Trees (1994) 8: 198–204

Structure and Function
Trees

Induction of rehydration and bud break by irrigation or rain in decidous trees of a tropical dry forest in Costa Rica

Rolf Borchert

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

Received 16 April/Accepted 3 August 1993

Summary. Clusters of 2–4 bare, deciduous hardwood trees and woody vines in a dry upland forest in Costa Rica were surrounded by scaffolding and rehydration was induced during the dry season by irrigation of 9–50 m^2 plots with 200 mm water. The resulting changes in water status preceding bud break were monitored. Following irrigation, stem water potentials increased from < –4 MPa to about –1.5 MPa within 24 h and to > – 0.3 MPa within 48 h. Rehydration of stem tissues by lateral transport, measured as an increase in electric conductivity, continued for 4–8 days. Terminal flower buds in *Tabebuia ochracea* began to expand 48 h after irrigation and trees were in full bloom 4 days later. In all experimental species, lateral vegetative buds began to expand 5–7 days after irrigation and leaves were fully expanded 2 weeks later. After the first rains of the rainy season (100 mm in 48 hr) all trees in the dry forest rehydrated and leaves emerged in synchrony slightly faster than after irrigation. In response to rain or irrigation drought-stressed tropical hardwood trees thus rehydrated at rates similar to those of desert succulents and their development resumed much faster than that of deciduous cold-temperate trees in spring.

Key words: Bud break – Irrigation – Rehydration – Tropical dry forest – Tropical hardwood trees

Introduction

In tropical wet forests with high temperature and good moisture supply throughout the year, shoot growth in broadleaved trees resumes as soon as a cohort of senescent leaves has been shed, i.e., bud break is the consequence of changing functional correlations within trees and is not induced by environmental change (Borchert 1991, 1992). In contrast, both in cold-temperate and tropical drought-deciduous forests the shedding of senescent leaves at the end of a growing season and the subsequent resumption of shoot growth are separated by rest periods of several months imposed by unfavorable environmental conditions, namely low temperature and drought, respectively. While similar in seasonal changes in physiognomy, the two forest types differ fundamentally with respect to the time course of the elimination of environmental stress and the physiological changes preceding bud break.

In temperate forests, gradual increases in temperature which eventually cause bud break and growth resumption extend over 2–3 months between March and May. Physiological changes following the breaking of dormancy by exposure to low temperature include dissolution of dormancy callose in the phloem, conversion of reserve starch to sugar, release of sugars into the xylem and development of xylem pressure (root pressure), refilling of vessels, resaturation of stem tissues, and hormonal changes in buds and stems. The time course of physiological events before bud break and of subsequent shoot growth varies widely between tree species (Zimmermann 1964; Braun 1984; Sperry et al. 1987; Borchert 1991).

Whereas all trees of a temperate forest are exposed to similar cold stress, the degree of water stress experienced by trees of tropical dry forests during the dry season varies widely, because the impact of prolonged climatic drought is buffered in many trees by access to subsoil water reserves or water storage in tree trunks. Consequently, the patterns of tree development (phenology) observed during the 6–7 month long dry season within the dry forest ecosystem of Guanacaste, Costa Rica, vary widely (Borchert 1993a). For instance, water storage in tree trunks enables prolonged flowering of bare lightwood trees at very dry sites, and trees having access to the groundwater table may remain evergreen and flower or exchange leaves during severe climatic drought. Only hardwood trees with low stem water storage growing at dry upland forest sites desiccate severely, to stem water potentials (ψ_{stem}) below –4 MPa, and remain inactive for the duration of climatic drought (Borchert 1993a). In such trees, which are the subject of this study, the transition from drought-imposed rest to active growth may be abrupt. Single, heavy rainfalls of 40–50 mm cause mass-flowering of desiccated trees

and woody vines (Opler et al. 1976; Reich and Borchert 1982; Bullock 1986), and the first heavy rains after the dry season trigger the rapid, synchronous resumption of shoot growth in all trees (Bullock and Solis-Magallanes 1990; Borchert 1993a). Bud break of deciduous tropical trees before the advent of rains, as repeatedly described in the literature, occurs only in trees with access to soil moisture or stem water storage (Bullock and Solis-Magallanes 1990; Borchert 1994).

Although deciduous dry forests are widespread in tropical regions with seasonal monsoon climates, the time course and extent of rehydration preceding the rapid rain-induced bud break, flowering and shoot growth have not been analyzed in the past. Such studies are complicated by the unpredictability of isolated rainfalls or the beginning of the rainy season and by the difficulty of measuring changes in water status in the crown of forest trees. In this study, clusters of bare forest trees in a dry upland forest in Costa Rica were surrounded by scaffolding, and changes in water status resulting in bud break were measured during rehydration caused by irrigation or heavy rainfall.

Materials and methods

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). Briefly, annual mean temperature is 27.8°C and mean annual 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. Phenology and changes in water status of more than 30 tree species were observed during two consecutive dry seasons between 1 January 1991 and 26 February 1992 (Borchert 1993a). With the exception of two trees growing at a moist lowland site, all observations described here were made in an open, dry, secondary upland forest growing on humus-rich, porous soil derived from vulcanic andesite conglomerates (see Borchert 1993a, Fig. 1).

Tabebuia ochracea ssp. neochrysantha Gentry (Bignoniaceae), common in dry upland forests, was chosen as the principal subject of this study, because in response to irrigation or heavy rain trunks expand rapidly by as much as 25–30 mm and flowers open within a week (Reich and Borchert 1982). Vines (*Cydista* sp., Bignoniaceae) and other trees, usually 10–15 m tall, of the following species were also studied: *Calicophyllum candidissimum* (Vahl) DC. (Rubiaceae), *Lonchocarpus minimifolium* Donn. Smith (Fabaceae), *Luehea candida* (D.C.) Mart. (Tiliaceae), and *Tabebuia impetigunosa* (Mart.) Standley. Except for *T. impetigunosa* and *T. ochracea* species will be referred to by genus name only.

To enable measurement of water status in tree crowns, four groups of 2–4 trees were surrounded by bamboo scaffolding with observation platforms at 5 and 10 m height. Woody vines were pulled down, spread horizontally and tied to tree trunks at breast height. Each terminal branch was labeled and its distance from the base of the vine's main stem was measured.

Water potential was measured with a pressure chamber in samples obtained with a tree pruner. For monitoring of seasonal changes in tree water status, triplicate samples were collected every 7–14 days between 0530 and 0700 hours, 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}) was obtained from leaves or leaf-bearing twigs. In a modification of 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. This technique is justified by the following considerations, which are discussed in more detail in Borchert (1994). Once xylem tension is released by the double cut, the retention of water depends only on the tension of tissues adjacent to the xylem. If these tissues are water saturated, xylem water will not be absorbed upon cutting a sample and liquid will be expelled by low compensation pressure, i.e., ψ_{stem} is high. Progressivly lower values of ψ_{stem} indicate increasing tension of stem tissues. For bare twigs, in which xylem tension is determined only by stem tissues, ψ_{stem} measured in double-cut twig sections with the modified pressure chamber technique (e.g., Figs. 1A, 2) was identical with that measured conventionally in adjacent terminal twigs (data not shown). Rehydration of stem tissues was indicated by increasing ψ_{stem} both in irrigated bare trees (Fig. 2) and in trees at moist sites bearing senescent leaves with low ψ_{leaf} (Fig. 1B). ψ_{stem} is thus independent of ψ_{leaf} or ψ_{xylem}, i.e., parenchymatic tissues near the xylem of a rehydrating branch may become water-saturated while xylem tension is high (Fig. 1B). Because of the high elastic module of wood, these parenchymatic tissues 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}. ψ_{stem} thus constitutes a measure of the water status of parenchyma cells near the xylem of twigs, which is uncoupled from daily variation in ψ_{xylem}, but depends on both predawn ψ_{xylem} (and hence soil water status) and the relative water content of adjacent stem tissues (Borchert 1994).

During rehydration of desiccated trees, ψ_{stem} permits the assessment of changes in the water status of thin branches, but not tree trunks. Stem expansion has been used as an indirect measure of rehydration in the outer, elastic tissues of the trunk and correlates well with changes in water potential in tropical tree species with a thick bark, but not in trees with a thin, hard bark (Daubenmire 1972; Reich and Borchert 1982, 1984; Ewers and Cruiziat 1991). Changes in electric resistance were therefore used to monitor rehydration of tree trunks. Resistance to AC of <1 kHz (or impedance) between electrodes in tree trunks varies with the amount and ion content of cell sap released by cells wounded during electrode insertion and thus reflects 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). 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. SM was found to be highly correlated with other measures of tree water status and developmental changes during the dry season (Borchert 1993a, b). Changes in stem circumference (girth) were measured using aluminum dendrometer bands (Liming 1957).

Experimental plots, located in a dry upland forest between 40 and 80 m from an irrigation ditch, were irrigated at rates of 1–1.2 m^3 h^{-1} using a portable generator, an electric pump, and garden hose (Table 1). Irrigation was initiated by pouring 0.8 m^3 water from 4 prefilled metal-drums within 15 min on the experimental plot. This water was immediately absorbed by the dry, porous soil. Thereafter water was distributed for 30-min periods over 2–4 m^2 sections by means of a 3-pronged outlet tube. The amount of irrigation water, expressed as millimeters per unit surface, was calculated from the irrigated area and duration and rate of irrigation. Measurements of tree water status were made before irrigation, at 12 h intervals during the first 3 days after irrigation, and daily thereafter. ψ_{stem} was measured in terminal tree branches, and girth changes and SM were measured at 1.5, 6, and 11 m trunk height.

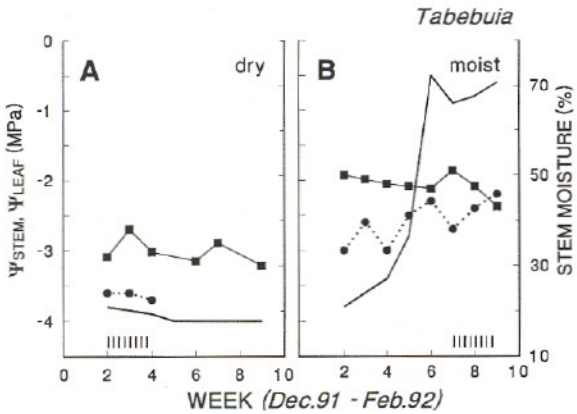

Fig. 1. Phenology and changes in water status of *T. ochracea* growing at a dry upland forest site (**A**) or a moist lowland site (**B**) during the dry season 1991/92 in Guanacaste, Costa Rica. Tree water status was assessed by monitoring ψ_{leaf}, ψ_{stem} and stem moisture (SM). |||| leaf fall; ●····●, ψ_{leaf}; —, ψ_{stem}; ■——■ stem moisture

Development of flowers and leaves after rehydration was monitored daily during the first week after irrigation, and every 3 days thereafter. Leaf length was measured with a ruler on accessible twigs and estimated on other twigs using binoculars.

Results

Rehydration of hardwood trees at dry sites

In trees growing at dry upland forest sites ψ_{leaf}, ψ_{stem} and SM declined to very low values within 4–6 weeks after the last major rainfall, and trees remained strongly desiccated for the rest of the dry season (Fig. 1 A; Table 2, day 0). The only rainfall occurring during the observation period (30 mm on 2 March 1991) did not cause rehydration and bud break in any upland-forest tree, but resulted in mass-flowering of *T. ochracea* at moist sites (Borchert 1993 a).

Measurement of tree rehydration at the beginning of the rainy season is impractical, because the timing of the first rains is unpredictable, and there is no opportunity for testing methods and repeating measurements. To study the time course of rehydration and growth resumption after rehydration, small plots containing 3–4 trees and in some cases a woody vine were irrigated with water from a small irrigation canal at least 4 weeks after all trees had shed their leaves (Table 1). The amount of water delivered to these plots over periods of 4–6 h (200–280 mm) was more than 4 times the minimum amount of rainfall known to induce rehydration and budbreak in dry forest trees (40–50 mm; Reich and Borchert 1982), but only a fraction of the area penetrated by the trees' root systems was actually irrigated (see below). The data given (Figs. 2, 3, Table 2) are representative of trees at several irrigated plots.

Before irrigation, all experimental trees and vines had a ψ_{stem} below the measuring range of the pressure chamber used (< –4 MPa; Figs. 1 A, 2; Table 2 A, B, day 0). Pressurized air passed freely through vine sections cut at both ends, indicating that the vessels were empty. Between 24 and 36 h after the beginning of irrigation, ψ_{stem} in the crowns of both small (Table 2 B, days 1–2) and 12–15 m tall *T. ochracea* (Fig. 2, days 0–2) began to increase notably, and after 48 h ψ_{stem} had reached saturation values (> –0.3 MPa) in most measured twigs of all experimental species. As indicated by wide variation in ψ_{stem} measured between 24 and 36 h after irrigation, the rate of rehydration in twigs of woody vines sampled 12–16 m from the base varied widely, but after 48 h all vessels were filled and sap was expelled by very low compensation pressures (Table 2 A, days 1–2). Irrespective of tree size, in 12 trees or vines of five species water absorbed by the root system started arriving in twigs 24 h after the beginning of irrigation, and ψ_{stem} had reached saturation values after 48 h.

SM and girth began to increase 36 h after the start of irrigation and, unlike ψ_{stem}, continued to do so for several days. In *T. ochracea* SM consistently reached its maximum after 4 days, while girth expansion lasted for up to 10–14 days (Fig. 2 and eight other trees in Expt. 3). In *Luehea* and

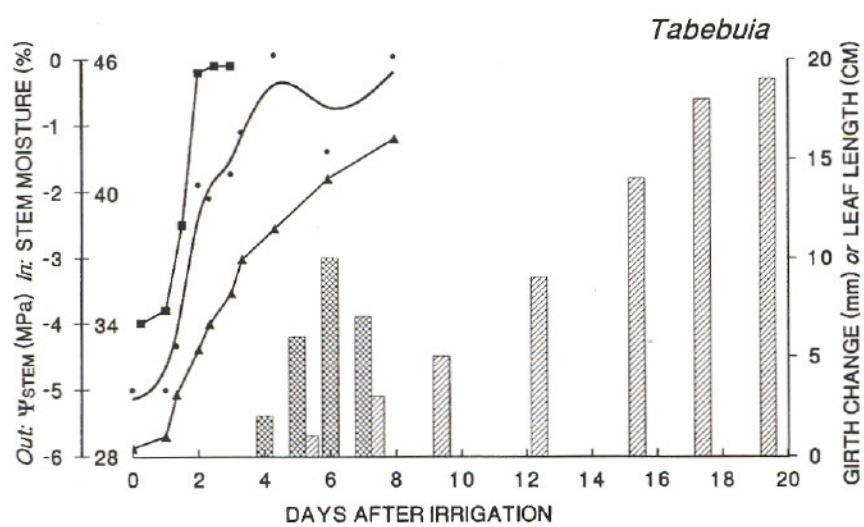

Fig. 2. Rehydration, flowering and leaf growth of *T. ochracea* induced by irrigating a 50 m^2 plot in a dry upland forest with 200 mm water (Table 1, Expt. 3). Rehydration was measured as increase in ψ_{stem} in twigs sampled at 12–14 m height (means of 3 samples), stem moisture (means of 9 values at 3 levels; curve fitted using a locally weighted regression procedure in the Axum program) and girth expansion at breast height. Flowering is in relative, developmental units. Leaf length is the length of the largest leaflet of the digitate leaf; data are means of measurements from 2 small, non-flowering *T. ochracea* and estimates of 2 large *T. impetigunosa* (Table 2 B, C). ■ ψ_{stem}; ● stem moisture; ▲ girth change; ▨ flowering; ▨ leaf length

Table 1. Irrigation of deciduous trees and woody vines in a dry tropical upland forest in Guanacaste, Costa Rica

	Experiment 1	Experiment 2	Experiment 3
Date	28 February 1991	4 February 1992	5 February 1992
Area	16 m^2	36 m^2	50 m^2
Water	280 mm	200 mm	200 mm
Species	*Cydista* sp. Four *T. ochracea* Two *T. impetigunosa* *Lonchocarpus* Eight other trees	*Lonchocarpus* *Luehea* *T. impetigunosa*	*Lonchocarpus* *Luehea* Two *T. ochracea* Twelve nearby trees

Lonchocarpus SM increased for 8 or more days (Fig. 3B, C). The rise in SM and girth was notably higher in *T. ochracea* and *Luehea* possessing a thick bark than in *Lonchocarpus* with a thin, hard bark (Figs. 2, 3A, B vs 3C).

To study the progress of rehydration from the base to the crown of tall trees or long vines, SM and changes in girth were measured at three levels above ground. In preliminary studies, SM readings in rehydrating, but not in fully rehydrated, tree trunks were found to vary widely. SM was therefore measured at 3 points along the stem circumference at each level. Consistently, both SM (Fig. 3A, B) and girth (data not shown) increased at the same rate at all levels, i.e., rehydration proceeded uniformly along the entire tree trunk. There was no measurable variation in SM or girth of woody vines.

Tree development induced by rehydration and heavy rain

The terminal flower buds of *T. ochracea* began to expand notably 2–3 days after irrigation, and most of the large, trumpet-shaped flowers were fully open after 6 days (Fig. 2, Table 2B). In all tree species and in the vine *Cydista* lateral vegetative buds started expanding 5–7 days after irrigation and were fully expanded after 3 weeks (Fig. 2, Table 2). Unexpectedly, several trees standing up to 9–11 m from the center of irrigated plots also produced a full crown of new leaves after irrigation (Table 2C),

Table 2. Rehydration and subsequent development induced by irrigation (280 mm water over 16 m^2) 28 February 1991 and 100 mm rain May 13/14 in trees and a woody vine at a dry upland forest site (Table 1, Expt. 1). A – the vine *Cydista* sp. was rooted in the center of the irrigated plot and its 12–25 m long stems where spread out horizontally and tied to nearby trees. B – 4 small (5–6 cm diameter) *T. ochracea* grew within 2–4 m of the irrigated plot; 2 of the trees were entirely vegetative, 2 formed flowers on some, leaves on other twigs. C – 2 large (36 and 28 cm diameter) *T. impetigunosa* stood 9 and 11 m from the plot's center. The single 30-mm rain-shower on March 3 did not cause any notable developmental response in non-irrigated trees of the surrounding dry forest. Stem and leaf water potentials (ψ_S, ψ_L) are given as –MPa

DAY	A *Cydista* sp. 12–16 m long	B *T. ochracea* 4 small trees	C *T. impetigunosa* 2 large trees
0	ψ_S <4	ψ_S <4	
1	ψ_S 4, 2.1, 1.5, 0.48, 0.21, 0.14, 0.07	ψ_S 1.58, 1.51, 1.14, 1.14	
2	ψ_S 0.07–0.03	ψ_S 1.1, 0.3, 0.24	
3	30 mm rain – no developmental response in dry forest		
4	Leaf buds expand	Flower buds expand	
6		Inflorescences fully expanded	Leaf buds expand
7	Leaves 4–8 cm long	Leaves 3–6 cm long Flowers abscising	Leaves 3–8 cm long
9	Leaves 6–9 cm		
12	Leaves 15–20 cm	Leaves 8–12 cm	Leaves 10–15 cm
20	Shoots up to 25 cm Leaves fully expanded, not turgid	Leaves fully expanded, turgid	Leaves expanded, not turgid
32	Herbivore damage	Leaves not turgid	Leaves not turgid
42	Heavy leaf damage	Leaves not turgid	Leaves not turgid
54	Heavy leaf damage ψ_L 4, 3.4, 2.9	Leaves not turgid ψ_L 3.3, 3.2	Leaves not turgid
74	Beginning of rainy season. 100 mm rain within 48 h		
75	No leaves left	Leaves half turgid	Leaves not turgid
76		Leaves fully turgid	Leaves fully turgid
85	New leaves expand	New leaves expand	No new leaves
92	Leaves fully expanded Full canopy of light-green leaves throughout dry forest	Leaves fully expanded	

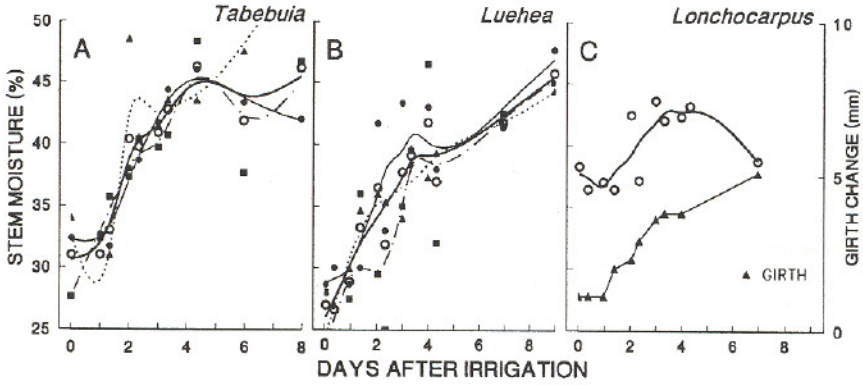

Fig. 3. Increase in stem moisture induced in 3 hardwood species by irrigating a 50 m^2 plot with 200 mm water (Table 1, Expt. 3). **A, B** – *T. ochracea* and *Luehea*: means of 3 SM-measurements at each of 3 levels (1.5, 6, 11 m above ground) and overall mean (9 values). **C** – *Lonchocarpus*: mean SM for whole tree (9 values) and girth increase at breast height. Curves for SM were fitted using a locally weighted regression as in Fig. 2. ○——○ mean; ▲---- ▲ 11 m; ■— ● —■ 6 m; ●——● 1.5 m

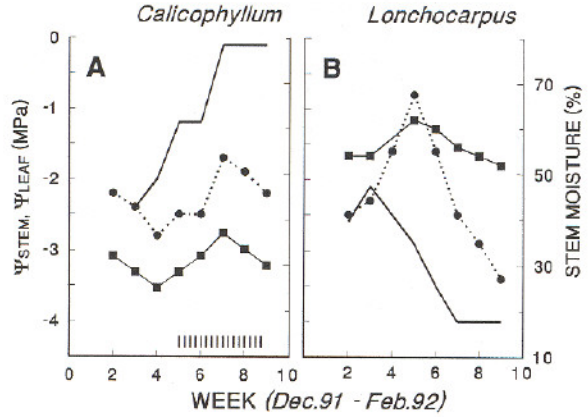

Fig. 4. Phenology and changes in water status of *Calicophyllum* and *Lonchocarpus* growing at a moist lowland site during the dry season 1991/92. Variables as in Fig. 1. *Lonchocarpus* shed leaves after the observation period shown. |||| leaf fall; ●----● ψ_{leaf}; — ψ_{stem}; ■——■ stem moisture

indicating that absorption of water by as little as 3% (16 of 452 m^2) of the trees' widespread root system was capable of supplying the entire tree crown with water. Extensive lateral transport must therefore take place in such trees. In contrast, leaf formation in a large tree of the water-storing *Bursera simarouba* was confined to the branches closest to a small irrigated plot 11 m away.

In two *T. impetigunosa* trees irrigated on 28 February 1991, the new, fully expanded, light-green leaves remained partially flaccid and thus had a low ψ_{leaf} during most of the 8 rainless weeks preceding the onset of the rainy season, but none were shed and irrigated trees constituted a green oasis in the otherwise bare deciduous forest (Table 2B, C, days 20–74). Within 48 h after the first rains of the rainy season leaves formed after irrigation regained turgidity. Newly emerging leaves on all bare trees were fully expanded within 18 days, i.e., somewhat faster than after irrigation (Table 2, days 74–92).

Rehydration at moist sites during climatic drought

Trees growing at moist lowland sites providing access of roots to the groundwater table maintained a higher ψ_{leaf} and SM and shed their leaves later than those at dry sites (Figs. 1A vs B, 4). ψ_{stem} commonly declined during the early dry season (Fig. 4B) and then increased to values near saturation well before leaves were shed. This resulted in large differences between ψ_{stem} and the low ψ_{leaf} of senescent leaves (Figs. 1B, 4A). Leaf shedding in resaturated trees was followed by flowering (in *T. ochracea, Luehea*) and flushing. At both dry and moist sites, *Lonchocarpus* maintained a higher SM, retained its leaves longer, and desiccated later than other species (Figs. 3C, 4B vs 1, 4A). Generally, trees at moist sites varied widely with respect to seasonal changes in water status and development (Borchert 1993a, 1994).

Discussion

Rehydration and rise of sap

The biophysical and biochemical mechanisms involved in water uptake and refilling of vessels in bare trees are likely to be similar in tropical and temperate trees. In the latter, the rise of sap is triggered in early spring by the mobilization of reserve starch and activation of acid phosphatases likely to be involved in sugar secretion into the xylem. Secretion of sugars and possibly mineral ions into the vessels presumably causes osmotic water uptake and development of xylem pressure responsible for refilling embolized vessels and upward water transport in bare trees (root or bleeding pressure; Kramer and Kozlowski 1979; Sauter 1980; Braun 1984). Because of the slow and irregular rise of temperature in spring, activation of the initial metabolic processes and subsequent water transport extend over several weeks. In a study of refilling of vessels in wild grapevine growing in the northeastern USA, root pressure was first observed on April 8. Two weeks later very few vines had become refilled entirely, but 1 month later, at the time of bud break, refilling of vessels was nearly complete (Sperry et al. 1987).

The large vessels of bare, desiccated vines were found to be empty (see Results) and, as in other hardwood trees, the majority of vessels are likely to have become embolized in strongly desiccated, bare hardwood twigs with $\psi_{stem} < -4$ MPa (Figs. 1A, 2; Tyree and Sperry 1989). During rehydration of irrigated trees and vines, water uptake by roots should result in the development of xylem pressure in the root system (root pressure), which is a

prerequisite for the refilling of embolized vessels (Sperry et al. 1987). Refilling of vessels and upward water transport after irrigation were much faster than during sap rise in bare temperate trees and vines. As indicated by increasing ψ_{stem}, in the twigs of 12–15 m tall trees and in vine segments 15–20 m from the base rehydration started between 24 and 36 h after the beginning of irrigation, and within 48 h parenchymatic tissues near the xylem had become saturated (Fig. 2, Table 2). These rates of rehydration are similar to those observed in much smaller desert succulents, in which maximum water conductivity of persisting, desiccated roots is reestablished within 16 h after rewetting, and water uptake and stomatal opening are induced within 36 h (Rundel and Nobel 1991). The timing of rehydration in twigs of tall trees indicates that within little more than 1 day all the processes involved in the establishment of root pressure were activated, many vessels became refilled and water was driven as much as 15 m up the stems of bare trees and vines at velocities of 0.7–1 m h^{-1}, similar to the highest observed rates of phloem transport (Richardson 1968). Apparently, this relatively fast long-distance water movement driven by osmotic water uptake is possible because the amount of water absorbed and transported in bare trees is very small as compared to that transported in leaf-bearing, transpiring trees (Braun 1984), only a fraction of this water is required for the initial refilling of vessels, and flow resistance in the xylem is low. The strong local variation in SM, observed in rehydrating trees (Figs. 2, 3) but not in those at equilibrium with soil moisture, indicates that refilling of vessels and rehydration of stem tissues proceeds irregularly in different parts of a tree trunk, as also observed for temperate woody vines (Sperry et al. 1987).

During sap rise in bare temperate trees, pressure developing in the xylem of water-saturated trunks may manifest itself as *bleeding*, i.e., exudation of sugar-containing sap from leaf scars, buds or cut twigs (Kramer and Kozlowski 1979). Bleeding has been also occasionally noted in tropical trees, e.g., during flushing of the "rain tree", *Pithecelobium saman* (Braun 1984), but was never observed during rehydration of irrigated, strongly desiccated dry-forest trees. In such trees root pressure is unlikely to become manifest as bleeding in the crown, because the xylem is surrounded by stem tissues with a very low water potential, constituting a large, potent sink for the small amount of water rising in the xylem. Refilling of vessels and subsequent rehydration of stem tissues, as indicated by increasing ψ_{stem}, thus replaces bleeding as a manifestation of xylem pressure. The relatively slow increase in SM and girth, proceeding at the same rate along the entire height of tree trunks (Figs. 2, 3), indicates that rapid refilling of the xylem is followed by much slower rehydration of tissues outside the xylem, which occurs via relatively slow, lateral water movement.

Tree development after rehydration

Terminal flower buds of *T. ochracea*, which retain good vascular connections with the supporting twig throughout the rest period (Braun 1960), began to expand, i.e., to absorb water, simultaneously with the rehydration of stem tissues, and trees were in full bloom 1–2 days after SM had reached its maximum (Fig. 2). Similarly, bare trees of many other species have been observed to bloom within 3–12 days after heavy isolated rains in Costa Rican and Mexican dry forests (Opler et al. 1976; Bullock 1986). In all eight irrigated *T. ochracea* trees (Table 1, Experiment 3) opening of the large flowers coincided with a distinct temporary decline in SM (Fig. 2, day 6) and was followed by stem shrinkage in earlier studies (Reich and Borchert 1982), suggesting that water from rehydrating stem tissues is absorbed to replace water loss by expanding flowers.

Vascular connections between lateral buds and the xylem are usually severed during growth in girth after bud inception. Initial growth of lateral buds giving rise to vegetative shoots is relatively slow, because they are supplied with water and nutrients via slow cell-to-cell transport from adjacent parenchymatic tissues (Braun 1960). Accordingly, lateral, vegetative buds in all experimental species began to expand later than terminal flower buds and at a time when resaturation of bark tissues, indicated by increased SM and girth expansion, was well advanced (Figs. 2, 3, days 5–8).

In all experiments, water supplied by a single irrigation was sufficient for the establishment of a full crown of new leaves, but not for maintaining turgidity of these leaves during continuing drought (Table 2C, days 20–74). The physiological basis for the unexpectedly high drought resistance of partially flaccid, young leaves surviving 8 rainless weeks is not known. Similarly, expansion of leaves on shoots emerging during the dry season in *Erythrina poeppigiana* and in water-storing lightwood trees of tropical dry forests remain arrested at an early stage, and leaves expand fully only after soils have become water-saturated by the first heavy rains (Borchert 1980; Bullock and Solis-Magallanes 1990).

Predictibly and consistent with prior observations (Reich and Borchert 1982, 1984), hardwood trees growing at moist sites desiccated less and hence retained their leaves longer than their conspecifics at dry sites. The observed decline in ψ_{stem} during the early dry season and its later rise in the presence of senescent leaves with a low ψ_{leaf} illustrates that in trees at moist sites ψ_{stem} may approach saturation values while ψ_{leaf} remains low (Figs. 1B, 4A). Indirect evidence suggests that increases in ψ_{stem} in the presence of water-stressed leaves are the result of root extension into moist subsoil layers, possibly in conjunction with osmotic adjustment in stem tissues (Borchert 1994). In contrast to the rapid and complete rehydration of bare trees after irrigation (Fig. 2), rehydration of leaf-bearing trees using subsoil-moisture always required several weeks and was limited to parenchymatic tissues near the xylem (increasing ψ_{stem}), while the water content of outer stem tissues (SM) rarely increased before transpirational water loss had been eliminated by leaf shedding (Figs. 1B, 4A). Without exception, establishment of a high ψ_{stem} precedes flowering and bud break of dry-forest trees during drought, which occurs only in trees which either store water in their trunks or have access to soil moisture (Bullock and Solis-Magallanes 1990; Borchert 1994).

Development of drought-deciduous tropical hardwood trees during the dry season is thus highly opportunistic and, unlike their temperate counterparts, bare trees are apparently never dormant. Strongly desiccated trees at dry sites rehydrated and resumed development rapidly whenever sufficient water became available, whereas trees at moist sites desiccated moderately while bearing senescent leaves and then rehydrated, flowered and flushed after leaf shedding at rates which varied with soil water availability.

In contrast to the dramatic effects of a single irrigation on the development of strongly desiccated, bare trees described here, maintenance of a high soil moisture content by frequent irrigation during the dry season did not affect development of most tree species of a tropical moist forest in Panama (Wright and Cornejo 1990), indicating that in such forests most trees are adequately buffered against moderate seasonal drought by soil moisture reserves (see Introduction).

Acknowledgements. I am very grateful to the more than 30 EARTHWATCH volunteers, whose financial support and reliable and enthusiastic collaboration made this study possible. Thanks are also due to the managers of La Pacifica, P. Nett and Ing. F. Estrada, for logistical support and permission to do field work in the hacienda, to W. Hagnauer, Finca Las Pumas, for advice and logistical support, and to M. T. Tyree, University of Vermont, for valuable suggestions during the planning for this project and revision of the manuscript.

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