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Water status and development of tropical trees during seasonal drought

Rolf Borchert

Department of Physiology and Cell Biology, University of Kansas, Haworth Hall, Lawrence KS 66045-2106, USA

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Summary. Bud break, shoot growth and flowering of trees involve cell expansion, known to be inhibited by moderate water deficits. In apparent contradiction to physiological theory, many trees flower or exchange leaves during the 6 month-long, severe dry season in the tropical dry forest of Guanacaste, Costa Rica. To explore this paradox, changes in tree water status during the dry season were monitored in numerous trees. Water potential of stem tissues (Ψ_{stem}) was obtained by a modification of the pressure chamber technique, in which xylem tension was released by cutting defoliated branch samples at both ends. During the early dry season twigs bearing old, senescent leaves generally had a low leaf water potential (Ψ_{leaf}), while Ψ_{stem} varied with water availability. At dry sites, Ψ_{stem} was very low in hardwood trees (<–4 MPa), but near saturation (>–0.2 MPa) in lightwood trees storing water with osmotic potentials between –0.8 and –2.1 MPa. At moist sites trees bearing old leaves rehydrated during drought; their Ψ_{stem} increased from low values (<–3 MPa) to near saturation, resulting in differences of 3–4 MPa between Ψ_{stem} and Ψ_{leaf}. Indirect evidence indicates that rehydration resulted from osmotic adjustment of stem tissues and improved water availability due to extension of roots into moist subsoil layers. In confirmation of physiological theory, elimination of xylem tension by leaf shedding and establishment of a high solute content and high Ψ_{stem} were prerequisites for flowering and bud break during drought.

Key words: Bud break – Drought – Stem water potential – Tree water status – Tropical dry forest

Introduction

Cell growth is the process most sensitive to water stress in plants (Hinckley et al. 1991). Tree growth should thus remain arrested during the 4–6 month long dry season characterizing tropical drought-deciduous forests and should resume during the early rainy season. Contrary to this prediction and in apparent violation of physiological theory, the majority of tree species in the dry lowland forest of Guanacaste, Costa Rica, flower or leaf out during the dry season after shedding their leaves (Frankie et al. 1974; Borchert 1991). In confirmation of earlier, preliminary studies (Reich and Borchert 1982, 1984), recent measurements of the changes in water status of many trees during two consecutive dry seasons revealed that, with few exceptions, trees rehydrate before vegetative or flower buds begin to expand. The degree of desiccation and the rate and timing of rehydration vary strongly with the availability of water stored in tree trunks or in the subsoil, which buffers the impact of seasonal environmental drought (Borchert 1993a). The time course of tree development during the dry season (phenology), seasonal changes in tree water status, stem water storage as a function of wood density, and soil water availability at different sites were found to be highly correlated and to characterize the adaptation of tree species to certain sites within the tropical dry forest ecosystem. Species with similar characters were tentatively grouped into ecophysiological types ("ecotypes"; Borchert 1993a) which are summarized in Tables 1 and 2 and illustrated by examples to be analyzed in this study.

Monitoring of seasonal changes in water status of dry forest trees raised questions concerning the feasability and usefulness of available measurement techniques. The merits of relative water content *vs* water potential in measurements of the water status of herbaceous plants is a topic of current debate (Sinclair and Ludlow 1985; Hinckley et al. 1991). Assessment of water status is considerably more difficult in trees because of their large size and complexity. For instance, steep gradients in water potential may develop between trunk and outer branches (Hinckley et al. 1991), and the water content of sapwood usually declines during the growing season with increasing xylem tension, while the bark water content doubles during the early growing season and declines later (Fig. 1; Gibbs 1958); i.e., the water content of adjacent tissues changes in opposite ways.

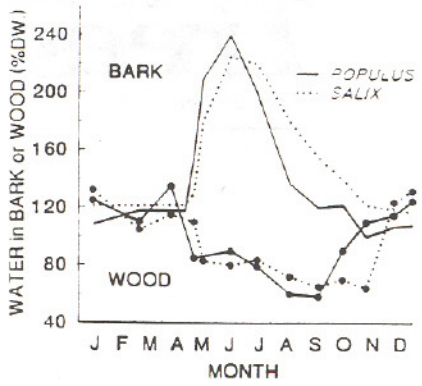


Fig. 1. Annual variation in water content of bark and wood of *Populus deltoides* and *Salix fragilis* (redrawn from Gibbs 1958)

Measurement of seasonal changes in the water status of tropical trees presents additional problems, which do not arise in temperate trees and hence have not been addressed in the past. For example, water storage in the trunks of many tropical trees with low-density wood enables flowering of bare trees during the early dry season or bud break during the late dry season, when stem shrinkage indicates water loss (Reich and Borchert 1984; Bullock and Solis-Magallanes 1990). Analysis of such phenomena requires methods to assess quantity and water potential of stored water and water transport to developing organs. In other species, large differences in the water status of organs within the same tree crown may arise because consecutive growth cycles of tropical trees are not as well separated in time as in temperate broadleaved trees. For example, the large, sclerophyllous leaves of *Tabebuia rosea* are shed gradually during the dry season. Leaf abscission starts in the upper part of the crown, and large flowers open on the bare, upper branches while the lower branches still carry old, strongly desiccated leaves lacking stomatal control (Reich and Borchert 1988). Similarly, in many leaf-exchanging species terminal or axillary buds begin to expand on branches bearing old leaves. Cell expansion in growing buds or flowers, supposedly sensitive to water stress, thus takes place in a crown or on branches bearing strongly water-stressed, senescent leaves.

In this study, the pressure chamber was used in a novel way to measure the water potential of stem tissues (Ψ_{stem}) after elimination of xylem tension. Establishment of a high Ψ_{stem} during drought, which depended on water availability and the presence of high solute concentrations in stem tissues, was found to be a prerequisite for flowering and bud break during the dry season.

Materials and methods

Field site. Field observations were made at Hacienda La Pacifica (Guanacaste, Costa Rica) located at 45 m elevation in the "Tropical dry forest, moist province transition" *sensu* Holdridge (Hartshorn 1983). Field site and climate have been described in detail elsewhere (Reich and Borchert 1982, 1984; Borchert 1993a). Annual mean temperature is 27.8°C and mean precipitation during the last decade was 1240±385 mm (Hagnauer 1993). More than 95% of annual rainfall occurs during the rainy season between late May and November.

Table 1. Sites and tree ecotypes in the tropical dry forest of Guanacaste, Costa Rica

DRY UPLAND FOREST. Tree roots have no access to the groundwater table. Soil water reserves are depleted early in the dry season in dense tree stands.
D_{hard} – Deciduous **hard**wood trees shed leaves gradually during the early dry season and desiccate strongly; rehydration and bud break occur only after the first heavy rains of the rainy season.
D_{light} – Deciduous **light**wood trees with high stem water storage shed mesomorphic leaves rapidly at the beginning of the dry season and retain a high water content throughout the dry season while stems shrink markedly. Most species flower over prolonged periods during the early dry season and bud break occurs late in the dry season before the beginning of rains.

UPLAND SAVANNA – Roots of widely spaced trees have no access to the groundwater table, but tap subsoil water reserves not accessible to the herbaceous vegetation.
D_{soft} – Deciduous **soft**wood trees rehydrate and flower after leaf shedding during the dry season.

MOIST LOWLAND SITES – Tree roots have access to subsoil moisture throughout the dry season.
EV_{soft} – **EV**ergreen **soft**wood trees exchange coriaceous leaves and flower during the dry season.
EV_{light} – **EV**ergreen **light**wood trees exchange leaves and maintain a high water content during the dry season

Phenology and changes in tree water status were observed during two consecutive dry seasons, January–June 1991 and December 1991–February 1992. The latter period, for which changes in tree water relations and phenology are reported here, was unusually dry: the last substantial rain fell on October 14 1991, and there was no precipitation exceeding 3 mm.

Experimental trees. Tree species used are given in Table 2. They are representative of more than 35 species studied in some detail (Borchert 1993a). Species names follow Hartshorn (1983), where author names may be found. Species will be referred to by genus name only. Experimental trees, ranging from 5 to 14 m in height, were studied at sites from very low (dry upland forest) to good soil moisture availability (Table 1). Tree development (phenology) was monitored weekly or biweekly as described in Borchert (1993a).

Measurement of tree water status. Water potential was measured with a pressure chamber in samples obtained from lower tree branches with a tree pruner or from the crown of 12 forest trees accessible from 10 m high bamboo scaffolding. Triplicate samples were collected weekly, usually between 05 30 and 07 00 hours, and immediately placed into plastic bags, stored in a cooler containing moist paper, and processed within 2 h after sampling. If variation among samples exceeded 0.3 MPa, measurements were repeated the next day. When maximum compensation pressure attainable with the pressure chamber used (4 MPa) was insufficient to cause emergence of xylem sap at the cut surface, a water potential of <−4 MPa was recorded. *Leaf water potential* (Ψ_{leaf}), a measure of xylem tension, was obtained from leaves or leaf-bearing branch sections. During the early dry season all leaves were 6–8 months old and somewhat senescent; stomatal conductance of darkened leaves rarely declined below 30–50% of leaves in light (C. Martin, personal communication). To measure equilibration of such leaves with soil moisture, leaves wrapped in aluminum foil and enclosed in plastic bags in the evening were collected the next morning at 06 00 hours for measurement of predawn Ψ_{leaf}.

In a modification of the standard pressure chamber technique, *stem water potential* (Ψ_{stem}) was measured in bare or defoliated, 10 cm-long branch sections *cut at both ends* to release xylem tension. Results obtained with this method will be evaluated in the discussion.

Electric resistance to AC of <1 kHz (or impedance) between electrodes in tree trunks varies with the amount and ion content of cell sap

Table 2. Experimental species and ecophysiological and phenological characteristics of tree ecotypes in the tropical dry forest of Guanacaste described in Table 1

ECOTYPE – *Species*	Phenology			Stem		Water status			Figure
	Shed	Flush month	Flower	Density g cm^{-3}	Max water % DW	Ψleaf MPa	Ψstem MPa	SM %	
	B	C	D	E	F	G	H	I	J
D_{hard}	*Means of 9 species:*			*0.94*	*32*	*–3.7*	*–3.9*	*31*	
Lysiloma seemanii	2–4	6–7	7	0.92	30	<–4	<–4	31	6C
Tabebuia ochracea subsp. *neochrysantha*	1–2	5–6	after rain	1.1	20	–3.9	<–4	29	3A
D_{light}	*Means of 6 species:*			*0.40*	*193*	*–1.5*	*–0.5*	*63*	
Enterolobium cyclocarpum	1–2	2–4	2–4	0.49	125	–2.3	–1.1	52	4A
Spondias purpurea	12	5–6	1–2	0.37	191		–1	69	4B
D_{soft}	*Means of 9 species:*			*0.71*	*65*	*–2.5*	*–2.4*	*47*	
Cordia alliodora	2–3	6	2	0.70	63	–3.7	<–4	37	3B
Guazuma ulmifolia	1–2	4–5	3–4	0.67	71	–2.5	–1.7	45	3C
Myrospermum frutescens	12–1	4–5	1–2	0.80	48	–3.5	–3.6	44	6D
Pterocarpus rohrii	12–1	4–5	2	0.52	114	–2	–2.2	42	3D
EV_{soft}	*Means of 9 species:*			*0.64*	*74*	*–2.5*	*–1.6*	*46*	
Andira inermis	11–1		2	0.70	64	–1	–0.3	44	6B
Licania arborea	irregular		1	0.59	100	–4	–0.5	50	2A–C
Pithecelobium saman	3		3	0.14	57	–2.7	–2.4	49	6A
EV_{light}	*Means of 5 species:*			*0.47*	*143*	*–2.0*	*–0.8*	*51*	
Eugenia salamensis	3–5	4–6	3–6	0.60	89	–3.5	–1.5	49	2D–F
Gmelina arborea	irregular		12–2	0.42	167	–1.6	–0.8	54	4C

Columns: A – Species (for authors and families see Borchert 1993a); B–D – Phenology: month of leaf shedding (D), flushing (E), flowering (F); E, F – Wood properties: E – wood density; F – percentage maximum water content of wood. G–I – Tree water status during the dry season. All measurements represent the lowest observed values during the dry season. G – Ψ_{leaf}; H – Ψ_{stem}; I – stem moisture. J – Reference to Figure in Results (data from Borchert 1993a)

released by cells wounded during electrode insertion and hence with abundance and water status of living cells in stem tissues (Blanchard et al. 1983). For avocado (*Persea*) and spruce (*Picea*), electric resistance, expressed as percent of the species-specific maximum, was found to be highly correlated with Ψ_{leaf} (Dixon et al. 1978). Because twigs for measurement of Ψ_{stem} are difficult to obtain for tall forest trees, measurements of electric resistance were used to estimate site- and species-specific differences in water status of numerous trees. For each measurement, a pair of parallel nails (40 mm long) was driven 20 mm deep and 10 mm apart into bark and sapwood of tree trunks. Resistance between these electrodes was measured with a Bouyoucos soil moisture meter (Model BN-2B using AC of 480 Hz, Beckman, Cedar Grove, N. J.). Instead of the instrument's inconvenient exponential scale for Ohm, the linear, arbitrary scale indicating "percent available soil moisture" was used and data are given as *percent stem moisture* (SM), which thus constitutes a *relative* measure based on electric resistance of the outer 20 mm of tree trunks. Measurements were found to be highly correlated with other measures of tree water status and developmental changes during the dry season (Table 2; Borchert 1993a; Borchert, in preparation).

Changes in stem circumference (*stem shrinkage*) were measured using aluminum dendrometer bands installed at breast height (Liming 1957). For light- and softwood trees, *wood density* and *maximum water content* (Table 2) were determined in wood cores excised with an increment borer (5 mm diameter, 30 mm long) and weighed fresh, after soaking for 24 h, and after oven drying (Schulze et al. 1988). For hardwood species resisting the increment borer, wood density of the same or related species was obtained from Barajas-Morales (1987), and maximum water content (MWC) was calculated as % MWC = (1 – D/1.5) 100 /D, where D = wood density and 1.5 is the mean density of wood substance. Values obtained with this formula were closer to measured values than those calculated using the relation % MWC = –0.93+1.02 /D, derived from measurements with tropical deciduous tree species (Schulze et al. 1988).

Osmotic concentration of bark and wood tissues was obtained from cores (9 cm long, 5 mm diameter) freshly excised with an increment borer. Sections of bark and wood (5 and 10 mm long, respectively) were squeezed with a pair of pliers and the osmolality of the expelled sap, absorbed onto filter paper disks (5 mm diameter), was measured in an osmometer (Model 5100A Vapor Pressure Osmometer, Wescor, Provo, Utah). Water content of bark and wood was determined by weighing sections after excision and after oven drying.

Field data were analyzed and graphed using the Quattro-Pro spreadsheet (Borland International, Scotts Valley, Calif.), Axum (Trimetrix, Seattle, Wash.) and a Hewlett-Packard Laser Printer.

Results

Differences between Ψ_{leaf} and Ψ_{stem}

At moist sites, *Licania* is an evergreen tree bearing the leathery, sclerophyllous leaves of 2–3 consecutive flushes on long, relatively thin branches, whose extension growth ends with the formation of a terminal inflorescence. Abscission of old leaves is irregular, and in older branches leaf-bearing sections alternate with 10–20 cm long bare sections. Using the pressure chamber, water potential was measured in March 1991 in sets of stem samples with or without attached organs, cut from the same branch (Fig. 2). Consistently, the water potential of bare stem sections (Ψ_{stem}) was quite high (often > –0.2 MPa), Ψ_{leaf} of adjacent branch sections bearing old, brittle leaves was very low (<–4 MPa), and branches bearing young leaves or developing fruits had water potentials between –0.6 and

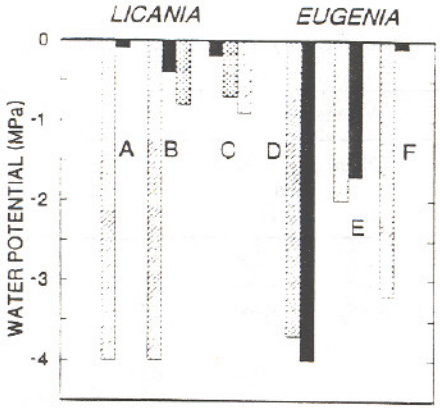
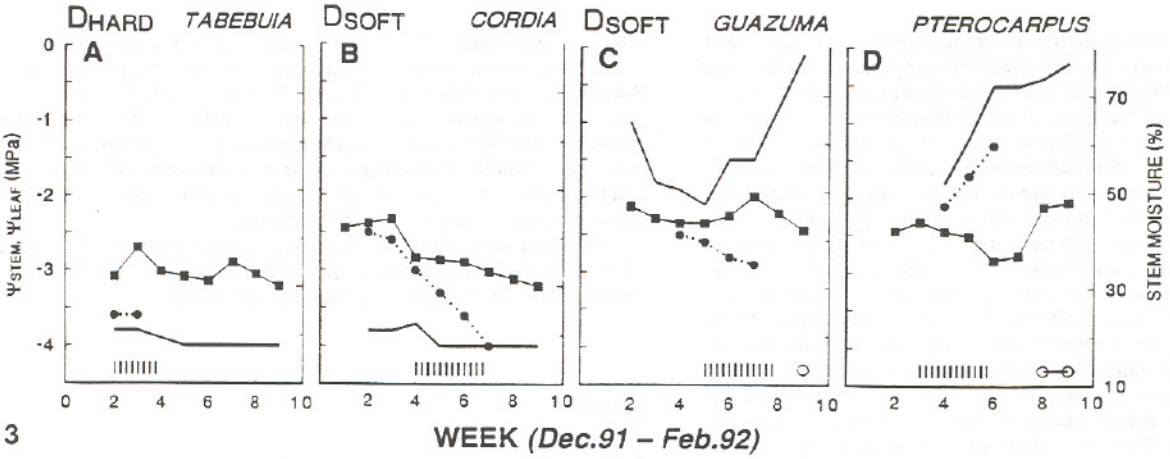


Fig. 2. Differences in water potential between stem sections and organs on the same branches of two tropical trees growing at a moist site. Water potential for each data set was measured during the dry season in the same branch in adjacent 10 cm-long sections cut at both ends. Branch sections were bare (Ψ_{stem}) or carried a leaf (Ψ_{leaf}) or a terminal infrutescence (Ψ_{fruit}). *Licania arborea*: *A* – bare stem and old leaf; *B* – bare stem, old leaf and infrutescence; *C* – bare stem, infrutescence and new leaf. *Eugenia salamensis*: bare stem and old leaf before (*D*, *E*) and 2 days after irrigation of the tree (*F*). ■ Stem; ▨ Old leaf; ▽ New leaf; ▩ Fruit

–1.0 MPa (Fig. 2 A – C). To eliminate the possibility that high Ψ_{stem} values resulted from expulsion of water from vessels extending through the entire length of the stem samples, stem segments comprising the last and first nodes of consecutive flushes, i.e., branch segments with discontinuous vessels, were tested and found to give the same results as segments from a single flush.

Measurements thus revealed dramatic differences between the water potentials of bare stem sections (Ψ_{stem}), in which xylem tension was released by cutting at both ends, and stem sections with attached organs, in which xylem tension persisted (Ψ_{leaf}, Ψ_{fruit}). There were also large differences between Ψ_{leaf} of old and young leaves on the same branch. In parallel to the paradoxical observations of *Tabebuia rosea* (see Introduction) these data show that young leaves and fruits were growing on branches carrying desiccated old leaves.

In *Eugenia* standing near the above *Licania*, Ψ_{stem} and Ψ_{leaf} of old leaves were both low during initial measurements of drought-stressed trees (Fig. 2D, E). Within 2 days after irrigation Ψ_{stem} increased to –0.1 MPa, while Ψ_{leaf} remained very low (Fig. 2F). Ψ_{stem} thus varied independently of Ψ_{leaf} with a change in tree water status. In *Enterolobium*, *Guazuma*, *Spondias* and a few other species, whose twigs contain large, thin-walled, often slimy pith cells (described for *Pseudobombax* in Roth 1981), liquid was repeatedly observed to emerge from the cut surface of branch segments as soon as they were exposed to the very low pressure generated by closing the lid of the pressure chamber ($\Psi_{stem} > -0.1$ MPa). For these species very low pressure was therefore sufficient to expel liquid from water-filled vessels and water-storing pith.



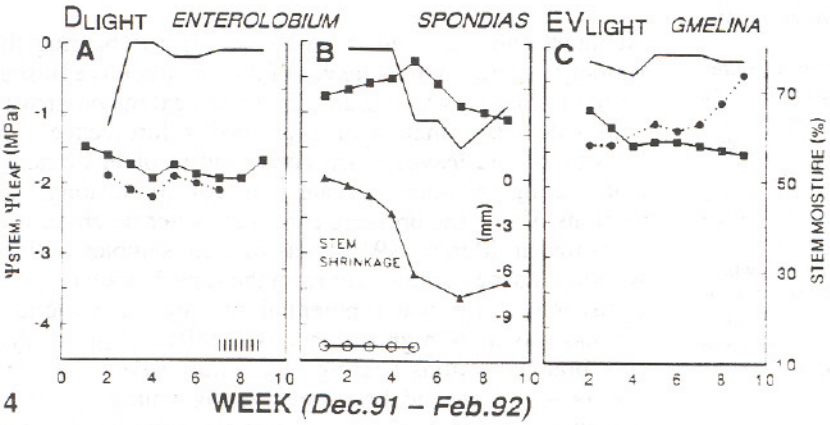


Fig. 3–4. Variation in phenology (bottom) and Ψ_{stem}, Ψ_{leaf}, and stem moisture (*upper curves*) in tropical dry forest trees of different ecotypes during the early dry season 1991/1992. For description of ecotypes (D_{hard}, etc.) and sites see Table 1.

Fig. 3. A – *Tabebuia ochracea* subsp. *neochrysantha* in a dry upland forest; B – *Cordia alliodora* in a dry savanna. C – *Guazuma ulmifolia* in a dry savanna; D – *Pterocarpus rohrii* at a moist lowland site.

Fig. 4. A, B – *Enterolobium cyclocarpum* and *Spondias purpurea* at a dry upland forest site. In B, stem shrinkage was measured at breast height. C – *Gmelina arborea* at a moist site. ——— Ψ_{stem}, ●– – – –● Ψ_{leaf}, ■——■ stem moisture; leaf fall: ○——○ flowering

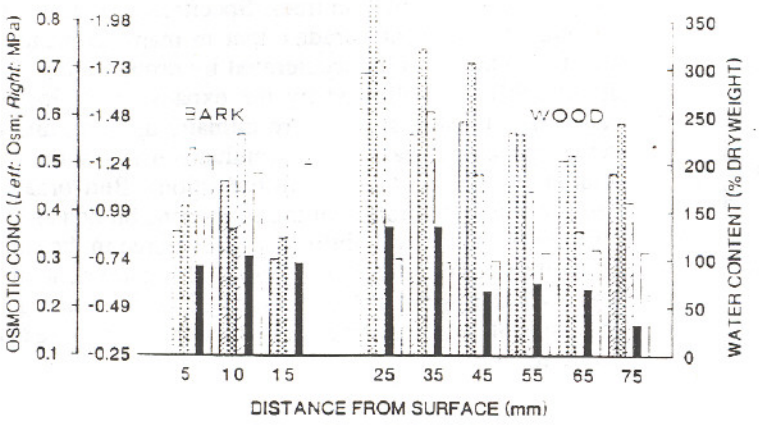


Fig. 5. Solute and water content in bark and wood of lightwood species. **A–D** – Osmotic concentrations in the deciduous species *Bursera simarouba*, *Cochlospermum vitifolium* and *Enterolobium cyclocarpum* at dry sites and in the evergreen *Gmelina arborea* at a moist site; **E** – water content in *Enterolobium*. Sap was expressed from 5 and 10 mm-thick core sections of bark and wood, respectively, and osmotic concentration (osmol) was determined with an osmometer. ▨ A – Cochlospermum; ▩ B – Bursera; ▨ C – Enterolobium; ■ D – Gmelina; □ E – Water content

The results obtained with *Licania* and *Eugenia* raise the following questions: (1) Which aspect of tree water status does Ψ_{stem} measure? (2) Is this measurement relevant for tree development during the dry season? (3) How can large differences in water potential exist within adjacent tissues or organs on the same branch? To address these questions changes in Ψ_{stem} and Ψ_{leaf} were measured in many trees belonging to different ecotypes and growing at sites ranging from very dry to moist during the early dry season 1991/92 (Figs. 3–6; Tables 1, 2).

Variation in Ψ_{stem} during the dry season

In *hardwood trees* at dry upland sites, Ψ_{leaf} and Ψ_{stem} declined to very low values early in the dry season and Ψ_{stem} remained low after drought-induced leaf shedding for the rest of the dry season. (Fig. 3A; Table 2 G-I; Borchert 1993a). Among softwood species at dry savanna sites, the degree of desiccation during the early dry season varied. *Cordia*, retaining its leaves long into the dry season, dehydrated as much as hardwood species and remained desiccated for the duration of drought (Fig. 3B; Table 2 G-I). Twigs of *Guazuma* dried out much less, Ψ_{stem} began to increase during leaf shedding and flowers emerged gradually after Ψ_{stem} had reached its maximum, i.e., after branches had fully rehydrated ($\Psi_{stem} = > -0.2$ MPa; Fig. 3C; Table 2 G-I). Young shoots started expanding slowly in late February (not shown). In *Pterocarpus* growing at a moist site, both Ψ_{stem} and Ψ_{leaf} of the last leaves to be shed increased during leaf fall and the bare tree flowered abundantly after full rehydration (Fig. 3D; Table 2 G-I). Stem moisture content (SM) in softwood species was higher than in hardwood trees but varied only little with increasing Ψ_{stem} (e.g. Figs. 3D, 6D).

In striking contrast to hardwood trees growing at the same very dry upland sites, water-storing lightwood trees, characterized by wood densities below 0.5 g cm^{-3} and a saturation water content above 125% dry weight (Table 2), maintained Ψ_{stem} near saturation level and well above Ψ_{leaf} before leaf shedding (Fig. 4A, B vs Fig. 3A). The high water content of the 15–20 mm-thick bark of such lightwood trees (Fig. 5E, *Enterolobium*) was reflected in high SM values. The weight of cut, thick branches of lightwood trees indicated that water content throughout the stem was as high as in the analyzed samples of the outer wood (Fig. 5); the amount of water stored in large trees is thus substantial (Table 3).

Spondias and other shallow-rooted lightwood species shed leaves rapidly during the early dry season (data not shown) and then flowered for prolonged periods. Use of stored water for flower expansion and evaporation from flowers is indicated by decreasing stem circumference, Ψ_{stem} and SM (Fig. 4B; Reich and Borchert 1984).

Solute concentrations of water stored in the extensive parenchymatic tissues of bark and wood of deciduous lightwood trees from dry sites (Roth 1981) ranged from 0.34 to 0.85 osmol, corresponding to osmotic potentials between –0.8 and –2.1 MPa (Fig. 5A–C). They were more than twice those measured in the evergreen lightwood species *Gmelina* growing at moist sites (Fig. 5D). In all species analyzed, osmotic concentrations were distinctly higher in the wood than in the bark and declined from the outer towards the inner layers of the wood.

Facultatively evergreen, leaf-exchanging softwood species with coriaceous leaves, adapted to moist lowland sites, desiccated only moderately and attained saturation Ψ_{stem} weeks before leaf fall (Fig. 6A, B). Following the increase in Ψ_{stem}, predawn Ψ_{leaf} of several trees increased in exposed leaves or in leaves wrapped in aluminum foil (Figs. 3D, 6A, D). Flowering or flushing often started before old leaves had been shed completely (Fig. 6B).

Deciduous hard- and softwood trees growing at moist lowland sites retained their leaves longer and maintained a higher SM than their conspecifics at dry upland sites (Fig. 6C, D *vs* Fig. 3A). As in evergreen trees at the same sites, Ψ_{stem} of such trees increased to saturation values before abscission of the senescent mesic leaves, resulting in large differences between Ψ_{stem} and Ψ_{leaf} (Fig. 6C, D), as first observed in *Licania* and *Eugenia* (Fig. 2). Facultatively evergreen lightwood trees at moist sites maintained a saturation Ψ_{stem} and a very high SM as well as a high Ψ_{leaf} throughout the dry season (Fig. 4C).

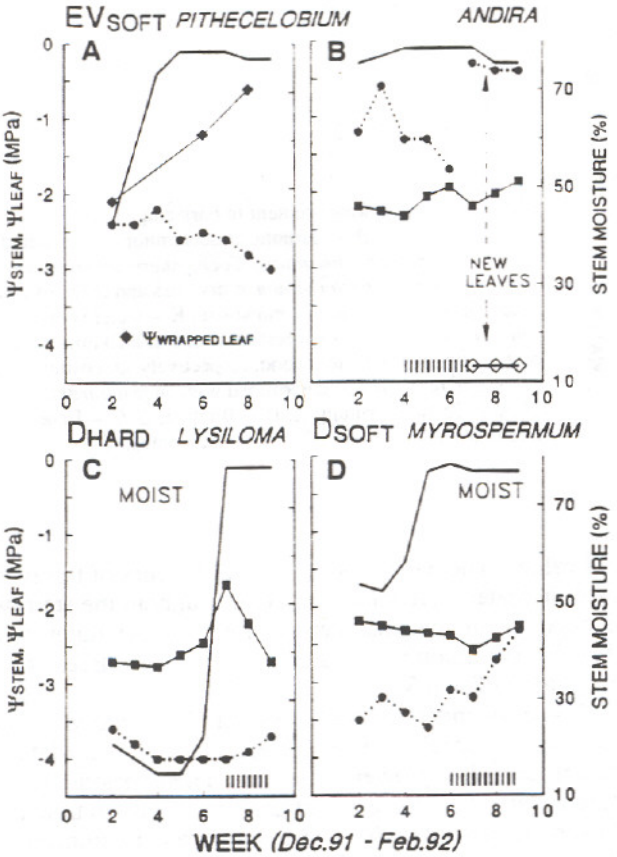


Fig. 6 A–D. Variation in phenology (*bottom*) and ψ_{stem}, ψ_{leaf}, and stem moisture (*upper curves*) in tropical dry forest trees of different ecotypes during the early dry season 1991/1992. **A, B** – *Pithecelobium saman* and *Andira inermis* at moist lowland sites. In **A**, leaves were wrapped in aluminum foil and plastic bags in the evening and predawn ψ_{leaf} was measured the next morning. In **B**, ψ_{leaf} was measured in old leaves before shedding and later in newly expanded leaves. **C, D** – *Lysiloma seemannii* and *Myrospermum frutescens* at a moist lowland site. Compare to hard- and softwood species at dry sites in Fig. 3A, B. ———, Ψ_{stem}; ●– – – –●, Ψ_{leaf}; ■———■, stem moisture; ▥ leaf fall

Discussion

Water status and the development of tropical trees during drought

Most studies of the relations between tree water status and physiological processes deal with the effect of water deficits on leaf functions such as stomatal conductance and photosynthesis or with drought resistance of leaves in temperate or tropical trees (Sobrado 1986; Hinckley et al. 1991; Olivares and Medina 1992). The role of tree water status in the growth of buds, flowers and shoots of trees has received much less attention (Hinckley et al. 1991). Consequently, the current debate on the merits of various measures of water status is mainly concerned with the value of Ψ_{leaf} *vs* relative leaf water content (RWC_{leaf}; Sinclair and Ludlow 1985). Likewise, most studies of osmotic adjustment, turgor loss and the role of the elastic modulus in sensing water deficits deal with leaves and rely on use of the pressure-volume technique (Pallardy et al. 1991). In contrast, this study is concerned with the effect of water stress on organ growth in trees. Specifically, it attempts to resolve the apparent paradox that in many tropical trees leaf fall, known to be accelerated by drought stress (Addicott 1991), is followed by the expansion of flower or vegetative buds during severe climatic drought, and that these processes may occur simultaneously on the same branch or tree crown (see Introduction). Bud break depends on the rehydration of the supporting branch and thus ultimately on the availability of water stored in the subsoil or in tree stems (Borchert 1993a). Measurement of the water status of stem tissues thus appears to be central to the analysis of tropical tree development during seasonal drought.

Measurement of Ψ_{stem} with the pressure chamber

In normal use of the pressure chamber, tension in the xylem of terminal organs (Ψ_{xylem} of bare stem, leaf, inflorescence or fruit; Fig. 2) is measured by interrupting the xylem with a single cut and compensating the tension pulling water into the organ's tissues by applying external pressure. If bare branch sections are cut at both ends, as done for measurements of Ψ_{stem} in this study (see Fig. 2; Material and methods), xylem tension is released and the retention of water should depend only on the pressure component of the water potential of parenchymatic tissues adjacent to the xylem and of apoplastic water in the wood. If tissues near the xylem are fully saturated, xylem water will not be absorbed upon cutting a branch section and can be be expelled by very low pressure in the pressure chamber (see Results). High Ψ_{stem}-values measured in stem sections including the apical and basal ends of consecutive flushes of shoot growth are unlikely to be the result of releasing water from long vessels extending through the entire experimental sample. Measurement of progressively lower values of Ψ_{stem} should indicate increasing water deficits of parenchymatic tissues in sapwood and bark, possibly in conjunction with increasing cavitation of vessel elements. Ψ_{stem} should increase upon irrigation of drought-stressed trees, as indeed observed (Fig. 2D–F; Borchert 1993b). Lightwood trees maintaining a high water content in bark and wood also maintain a Ψ_{stem} near saturation at very dry sites (Figs. 4A, 5), where hardwood trees desiccate to values of Ψ_{stem} below –4 MPa (Fig. 3A). Ψ_{stem} thus constitutes a measure of tree water status which is different from and independent of Ψ_{leaf} or Ψ_{xylem} (Figs. 3–6). The roles of Ψ_{stem} and Ψ_{leaf} in tree development will be discussed below.

The observed differences of 3–4 MPa between Ψ_{stem} and Ψ_{leaf} of the same twig (Figs. 2; 6C, D) illustrate the problem of measuring tree water status and show that parenchymatic tissues near the xylem of a rehydrated branch may be water-saturated while xylem tension is high. Because of the high elastic module of wood, these parenchymatic tissues – likely to have a high solute content (see below) – apparently reach the turgor loss point and equilibrium with Ψ_{xylem} with minimal water loss and change in cell volume (Pallardy et al. 1991), such that a high Ψ_{stem} is measured after elimination of Ψ_{xylem} by defoliation and double cutting the branch. These considera-

tions suggest that Ψ_{stem} constitutes an indirect measure of the relative water content of parenchyma cells near the xylem (RWC_{stem}), which is uncoupled from daily variation in Ψ_{xylem} and depends on both predawn Ψ_{xylem} and the RWC of adjacent parenchymatic stem tissues. In analogy to RWC_{leaf} (Sinclair and Ludlow 1985), Ψ_{stem} appears to be relatively stable and tends to integrate the water balance of stem tissues over days or weeks (see time scale in Figs. 3, 4, 6). In hardwood trees with little stem water storage Ψ_{stem} should vary mainly with changes in predawn Ψ_{xylem} and thus provide an estimate of the water status of soil layers accessible to the tree's root system (see below).

Measurements of SM indicate electric resistance and reflect the amount of cell sap released by insertion of electrode nails into the outer 20 mm of tree trunks. SM thus constitutes a crude, *relative* measure of water storage in the outer tree trunk, as opposed to Ψ_{stem}, which indicates the water status of parenchymatic tissues near the xylem of twigs. Accordingly, SM ranged from high values in water-storing lightwood trees (Fig. 4; Table 2) to lower values in trees with low water storage growing at moist (Fig. 6C, D) or dry sites (Fig. 3A, B). SM was found to be well correlated with wood density, stem water storage and minimum Ψ_{stem} in more than 30 species (Figs. 3–6; Table 2; Borchert 1993a). During rehydration of strongly desiccated hardwood trees after irrigation, a rise in Ψ_{stem} from <-4 to >-0.2 MPa within 48 h was accompanied by an increase in SM to maximum values within 6–8 days, indicating that rapid refilling of vessels and rehydration of tissues near the xylem of twigs was followed by a slower rehydration of outer trunk tissues supplied by slow lateral water transport (Borchert 1993b). In contrast, slower increases in Ψ_{stem} during climatic drought were only rarely followed by a distinct rise in SM (Figs. 3–6), suggesting that physiologically significant increases in Ψ_{stem} of twigs may occur in the absence of full saturation of trunk tissues.

Water deficits and leaf abscission during drought

In confirmation of earlier observations (Addicott 1991), Ψ_{leaf} generally reached its minimum just before leaf shedding (Figs. 3A–C; 6A–C), but in some trees at moist sites Ψ_{leaf} of the last leaves to be shed increased in parallel with a simultaneous increase in Ψ_{stem} (Figs. 3D; 6D). The observed minima of Ψ_{leaf} were strongly correlated with the minima of Ψ_{stem} and SM, which in turn varied with the availability of stored water in tree stems or in the subsoil (Table 1: Sites; Table 2F–I; Borchert 1993a). Hard- and softwood trees growing at dry sites had the lowest Ψ_{leaf}, Ψ_{stem} and SM (Fig. 3A, B; Table 2G–H). With increasing soil moisture availability these values became larger (Figs. 3C, D; 6). The highest values were maintained in water-storing lightwood species at dry and moist sites (Fig. 4A, C; Table 2E–I).

Ψ_{stem} and bud development

Bud break and subsequent growth of flowers or shoots involve cell expansion, known to be inhibited by even moderate water stress (Hinckley et al. 1991). Water supply to expanding buds is strongly affected by the vascular connections between a bud and its supporting stem (Braun 1960). Resting terminal buds usually remain connected to the vascular system of the stem and expand rapidly after bud break. In resting lateral, axillary buds of broadleaved trees vascular connections are severed during growth in girth after bud inception and initial growth after bud break is slower, because water and nutrients have to be supplied to the growing tissues via cell-to-cell transport from the adjacent parenchymatic pith or bark tissues. Formation of new vascular connections begins only during early leaf expansion in the young shoot (Braun 1960). Water saturation of stem tissues, as indicated by a high Ψ_{stem}, should thus be a prerequisite for early bud growth. In keeping with these considerations, in almost all observed trees Ψ_{stem} approached saturation before flowering or flushing (Figs. 3C, D; 4B; 6A, B; Borchert 1993a). In leaf-bearing branches with a high Ψ_{stem} bud development rarely progressed beyond initial swelling, being apparently inhibited by low Ψ_{leaf}.

Differences in location and developmental status are likely to determine the priority of bud break in flower and vegetative buds of rehydrating trees. For example, the terminal flower buds of *Tabebuia ochracea* begin to expand within 2 days after irrigation or rain, as soon as Ψ_{stem} has increased to >-0.2 MPa, and are fully expanded after 6 days; expansion of lateral vegetative buds begins later and leaf expansion is completed only about 3 weeks after irrigation (Borchert 1993b). Similarly, only well vascularized flower buds in *Coffea arabica* open after rain (Crisosto et al. 1992).

Increase in Ψ_{stem} during climatic drought

Measurements of Ψ_{stem} given in Figs. 3–6 started on 8 December, 1991, i.e., 8 weeks after the last rainfall. Rehydration of stem tissues shown in Figs. 3 and 6 thus occurred after trees had been exposed to 3–4 months of high evaporation stress in the absence of rain (Reich and Borchert 1984). This raises questions as to the source of water enabling rehydration.

Rehydration of stem tissues should be preceded by an improvement of the tree's water balance due to changes in the soil-plant-atmosphere continuum, such as an increased capacity for water absorption or a reduction of water loss (Borchert 1991). Rehydration of hard- and softwood trees storing little water in their trunks will depend on the absorption of water remaining in the subsoil after the drying of upper soil layers during the early dry season. The inability of hardwood trees in dry upland forests to rehydrate after leaf fall indicates that accessible subsoil moisture reservoirs had been depleted (Fig. 3A). Among widely spaced savanna trees subsoil moisture was adequate to balance the water economy after the elimination of transpirational water loss (Fig. 3C). Predictably, in such trees

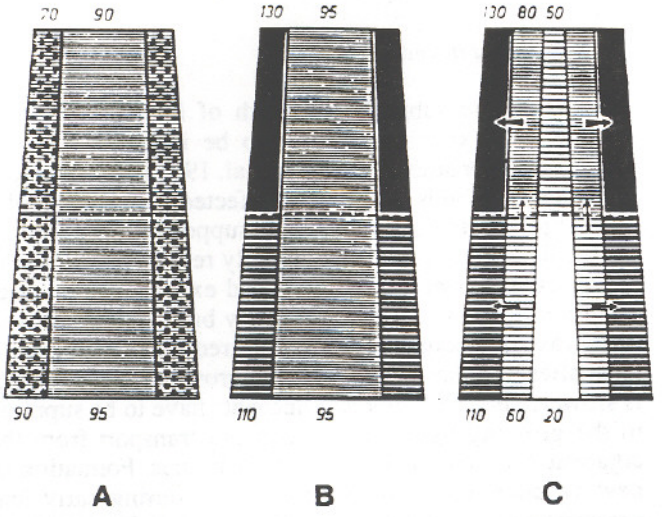


Fig. 7 A–C. Changes in water content due to starch degradation, osmotic water uptake and water shifting in upper (*top half*) and lower stems (*lower half*) of *Populus* before bud break in spring. **A, B** – Stem sections of intact young trees (6 cm stem diameter) in February (*A*) and April (*B*); **C** – Stem sections of a rootless young tree, cut in February and analyzed in April (redrawn from Braun 1961). Water content □ <40%; ▤ 41–60%; ▤ 61–80%; ▤ 81–100%; ▤ 101–120%; ■ >120%; ▨ Starch

ignore timing and rate of stem rehydration varied widely with site water availability and the time of leaf fall (Figs. 3B–D; Borchert 1993a). Similarly, in seven dry forest species stem shrinkage during leaf shedding, indicative of a declining RWC_{stem}, was followed by moderate stem expansion, i.e., partial rehydration, in the absence of rain. This rehydration resulted in flushing accompanied by renewed stem shrinkage indicating water loss by new foliage (Daubenmire 1972).

In contrast to trees at dry sites, rehydration at moist sites was sometimes remarkably fast, occurring well before leaf fall and in the absence of apparent changes in the soil-plant-water continuum (Fig. 6). Extension of fine roots into moist subsoil layers and increased absorbing capacity of tree tissues due to osmotic adjustment will be considered below as possible causes for rehydration.

Water-storing lightwood trees growing at very dry sites have shallow root systems (Olivares and Medina 1992) and shed their mesic leaves during early drought, i.e., such trees neither transpire nor absorb water during most of the dry season. Saturation water content of lightwood trees is roughly 3 and 6 times that of soft- and hardwood trees, respectively (Table 2). Both soft- and lightwood trees deplete about 30% of their stored water during the dry season, but the remaining water content in the latter is more than twice the saturation water content of the former (153 vs 67% DW; Schulze et al. 1988). Reflecting their high water content, Ψ_{stem} and SM are generally high in lightwood trees (Fig. 4). Water consumption during flower expansion, possibly in conjunction with evaporative water loss through the bark, caused not only a decrease in Ψ_{stem}, but also a decline in SM and shrinkage of the trunk (Fig. 4B; Reich and Borchert 1984). This implies that stored water used in the branches was replenished in part by water from the trunk. Similarly, bud break in many lightwood species occurs during the late dry season while trunks continue to shrink. However, root and leaf expansion remain arrested at an early stage until the first heavy rains enable resaturation (expansion) of the trunk and full leaf expansion (Reich and Borchert 1984; Bullock and Solis-Magallanes 1991). Shoots and roots also sprout readily from cut branches of *Bursera* and *Spondias*, which are widely planted as living fences.

Water shifting in leafless temperate trees

Slow, upward water transport in the xylem resulting from osmotic water uptake by stem tissues or expanding buds in bare trees (*water shifting*) has received little attention in recent discussions of tree water relations (e.g. Hinckley et al. 1991), although it plays an important role in the water relations of both temperate and tropical trees before and during bud break (Braun 1984). Some rarely cited studies of water shifting in temperate trees will be therefore reviewed as a basis for understanding dry-season development of tropical trees.

Parenchymatic tissues in stem and bark obtain water via osmotic water movement along gradients in water potential. In bare temperate trees, rising temperatures in early spring cause the transformation of starch into sugars and osmotic water uptake by bark tissues followed by slow upward water shifting from the root system through the wood (Fig. 7; Braun 1961; Sauter 1966). The amount of water absorbed and moved before bud break is much smaller than that transported in leaf-bearing, transpiring trees (e.g. *Betula*: 0.05 dm^3 day^{-1} March 12–April 9 *vs* 4.3 dm^3 day^{-1} May 7–13; Braun 1984). In intact temperate trees water shifting is usually accompanied by water transport driven by root pressure, but in rootless trees water shifting to the bark tissues of the upper branches results in a decreasing water content of the lower trunk (Fig. 7C); such trees dry out and die when leaves start expanding. A declining water potential of parenchymatic bark tissues due to increasing solute content, i.e. osmotic adjustment, thus causes an increase in symplastic water content of these tissues and a decreasing water content in the wood apoplast (compare Fig. 1). The resulting high water and sugar content of bark tissues is a prerequisite for subsequent bud break (see above).

In contrast to most other temperate hardwood trees, in walnut (*Juglans regia*) >90% of fine roots die during the winter and leaf development is unusually slow (Fig. 8; Bode 1959). In parallel with rootless temperate trees and drought-stressed tropical lightwood trees (Figs. 4B, 7C), the water content of short-shoots declined after bud break during flowering and initial leaf expansion, indicating that water absorbed by expanding young shoots and flowers was not fully replaced (Fig. 8, day 0–7). Subsequent, enhanced starch-sugar conversion resulted in rehydration of shoots and bleeding from leaf scars (Fig. 8, day 7–10). Osmotic water uptake by growing shoots was thus accompanied by the development of xylem pressure. Such pressures, referred to variously as bleeding pressure, stem or

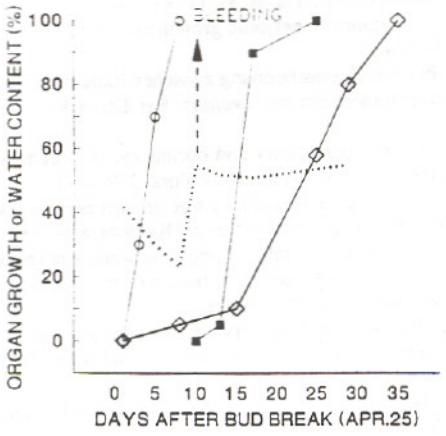


Fig. 8. The time course of bud break, root growth and leaf expansion in walnut (*Juglans regia*) during spring. The water content of short shoots bearing expanding buds decreased during growth of male flowers (catkins) and initial leaf expansion. Subsequent rehydration was followed by bleeding, rapid growth of fine roots and leaf expansion (redrawn from Bode 1959). ◇ Leaves; ○ Flowers; ■ Roots; - - - - Shoot water

root pressure, presumably result from secretion of sugars into the xylem sap (Sauter 1980; Braun 1984) and cause refilling of embolized vessels. A burst of fine root growth followed rehydration of shoots and enabled increased water absorption and accelerated shoot and leaf expansion (Fig. 8, day 10–35). In *Juglans*, as in tropical lightwood trees, a phase of slow initial shoot development relying on use of stored water and water shifting thus precedes rapid shoot growth and leaf expansion, which require moist soil, a well-developed root system and rapid water transport driven by water loss in the expanding foliage.

Differences in the water content of bark and wood are enhanced after the unfolding of leaves. Wood water content declines throughout the summer with increasing transpiration, while bark water content almost doubles during early summer, when soluble products of photosynthesis abound, and then declines during late summer, when starch accumulates at the expense of the solute content of bark parenchyma (Fig. 1; Gibbs 1958; Sauter 1966). Wood water content increases again in fall after the elimination of transpirational water loss by leaf abscission.

Osmotic water transport and water shifting in tropical trees

As in temperate trees, water content of the bark in bare tropical lightwood trees was about twice that of the wood, a fact more likely to reflect the higher dry weight of wood than significant physiological differences (Fig. 5). In all species analyzed, solute content was distinctly higher in the wood than in the bark and had a maximum in the outermost layer of the wood (Fig. 5), found to be free of starch deposits in *Bursera* and other lightwood species (Fink 1982). Although such trees lack distinct annual rings and a distinction between sap- and heartwood, there is a

Table 3. Water and solute content of a fallen *Cochlospermum* trunk based on data in Fig. 5

Height of main trunk	12.15	m
Base diameter	42.6	cm
Top diameter	16.6	cm
Volume	836	dm^3
Wood density	0.19	$g.cm^{-3}$
Water content (estimated 70%)	**585**	**dm^3**
Solute content (estimated 0.4 osmol)	234	mol
Sucrose, 234 mol	**80**	**kg**

clear physiological zonation with respect to solute content and starch deposition. The parenchymatic sheath surrounding the vessels (paratracheal contact parenchyma) usually remains free of starch and contains acid phosphatases, enzymes involved in the secretion of sugars into the xylem, which are found only around functioning, water-conducting vessels and are most active during bud break in temperate and tropical trees (Fink 1982; Braun 1984).

Maxima of solute concentrations in the outer wood containing the vessels active in water transport indicate a Ψ_{osm} between −1.7 and −2.1 MPa at the lowest end of a water potential gradient ($\Delta\ \Psi$ approx. 1 MPa) drawing water from the inner to the outer layers of the wood (Fig. 5). This gradient is similar to, but much more extended than, gradients measured 70 years ago (>60 mm *vs* 10 cell layers; Ursprung and Hayoz 1922). To enable upward water shifting, Ψ_{osm} in branches should be even more negative than in the trunk.

In the the evergreen lightwood-tree *Gmelina* growing at a moist site, Ψ_{leaf} and Ψ_{osm} of the wood parenchyma were about twice as high (Figs. 4C, 5D) as in the drought-tolerant lightwood species *Enterolobium* (Figs. 4A, 5C). Extrapolation of the solute content of stem cores to the volume of a whole tree yields substantial quantities of soluble carbohydrates (Table 3; Fig. 5), which were not reduced during growth of lightwood species (Bullock 1992).

In leaf-exchanging tropical trees acid phosphatase activity around vessels is less seasonal than in temperate trees, and guttation or bleeding, indicative of xylem pressure, have been observed repeatedly (Fink 1982). *Pithecelobium*, which rehydrates before leaf shedding (Fig. 6A), is referred to as "rain tree" because of the abundant guttation of young shoots expanding after leaf fall during the dry season (Fink 1982; Braun 1984). In view of such observations and the seasonality of fine root proliferation in tropical dry forests (Kummerow et al. 1990), it appears likely that as in *Juglans* (Fig. 8) extension of roots into moist soil layers as well as osmotic adjustment in stems contribute to the increase in Ψ_{stem} before leaf fall (Fig. 6). Increased availability of subsoil water or osmotic adjustment in leaves are indicated by the observed increases in predawn Ψ_{leaf} during rehydration of stem tissues (Fig. 6A, D). As in leaves, osmotic adjustment of stem tissues of tropical trees is likely to be triggered by water stress (Pallardy et al. 1991).

Flowering and flushing after leaf fall during the dry season were proposed earlier to result from balancing tree water economy by leaf shedding (Reich and Borchert 1984; Borchert 1991, 1992). The comparative analysis of bud break and flowering under a variety of conditions indicates that the prerequisites for rehydration and bud break are more complex. In tropical as in temperate trees establishment of relatively high solute concentrations in stem tissues by osmotic adjustment is needed both to provide the driving force for rehydration of desiccated branches and as a supply in organic nutrients for growing buds (Figs. 6, 7). Once water supply is adequate and embolized vessels have been refilled, osmotic water uptake by stem tissues will establish a high Ψ_{stem}. Correspondingly, continued maintenance of a high Ψ_{stem} depends on maintaining a high solute concentration (e.g. bare D_{light} trees, Fig. 5; shoots bearing young, mature leaves, Fig. 1 May–June). Vegetative or reproductive buds will expand and shoot growth will be sustained only if and as long as both Ψ_{stem} and Ψ_{xylem} ($= \Psi_{leaf}$) remain higher than the growth-induced water potential generated by the expanding cells of a growing organ (Boyer 1988).

Characterization of tree water status by two variables, Ψ_{stem} and Ψ_{leaf} ($= \Psi_{xylem}$), as recommended earlier (Bradford and Hsiao 1982), proved crucial for understanding the observed patterns of tree development during seasonal drought. For example, flowering or bud growth remain inhibited in rehydrated branches with a high Ψ_{stem} by the presence of senescent leaves with a low Ψ_{leaf} (Fig. 6) or may be arrested by a decrease in Ψ_{stem} resulting from insufficient replenishment of water via water shifting (Figs. 4B; 8, 0–7 days; arrest of early shoot growth in drought-stressed lightwood trees). Similarly, growth of new organs on shoots bearing young leaves with high solute production, such as prolonged shoot extension (e.g. *Populus*, *Salix*), recurrent flushing (e.g. *Quercus*) or flowering at the end of a flush of shoot growth (hapaxanthic flowering of many tropical trees) should occur only as long as soil moisture is plentiful and a high Ψ_{leaf} is maintained.

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