; see Methods) measured from 1 h after the start of dehydration to its end (Figures 6A, 6C and 6E). Increase in water potential of covered leaves (Ψ_{LCOV}, in MPa h^{-1}, from Figures 6A, 6C and 6E) and the initial rate of water uptake (in g min^{-1}, from Figures 6B, 6D and 6F) are given as measures of rehydration. Minimum leaf water potential (in MPa) is from Borchert (1994) and Borchert et al. (2002).

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Species	Dehydration	Rehydration		Field
	Capacitance	$\Delta\Psi_{LCOV}$	Water uptake	Min Ψ_{LEAF}
Deciduous Hardwood Species				
Calycophyllum candidissimum (Vahl.) DC	0.97	16.6	0.55	−5.6
Cordia alliodora (Ruiz & Pav.) Oken	0.97	13.1	0.33	−4.5
Guazuma ulmifolia Lam.	1.00	8.5	0.35	−4.3
Tabebuia neochrysantha A. Gentry	2.67	5.6	0.41	−6
Mean	1.4 ± 0.84	10.9 ± 4.9	0.41 ± 0.1	−5.1 ± 0.8
Leaf-exchanging Species				
Albizia guachapele (Kunth) Dugand	4.55		0.33	−1.8
Cassia grandis L.f.	3.75	0.1	0.12	−2.2
Dalbergia retusa Hemsl.	20.00		0.10	−2.2
Hymenea courbaril L.	4.00	0.6	0.15	−2.6
Licania arborea Seem.	6.25	3.6	0.17	
Samanea saman (Jacq.) Merr.	5.29	1.2		−2.7
Simarouba glauca DC	12.00	0.5	0.13	−1.5
Mean	8.0 ± 6.0	1.2 ± 1.4	0.16 ± 0.08	−2.2 ± 0.5
Stem-succulent Species				
Bombacopsis quinata (Jacq.) Dugand	15.71	0.0	0.02	−0.6
Spondias purpurea L.	12.22	0.0		−1
Mean	14.0 ± 2.5	0	0.02	−0.8 ± 0.3

Materials and methods

Experimental trees and sites

Experiments with cold-temperate, deciduous hardwood species were done between July and September mainly with Bradford pear (*Pyrus calleryana* Dcne.). Long, forked branches with many medium-sized leaves were readily obtained from small trees on the campus of the University of Kansas in Lawrence. Additional measurements were made with crabapple (*Malus* spp.), sugar maple (*Acer saccharum* Michx.), white ash (*Fraxinus americana* L.) and weeping willow (*Salix babylonica* L.), also collected from campus. Experimental species native to the semi-deciduous neotropical forests of Guanacaste, Costa Rica, are listed in Table 1 and are referred to by genus name in the text. Experiments were done with trees bearing leaves of different ages in July, October and January–March at Hacienda La Pacifica, Cañas, Guanacaste, the site of earlier ecophysiological studies (Borchert 1994*a*, Borchert et al. 2002).

Branch dehydration

In most experiments, 1–1.5-m-long forked branches bearing several twigs were cut in the afternoon, immediately placed into water and covered with a plastic bag overnight. For measurement of changes in water potential during dehydration and rehydration, about 20–30 leaves on one arm of a forked branch were left to transpire during dehydration (exposed leaves). On the other arm, 10–20 leaves were wrapped individually with aluminum foil and all other leaves were removed, or entire twigs were enclosed in plastic bags to eliminate transpiration (covered leaves).

At the start of dehydration, the freshly cut branch was sealed with vacuum grease to prevent the formation of air emboli at the base of the stem that might inhibit subsequent re-hydration. Branches of cold-temperate trees were dehydrated in an illuminated growth chamber (irradiance = 500 mmol m^{-2} s^{-1}; temperature = 29 °C; relative humidity = 45–50%) to favor water loss. The water potential of exposed leaves (Ψ_{LEX}), used as an indicator of increasing xylem tension, was measured periodically until it stabilized around −3.5 MPa. Branches of tropical trees were suspended in light shade on an open porch, where daytime temperature ranged from 28–35 °C and relative humidity varied between 60–85%. Water potential of exposed leaves was measured until it stabilized below −4 MPa or, if the decline was very slow, for at least 6–8 h or until dusk.

For measurement of Ψ_{LEX}, at each sampling time, two leaves were placed in a plastic bag and stored in a plastic cooler lined with moist paper. Water potential of exposed leaves was measured with a pressure chamber (Model 1000, PMS, Corvallis, OR) within 30 min after sampling. Recorded values of Ψ_{LEX} are means of the two sample leaves, which rarely varied by more than 0.1 MPa.

Water loss during dehydration was measured by weighing the entire branch on a top-loading electronic balance (Sarto-

rius, Göttingen, Germany, Model 2224; sensitivity 10 mg) and expressed as percent of total branch fresh weight. In some branches of stem-succulent species, stem shrinkage during dehydration was measured with a caliper to the nearest 0.1 mm.

Changes in capacitance during dehydration of *Pyrus* branches were calculated from Ψ_{LEX} and branch weight measured at regular intervals. As a substitute for the conventional relative water content (RWC), which normalizes water content to dry mass and thus requires destructive sampling, changes in the water content of entire branches were normalized by initial branch fresh mass and expressed as normalized branch water content (nBWC):

$$\text{nBWC} = \frac{(\text{FM}_\text{I} - \text{WL}_\text{T})}{\text{FM}_\text{I}} 100 \quad (1)$$

where FM_I = initial branch fresh mass and WL_T = total water loss during dehydration at time *T*.

To test this method and assess the effect of leaf sampling for Ψ_{LEX} measurements on changes in stem tissue capacitance during dehydration, the decline in Ψ_{LEX} and branch water content was measured simultaneously in three *Pyrus* branches of different size. In these branches, the stem fresh mass/leaf fresh mass ratio was adjusted initially to values greater than 1 by partial leaf removal (Figure 3). This ratio increased further during dehydration with the sampling of leaves for the measurement of Ψ_{LEX}. In all branches, the decline in nBWC and Ψ_{LEX} during branch dehydration followed the same characteristic time course (Figure 3A and 3B). The time course of Ψ_{LEX} during dehydration appears to be affected little by moderate variation in the rate of decline in nBWC and hence by leaf removal. The equation for capacitance (*C*):

$$C = \frac{\Delta\text{RWC}}{\Delta\Psi} \quad (2)$$

can therefore be transformed to:

$$C = \frac{\text{constant}}{\Delta\Psi} \quad (3)$$

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i.e., *C* is inversely proportional to the rate of decline in Ψ_{LEX}, $d\Psi/t$. Changes in capacitance during consecutive phases of branch dehydration can thus be identified by measurement of Ψ_{LEX} at regular intervals (Figure 3B) and *C* can be expressed in h MPa^{-1}. This method was used for calculation of capacitance during dehydration of tropical tree branches (Table 1). Confirming the validity of this method, the time course of capacitance calculated from the measured decline in nBWC was identical to that calculated with an assumed, constant rate of decline in stem water content (Figure 3C, open symbols versus closed symbols).

Branch rehydration

Except for one experiment (shown in Figure 4), all exposed leaves were removed before branch rehydration. To start rehydration, the greased, basal end of the branch was excised and

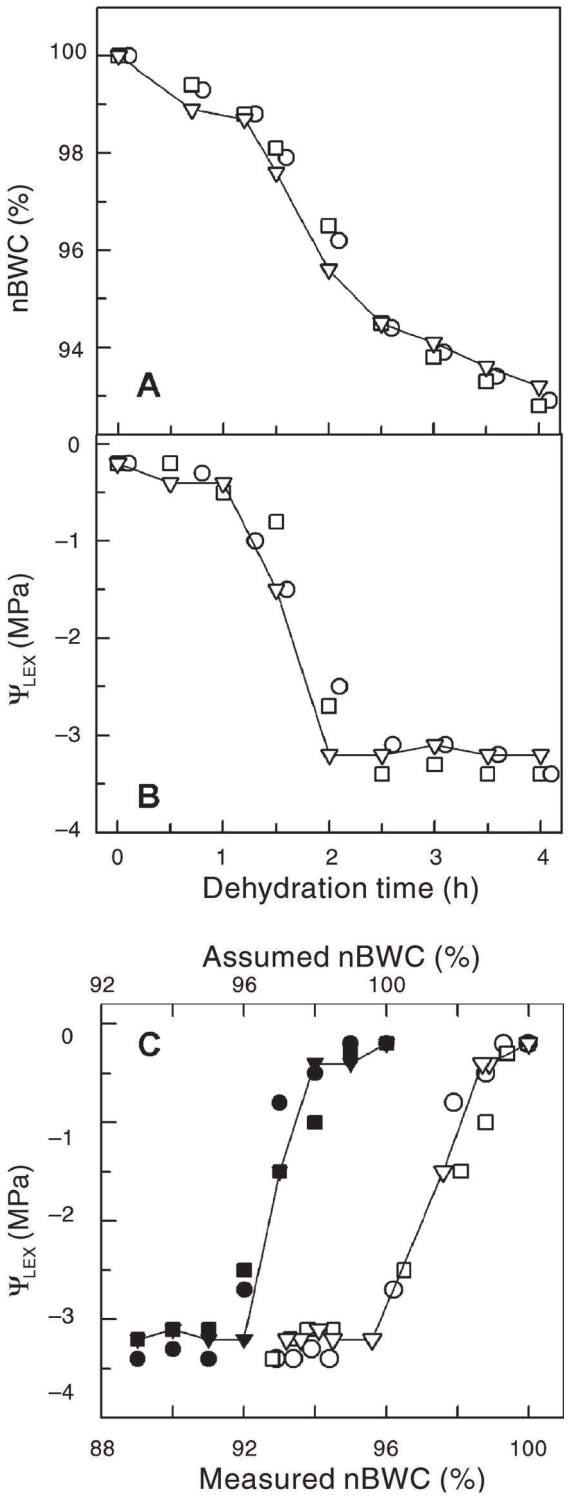

Figure 3. Dehydration in three branches of *Pyrus*, in which the ratio between water storing stem tissues (stem fresh mass) and transpiring leaf surface (leaf fresh mass) was adjusted to values greater than 1 by partial removal of leaves. (A) Decline in normalized branch water content (nBWC) during dehydration of three branches (□, ○, ▽). (B) Decline in water potential of exposed leaves (Ψ_{LEX}) during dehydration. (C) Changes in Ψ_{LEX} as a function of a decline in measured (□, ○, ▽) and assumed (■, ●, ▼) nBWC. Branch diameters (mm) and stem and leaf masses (g), respectively, for: □ = 15.1, 213.8 and 107.8; ○ = 12.7, 158.8 and 62.4; and ▽ = 9.2, 41.6 and 37.1.

the cut end was immediately immersed in water. To monitor the decrease in xylem tension during rehydration, the Ψ of covered leaves (Ψ_{LCOV}) was measured periodically (see above). For measurement of water uptake during rehydration, the re-cut branch was placed in a plastic beaker, containing 60–70 ml water, on a top-loading electronic balance (Ohaus, Florsham Park, NJ, Model TS120; sensitivity 0.1 mg). Beginning about 1 min after immersion of the branch, the beaker's weight was recorded every 1–4 min and the rate and cumulative amount of water uptake were calculated, graphed and monitored throughout the measurement. All experiments were repeated with two to three branches of the same species on the same day or over two consecutive days.

Results

Dehydration and rehydration in Pyrus

Three distinct phases, characterized by different rates of decline in Ψ_{LEX}, were evident during dehydration of *Pyrus* branches. Initially, Ψ_{LEX} declined slowly to about –0.5 MPa, then rapidly to –2.5 to –3 MPa, then slowly again at values below –3 MPa (Figure 3B). Water potential of covered leaves declined to the same values as Ψ_{LEX} (Figure 4), confirming that changes in Ψ on the transpiring side of the forked branch were transmitted throughout the branch. When water loss was expressed as changes in nBWC, the time course of dehydration was similar among branches of different size in which stem fresh mass exceeded leaf fresh mass (Figure 3A). The nonlinearity in the relationship between Ψ_{LEX} and nBWC indicates that the amount of water extracted from tissue storage varied throughout the different phases of the dehydration process (Figure 3C). The low rate of change of Ψ_{LEX} during the initial and final phases of dehydration indicates that water extraction occurred from capacitance. In contrast, the rapid change in Ψ_{LEX} during the middle phase of dehydration indicates that, during this phase, water was lost from tissues with low capacitance.

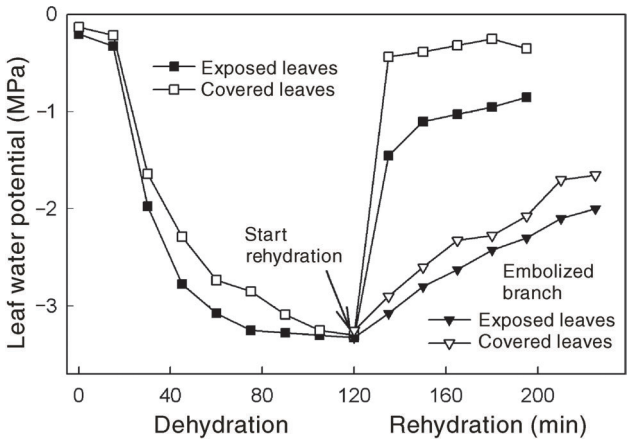

Figure 4. Dehydration and rehydration in a bifurcated branch of *Pyrus*. Changes in the water potential of exposed (■) and covered leaves (□) during dehydration of the branch in a growth chamber (0–120 min) and after rehydration started by immersing the re-cut branch base in water (120–240 min). Symbol ▼ = rehydration in a different branch embolized by exposure of the re-cut base to air for 5 min.

During rehydration of *Pyrus* branches, Ψ_{LCOV} increased to high values (about –0.5 MPa; Figure 4) within 15–20 min and Ψ_{LEX} rose to somewhat lower values (Figure 4). The rate of rehydration was reduced when the cut end of re-cut branches was exposed to air for 5 min before immersion in water, presumably because the amount of functional xylem was reduced by the introduction of air emboli (Figure 4).

According to a simple analogy with Ohm's law, the rate of water uptake by a branch (F) is described by $F = \Delta\Psi/R$, where $\Delta\Psi$ is the water potential difference between living cells in the branch and water in the beaker ($\Psi_{BEAKER} - \Psi_{LCOV}$) and R is the resistance to flow. For a given value of R, the rate of water uptake during rehydration should decline as Ψ_{LCOV} increases and approaches Ψ_{BEAKER}. The maximum rates of water absorption and total water uptake during rehydration varied widely with branch length and diameter (Figure 5A); however, these temporal variations were proportional, as indicated by the strong linear relationship between these variables (Figure 5C).

If the rate of water uptake (F_T) during rehydration followed a simple exponential decay of the initial rate (F_0), an equation of the form:

$$F_T = Ae^{F_0/-T} \quad (4)$$

(Keen and Spain 1992) should describe the response, where T is time and A is a constant. A logarithmic plot of the decline in water uptake during rehydration in a large and a small branch did not yield straight lines (Figure 5B). Instead, linear regressions through initial and final subsets of the data in each curve revealed two consecutive phases of re-hydration fitting a simple exponential decay. The initial phase exhibited rapid rehydration, followed by a second phase characterized by a lower rate of water uptake (Figure 5B, solid and dashed lines).

Results obtained with branches of *Malus* (data not shown) were identical to those described for *Pyrus*. In contrast, neither leafless nor leaf-bearing dehydrated branches of *Acer*, *Fraxinus* or *Salix* absorbed water at initial rates above 0.03 g min^{-1}, suggesting that the vessels of these branches were completely embolized by the end of dehydration (data not shown).

Branch dehydration and rehydration in tropical trees

Branch dehydration was associated with decreases in Ψ_{LEX} that varied widely across the different functional groups. In tropical deciduous species, Ψ_{LEX} declined to values between –4 and –5 MPa within 3–4 h (Figure 6A). In leaf-exchanging and stem-succulent species, the response of Ψ_{LEX} during dehydration differed fundamentally from those observed in *Pyrus* and tropical deciduous species. After a brief and rapid initial drop to values between –1 and –2 MPa, Ψ_{LEX} declined very slowly for many hours (Figure 6C and 6E). Water potential of exposed leaves generally remained above –2 MPa for > 8 h in stem-succulent species (Figure 6E) and declined from –2 to –3 MPa over a period of 4–8 h in leaf-exchanging species (Fig-

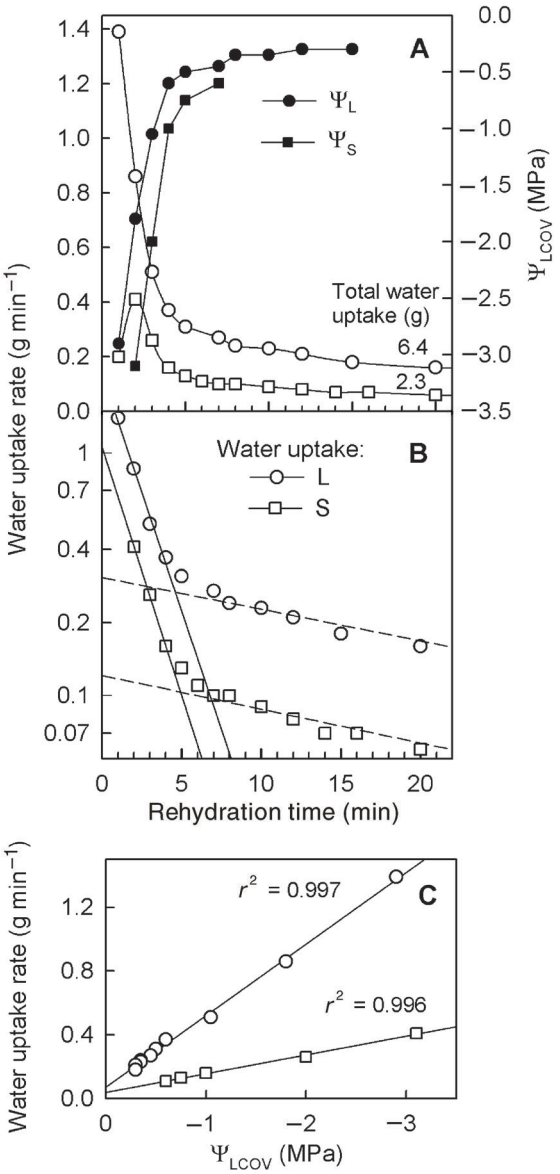

Figure 5. (A) Simultaneous measurement of the water potental of covered leaves (Ψ_{LCOV}; ■, ●) and water absorption (□, ○) during rehydration of a large (L) and a small (S) *Pyrus* branch. (B) Logarithmic plot of water uptake shown in A. Regressions were calculated for the first 3–4 (——) and last 5–6 measurements (– – –). (C) Regression of Ψ_{LCOV} against water uptake in A.

ure 6C). During these long dehydration periods, immature, unlignified shoot tips wilted on exposed and covered twigs; the smooth bark of the branches became progressively more wrinkled; branch diameter decreased (Figure 6E, stem shrinkage); and shriveling of the thin-walled, mucilage-filled pith cells of stem-succulent species (*Bombacopsis*, *Spondias*) resulted in the formation of air-filled cavities in the pith of twigs. Although branches were too heavy to be weighed on the available balance, these observations show that substantial amounts of water were lost during periods of minimal decline in Ψ_{LEX}, indicating that stem capacitance in these species was high.

During rehydration of deciduous species, the rapid rise in Ψ_{LCOV} (Figure 6A) and the biphasic decline in the rate of water uptake was similar to that of the temperate deciduous *Pyrus* described above (Figure 6B). In rehydrating branches of leaf-exchanging species, Ψ_{LCOV} increased by about 1 MPa over a period of 30–60 min (Figure 6C). The initial rate of water uptake during re-hydration ranged from a maximum of 0.33 to a minimum of 0.02 g min^{-1} (Figure 6D). These values were always significantly lower than in deciduous species (Table 1; compare Figures 6B and 6D). In stem succulents, immersion of re-cut leafless branches in water never caused Ψ_{LCOV} to increase (Figure 6E) or water uptake rate to exceed 0.03 g min^{-1} (Figure 6F). Branches of stem succulents with exposed, transpiring leaves exhibited relatively high rates of water uptake. However, these rates declined to low values immediately after defoliation (Figure 6 F), suggesting that leaves were responsible for the higher rates of water uptake observed before they were excised.

The distinct trend from rapid dehydration in branches of deciduous species to slow dehydration in stem-succulent species (Figure 7A) and the corresponding trend from low to high water-storage capacitance (Figure 7B, Table 1) were correlated with trends in the initial rate of water uptake during rehydration (Figure 7C, Table 1) and in the minimum Ψ_{LEAF} observed during the dry season in the field (Figure 7A, right; Table 1). Regressions in Figure 8 confirmed that correlations between water storage capacitance and these variables are indeed high for the means of the three functional types.

Discussion

Water storage capacitance and tree water relations

The data presented here demonstrate that wood structure strongly influences drought response across a diverse group of temperate and tropical tree species. Wood anatomy, particularly the amount and distribution of parenchyma, varies widely among the tropical dry forest species studied (Figure 2; Borchert 1994*a*, 1994*b*, Borchert et al. 2002) and was strongly correlated with tissue capacitance during dehydration. The close association between leaf phenology (Borchert 1994*a*, 1994*b*) and water storage capacitance illustrates the range of different trait combinations that may succeed in a particular environment.

The dehydration and rehydration responses observed in isolated branches (Figure 7) represent a distinct progression from low water-storage capacitance in deciduous hardwood species (Figures 6A and 6B) to large capacitance in stem-succulent species (Figures 6E and 6F). The basis for the differences in capacitance across these groups is reflected in the correspondence between wood density, saturation water content (Figure 1) and wood anatomy (Figure 2). Water storage capacitance was highly correlated with the minimum Ψ attained during dehydration (Figures 7A and 8C) and the rate of water uptake during rehydration (Figures 7C and 8B). Similar patterns were observed in tropical semi-deciduous forests in Hawaii (Stratton et al. 2000) and Panama, where sapwood capacitance ranged from low values in the deciduous *Cordia allio-*

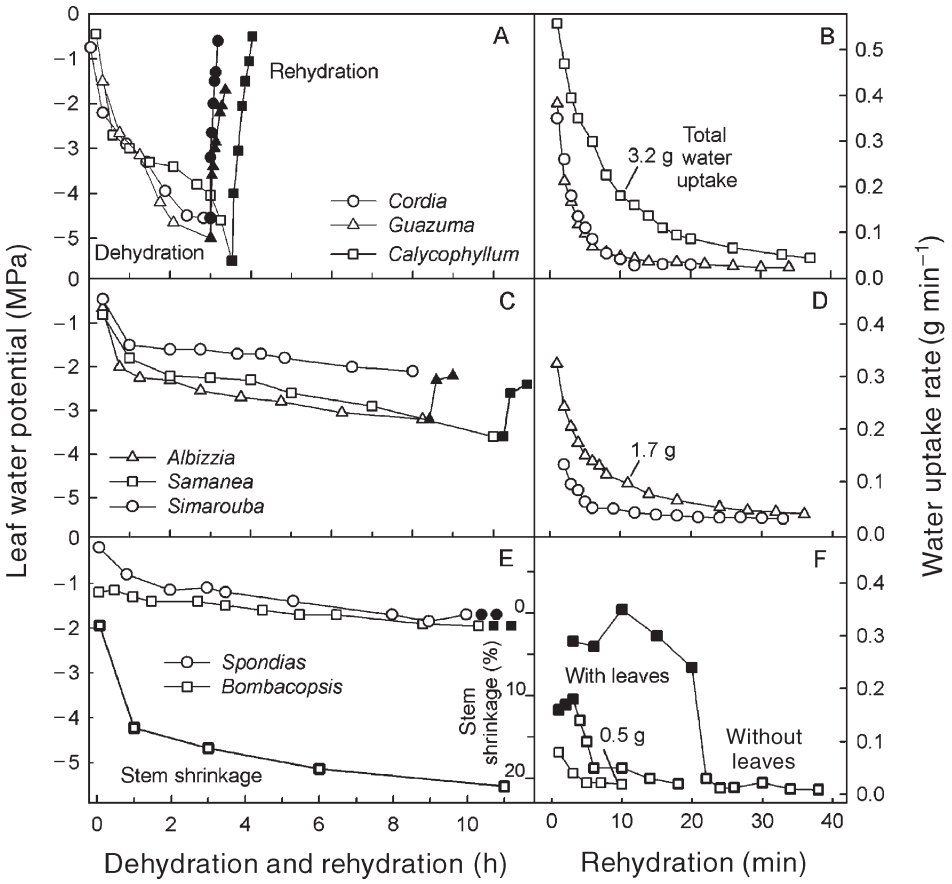

Figure 6. Dehydration of exposed leaves (○, △, □) and rehydration of covered leaves (●, ▲, ■; A, C and E) and water uptake (B, D and F) in tropical tree species of different functional types in the semi-deciduous forest of Guanacaste, Costa Rica. (A and B) Deciduous species (*Calycophyllum candidissimum*, *Cordia alliodora*, *Guazuma ulmifolia*). (C and D) Leaf-exchanging species (*Albizzia guachapele*, *Licania arborea*, *Samanea saman*, *Simarouba glauca*). (E and F) Stem-succulent species (*Bombacopsis quinata*, *Spondias purpurea*). Stem shrinkage during dehydration is shown for *Bombacopsis* in E. In F, water uptake of *Bombacopsis* during rehydration was measured in both leafless stems (□) and in stems with exposed leaves before (■) and after defoliation (◘).

dora (compare Table 1) to high capacitance in the evergreen *Schefflera morototoni* (Meinzer et al. 2003).

The dehydration and rehydration responses observed in excised branches correspond to seasonal observations of whole-tree water relations in tropical dry forests. The minimum Ψ attained during dehydration of branches in this study corresponded closely to the Ψ measured in these same species at peak drought in the field (Figure 7A; Borchert 1994*a*). This correspondence indicates that the differences in capacitance observed here contribute, in the same manner, to the drought response of intact trees. Other studies have reported strong relationships between water storage capacitance and other variables, including minimum branch Ψ, soil-to-branch hydraulic conductance, daily utilization of stored water and water movement between the xylem and wood parenchyma (Meinzer et al. 2003). Rooting depth is also likely to be important because even the high-capacitance species discussed here must replace most daily transpiration with soil water (Holbrook 1995). These and other observations make it increasingly apparent that whole- tree physiology is constrained by suites of traits related to size, architecture and tissue properties (Meinzer 2003). The species-independent scaling of several aspects of tree water relations with water storage capacitance (Figure 8; Meinzer et al. 2003) indicates that the extent of intra- versus extracellular water storage in woody stems, as determined by wood anatomy (Figure 2), constitutes one of the principal constraints of tree physiology in seasonally dry tropical forests.

Water storage capacitance of stem tissues appears to be the principal determinant of the two major strategies observed among tropical tree species adapted to severe seasonal drought (Ludlow 1989). Drought tolerance is limited to deciduous species with low capacitance, whose tissues tolerate desiccation to low water potentials and saturate quickly during experimental rehydration (Figure 6A) and after heavy rain or irrigation in the field (Borchert 1994*c*, Borchert et al. 2002). All species with paratracheal parenchyma and extensive wood parenchyma are drought avoiders, which generally maintain Ψ_{STEM} well above the turgor loss point. In these species, cavitation remains low despite daily loss and replacement of as much as 15–20% of the water stored in stems (Machado and Tyree 1994, Goldstein et al. 1998). During experimental dehydration of the succulent stems of *Ochroma* and *Pseudobombax*, turgor loss and frequent cavitations started at Ψ_{STEM} below –1.2 MPa (Machado and Tyree 1994). However, in the field, Ψ_{STEM} of such species was never observed to decline below –0.7 MPa during the dry season, making cavitation unlikely (Borchert 1994*a*, Borchert et al. 2002).

The range of water storage capacitance of tropical dry forest species is likely to influence their regulation of transpiration during drought. Modeling studies have demonstrated clear physical limits to soil water extraction and xylem water transport (Sperry et al. 1998, 2002). Field studies using this modeling framework have shown the relevance of these physical

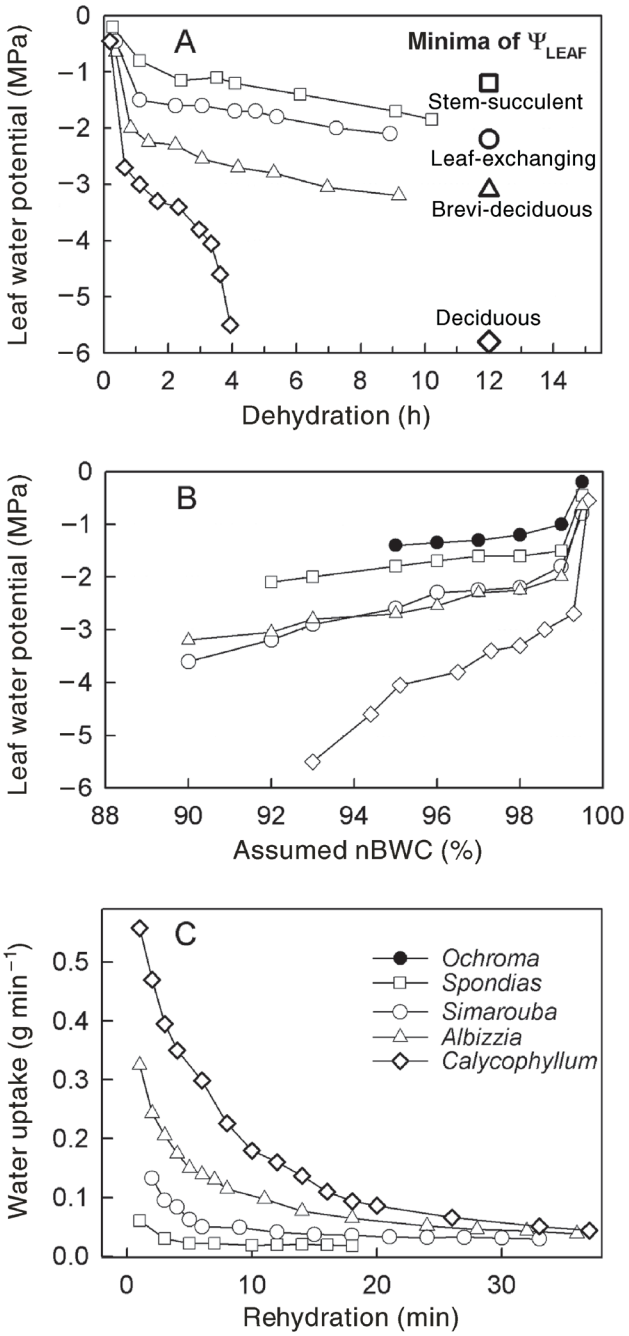

Figure 7. Comparison of dehydration and rehydration curves for branches from tropical trees of different functional types. (A) Experimental dehydration (left) and minima of leaf water potential (Ψ_{LEAF}) observed in the field during seasonal drought (right; data from Borchert et al. 2002). (B) Relationship between water potential of exposed leaves and nBWC declining at an assumed rate of 2 g h^{-1}. The dehydration curve for isolated stem sections of the tropical stem-succulent species *Ochroma pyramidale* (●) is redrawn from Machado and Tyree (1994). (C) Water-uptake during rehydration.

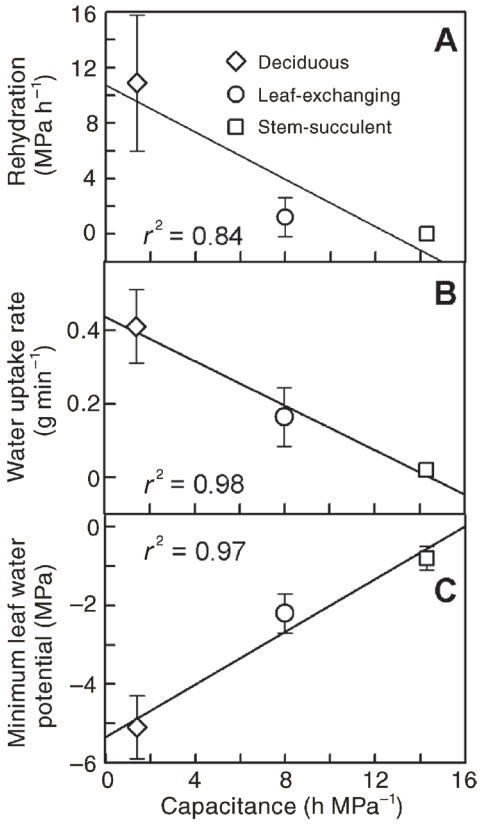

Figure 8. Correlations between water storage capacitance and increase in water potential of exposed leaves during rehydration (A), initial rate of water uptake during rehydration (B) and minima of leaf water potential observed during the dry season among trees of three functional groups. Means and errors from Table 1.

limits to water transport during drought (e.g., Sperry and Hacke 2002). However, water storage capacitance has yet to be fully explored in the context of these physical limits. Modeling efforts have, so far, focused largely on simpler steady state conditions, whereas field data in this area come primarily from temperate species with low water-storage capacitance. This and other studies of tropical trees show that capacitance contributes significantly to daily transpiration and drought response (Tyree et al. 1991, Goldstein et al. 1998). By relaxing the requirement for immediate soil water uptake to replace transpiration, water storage capacitance in species like the leaf-exchanging and stem-succulent ones studied here may allow trees to remain within the hydraulic limits associated with water transport during prolonged drought. The details of this effect await comparative studies across the range of capacitance observed here.

Branch dehydration

Variation in water storage capacitance during different phases of branch dehydration has been observed in all temperate and tropical tree species analyzed to date (Figures 3C and 7B; Tyree and Wang 1990, Tyree et al. 1991, Machado and Tyree 1994). These patterns of dehydration correspond to species-specific differences in the characteristics of living and dead cells from which water is lost during branch dehydration (Figure 2). Water is typically released from capillary spaces (inter-

Au: Tyree and Wang 1990 is not in Refs.

cellular spaces and cavitated xylem conduits) at water potentials above –0.6 MPa (Holbrook 1995). The amount of water released from intracellular storage depends on the quantity of living cells and their water relations parameters (elastic modulus, turgor loss point, etc.), with the greatest capacitance often occurring after turgor loss (Brodribb and Holbrook 2003). Finally, release of water by cavitation in xylem conduits can occur at pressures that vary widely across species (e.g., Pockman and Sperry 2000).

Branch dehydration in *Pyrus* was similar across branch sizes (Figure 3A) and occurred in three phases: an initial phase of relatively high capacitance ($\Psi_{LEX} > -0.5$ MPa), a second phase with very low capacitance and a final phase with higher capacitance at Ψ_{LEX} below –3 MPa (Figures 3B and 3C). The tropical deciduous species exhibited a similar response but, notably, did not exhibit the same initial period of high capacitance (compare Figure 3B with Figures 6A, 6C, 6E and 7A). The reasons for this difference are unknown but could reflect differences in the amount of capillary storage between *Pyrus* and the tropical deciduous species. Alternatively, partial refilling of embolized xylem during rehydration of *Pyrus* prior to dehydration could have artificially increased the observed capacitance.

In the absence of more detailed measurements, the degree of capacitance and prevailing tissue water potentials suggest the likely source of the water lost during each phase. The low-capacitance phase, observed in temperate and tropical deciduous species, probably corresponds to the depletion of capillary water at relatively high Ψ (Figure 7A and 7B; Holbrook 1995). Once capillary water is exhausted, tissue capacitance will be much lower until living cells or cavitation of functional xylem, or both, release significant quantities of water at lower Ψ (Tyree and Wang 1990). During dehydration of other cold-temperate species, acoustic emissions associated with xylem cavitation have been observed at Ψ_{STEM} below –2.5 MPa, corresponding to the inflection point between low- and high-capacitance phases (Tyree and Yang 1990). Although living cells in the small number of attached leaves on each sample could have contributed to the capacitance observed during dehydration, this effect should be minimized by the large difference between the amount of leaf tissue and stem tissue in the large branches measured. In future studies, this effect could be avoided by measuring Ψ with stem psychrometers to further decrease the amount of leaf area attached to branches (Dixon et al. 1984).

Au: Tyree and Wang is not in Refs.

Whereas the temperate (Figure 3) and tropical deciduous species (Figures 2A and 7B, *Calycophyllum*) exhibited periods of low capacitance during dehydration, the stem-succulent species with extensive intracellular water storage demonstrated high capacitance (Figures 2C and 7B, *Ochroma*, *Spondias*). The long duration of high capacitance and the large number of living cells in the stem-succulent species suggest that intracellular water storage released water throughout most of the dehydration period. Water released from xylem cavitation may also contribute to the second phase, a possibility that could be evaluated by comparing vulnerability curves for these species. The distinct differences between the dehydration curves of temperate and deciduous tropical species (Figures 3A and 3B versus Figures 7A and 7B, *Calycophyllum*) may reflect qualitative differences in wood anatomy, such as the fraction of tracheids in the wood (Figures 2A and 2D).

Branch rehydration

The rehydration patterns observed across the functional groups studied here also reflect differences in anatomy and water storage capacitance. The driving force for water uptake (Ψ_{LCOV}; Figure 5A) was linearly related to the rate of water uptake by *Pyrus* branches (Figure 5C). However, logarithmic plots of water uptake indicated that the decline in water uptake did not correspond to simple exponential decay of the initial rate. Rather, the rehydration response was the composite of two transport processes with different rates (Figure 5B). This biphasic decline in water uptake during re-hydration, previously observed in non-transpiring *Pelargonium* leaves, has been ascribed to water uptake by extracellular and then intracellular compartments of the leaf (Weatherley 1963). In *Pelargonium*, rapid water uptake was completed within 15–20 min, while osmotic water uptake by living cells lasted for hours. In *Pyrus*, rapid water uptake was completed during the first 10 min of rehydration (Figures 4 and 5A), after which the rate of water uptake was low. After Ψ_{LCOV} had exceeded –0.5 MPa, parenchymatic tissues in stem and leaves apparently continued slow osmotic uptake of water lost during dehydration (Figure 5A, right). In accordance with wood anatomy (Figure 2A), the dehydration and rehydration curves of isolated branches of *Pyrus* and tropical deciduous species (Figures 6A and 6B) indicate the predominant role of extracellular water storage in branch water relations.

In contrast, rehydration of stem-succulent species illustrates the role of the large capacitance resulting from extensive intracellular water storage. Within 1–3 min after the cessation of transpiration, xylem tension was largely eliminated by reverse osmosis, as indicated by a rapid decline of water uptake to low rates (Figure 6F). Correspondingly, there was no notable increase in Ψ_{LCOV} (Figure 6E). Complete rehydration of parenchymatic stem tissues and the corresponding stem expansion are likely to last at least as long as the decline in Ψ_{LEX}, and stem diameter measured during dehydration and was not monitored to completion (Figure 6E). During early rehydration, measurement of relatively low values of Ψ_{LCOV} (Figure 6E; about –2 MPa) in the absence of xylem tension resulting in water uptake (Figure 6F) suggests that Ψ_{LCOV} is determined by the osmotic potential of the paratracheal parenchyma. During early rehydration of leaf-exchanging species, moderate water uptake resulted in an increase of Ψ_{LCOV} by about 1 MPa, likely to indicate the elimination of xylem tension caused by loss of extracellular water (Figure 6C).

The extent of changes in hydraulic conductance during dehydration and rehydration is difficult to assess. The difference in *Pyrus* rehydration rate with and without the formation of air emboli (Figure 4), and the linear relationship between Ψ and water uptake during rehydration (Figure 5C), suggest that embolism frequencies were not high at the end of the dehydration phase of the experiment. Yet one interpretation of the third

phase of dehydration of *Pyrus* branches is that the observed capacitance was a result of water released by xylem cavitation. Stem water potentials during phase three were sufficiently low, and the quantity of parenchyma sufficiently small, that release of water from intracellular or capillary storage are unlikely explanations, although some water was probably released from plasmolyzed cells during phase three. Direct measurements during dehydration and rehydration are required to assess changes in hydraulic conductance. However, in the absence of such data, it should be noted that small amounts of cavitation may release sufficient water to account for the observed capacitance at low water potentials (Dixon et al. 1984, LoGullo and Salleo 1992). Such cavitation may have only a small effect on stem hydraulic conductance, particularly if cavitation occurred in tracheids or small vessels that carry only a small portion of flow through the xylem. Another possibility is that rapid refilling restored the function of these conduits. Refilling has been observed without the development of positive pressure (Holbrook et al. 2001) and the mechanisms are still a matter of continuing study (e.g., Holbrook and Zwieniecki 1999).

The results of this study demonstrate the anatomical basis for the observed correlations between water storage capacitance and leaf phenology. When these data are combined with published observations (Tyree et al. 1991, Meinzer et al. 2003), the trends appear to be robust across temperate and tropical tree species representing the full range of leaf phenology from drought- and winter-deciduous to evergreen species. The different patterns that we observed are likely to have important consequences for regulation of transpiration on daily and seasonal time scales that deserve continuing study.

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