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Ecology, Vol. 75, No. 5. (Jul., 1994), pp. 1437-1449.

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Ecology, 75(5), 1994, pp. 1437–1449
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SOIL AND STEM WATER STORAGE DETERMINE PHENOLOGY AND DISTRIBUTION OF TROPICAL DRY FOREST TREES[1]

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Abstract. Many trees of tropical dry forests flower or form new shoots soon after leaf shedding during the dry season, i.e., during a period when trees are likely to be severely water stressed. To resolve this apparent paradox, phenology and seasonal changes in tree water status were monitored during two consecutive dry seasons in >150 trees of 37 species growing at different sites in the tropical dry lowland forest of Guanacaste, Costa Rica.

Tree development during the dry season varied considerably between species and between sites of different moisture availability. Leaf shedding, flowering, and shoot growth (flushing) were strongly correlated with seasonal changes in tree water status, measured by conventional and newly developed techniques. Tree water status varied with the availability of subsoil water and a variety of biotic factors such as structure and life-span of leaves, time of leaf shedding, wood density and capacity for stem water storage, and depth and density of root systems. Observed tree species differed widely in wood density (from 0.19 to 1.1 g/cm^3) and stem water storage capacity (400–20% of dry mass), which was highly correlated with the degree of desiccation during drought. Only hardwood trees at dry upland sites, lacking stem water storage and access to subsoil water, desiccated strongly (stem water potential <-4 MPa) and remained inactive throughout the dry season. In all other trees elimination of transpirational water loss during leaf shedding in conjunction with utilization of residual water enabled rehydration of stem tissues and subsequent flowering or flushing during the dry season. Rate and degree of rehydration varied strongly with the availability of water stored in tree trunks or in the subsoil. Stored water buffers the impact of seasonal drought and enables flowering and flushing during the dry season. Climatic data are thus not sufficient to explain tree phenology in seasonally dry tropical forests.

Phenology, seasonal changes in water status, and water storage capacity of tree species are highly correlated. Tree species cluster into a number of distinct functional types ranging from deciduous hardwood trees and water-storing lightwood trees in dry upland forests to evergreen light- and softwood trees confined to moist lowland sites. Seasonal variation in tree water status thus appears to be the principal determinant of both phenology and distribution of tree species in tropical dry forests.

Key words: Costa Rica; seasonal drought; soil water storage; stem water storage; tree phenology; tree water status; tropical dry forest.

INTRODUCTION

Tropical dry forests grow under a range of annual rainfall from 600 to 1800 mm and are characterized by a dry season of 2–7 mo during which <10% of annual precipitation occurs (Murphy and Lugo 1986). Dry forests represent a larger fraction of tropical forests than rain forests, yet knowledge of the ecophysiology of dry forest trees is scant (Olivares and Medina 1992, Holbrook et al. 1994), and their phenology is not well understood (Murphy and Lugo 1986). Water is commonly considered to be the most important environmental factor affecting growth and distribution of trees (Hinckley et al. 1991). Seasonal water stress is thus likely to determine the timing of phenological events in dry forests, but the mechanism of its action remains obscure (Murphy and Lugo 1986). Most trees in tropical dry forests shed their leaves during the dry season, and many species flower or flush soon after leaf shedding. Flower expansion and shoot growth involve cell expansion, known to be inhibited by even moderate water deficits (Bradford and Hsiao 1982). The question is, then, how these growth processes can occur during severe climatic drought.

Using seasonal changes in stem diameter as an indirect measure of changes in tree water status, we found earlier that leaf shedding usually followed increasing water stress during early drought. Many trees rehydrated after leaf shedding, and rehydration always preceded flowering or flushing (Borchert 1980, 1991, Reich and Borchert 1982, 1984). In this study the relationship between changes in water status and tree development during two dry seasons in the tropical dry lowland forest of Guanacaste, Costa Rica, was analyzed in more detail. Changes in tree water status during the dry season were measured in many trees by conventional and

[1] Manuscript received 9 November 1992; revised 9 August 1993; accepted 22 October 1993.

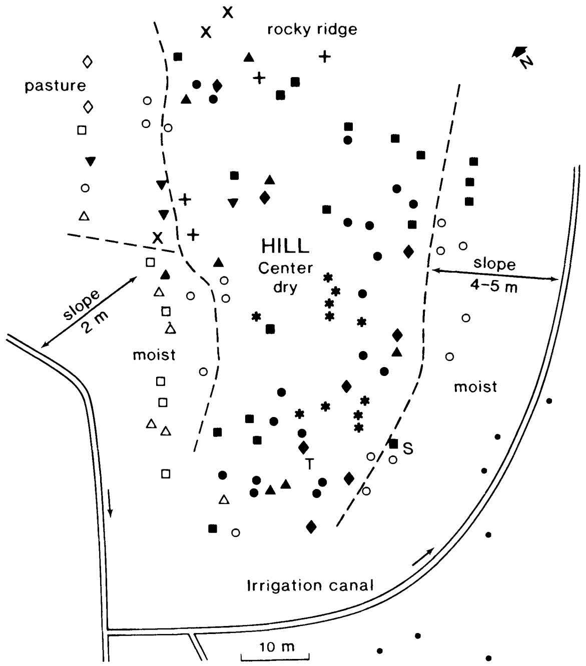

FIG. 1. Distribution of experimental trees of four functional types (D_{hard}, D_{soft}, D_{light}, EV_{soft}; see Table 2) at the HILL upland forest site at Hacienda La Pacifica. Dashed lines mark the boundary between the very dry forest center and the adjacent, moister sites. D_{hard} species: ▼, *Apeiba, Astronium, Calicophyllum*; ▲, *Lonchocarpus, Lysiloma, Machaereum*; ◆, *Luehea*; ■, *Tabebuia impetigunosa*; *Tabebuia ochracea*: ○, flowering, ●, not flowering after 30 mm rain on 3 March 1991. D_{light} species: ×, *Bombacopsis, Enterolobium*; +, *Bursera, Spondias purpurea*; *, *Cochlospermum*. D_{soft} species: ◇, *Cassia emarginata, Myrospermum*; □, *Cordia*; △, *Guazuma*. EV_{soft} species: S, *Schoepfia*; T, *Thouinidium*. ●, D_{hard} trees at wet site near irrigation canal.

newly developed methods, and were found to be the principal determinant of the observed tree development.

FIELD SITES, MATERIALS, AND METHODS

Research area and climate

Field observations were made at Hacienda La Pacifica, Canãs, Guanacaste province, Costa Rica, which is located at 45 m elevation in the "tropical dry forest, moist province transition" life zone of Holdridge (Hartshorn 1983) and has been the site of earlier studies of dry forest trees (Frankie et al. 1974, Reich and Borchert 1982, 1984). Generally, the dry season lasts from late November to mid-May, and >95% of the annual precipitation falls during the remaining months. Following extensive deforestation annual precipitation has declined continuously over the past 50 yr, from a mean (± SE) of 1950 ± 553 mm during 1931–1940 to 1240 ± 385 mm for 1981–1990; annual rainfall below 1000 mm was never recorded before 1971, but has been measured in 7 yr since then (Hagnauer 1993). Only 903 mm of rain fell in 1991, an exceptionally dry year (J. Herrick, *personal communication*). Field work was done during two consecutive dry seasons. The first period (1 January 1991 to 12 June 1991) comprised the greater part of the 1990/1991 dry season and the early rainy season. The second period started 1 December 1991, 6 wk after the last rainfall, and ended at the height of the dry season (25 February 1992). Monthly precipitation did not exceed 3 mm during this period.

Field sites

The HILL site (Fig. 1) is located in the "Bosque La Rana" ≈1 km from and 10–15 m above the Corobici River in the eastern part of Hacienda La Pacifica. It consists of secondary forest regenerated after the last burning of the forest ≈40 yr ago (W. Hagnauer, *personal communication*). Larger trees are 12–15 m tall and have diameters up to 40 cm. The underlying, partially exposed geological formations are andesite agglomerates giving rise to porous, volcanically derived soils (D. Smith, *personal communication*). The HILL site borders on one side with a pasture and elsewhere with a small irrigation canal carrying water at least twice weekly throughout the experimental period. The following subsites can be distinguished (Fig. 1): dry forest in the HILL center, >25 m from and 4–7 m above the irrigation ditch; moist slopes between HILL center and irrigation canal; wet sites within 3 m of the canal; dry savanna, i.e., open stands of trees at the forest margin with the adjacent pasture. The borders shown in Fig. 1 between the dry center of the HILL forest and the adjacent moister sites were drawn based on phenological observations and measurements of tree water status described in the *Results*.

The very dry TUFF site is located in the western part of La Pacifica, ≈1 km from and 15 m above the Tenorio River. Outcroppings of vulcanic tuff are covered by very little topsoil and bear groups of scattered trees. The moist HOTEL site comprises the grounds of the Hotel La Pacifica and several small lowland sites along a nearby farmroad. This flat site, crossed by several irrigation ditches, has heavy, lateritic soils and is between 4 and 6 m above the Corobici River.

Soil moisture availability.—Throughout the research area, the upper 30–40 cm of the soil dry out completely within 1 mo after the last heavy rainfall (Reich and Borchert 1984). Subsoil water reserves available to tree roots cannot be measured directly and were inferred from site topography, phenology, and tree water relations (see *Results*). Water reserves at the dry upland sites were depleted during the first 2 mo of drought, while at moist and wet sites near HILL and at HOTEL subsoil water was available to various degrees throughout the dry season.

Observed tree species

Trees growing at sites ranging from very dry to wet, and suitable for assessment of water status and phe-

TABLE 1. Tree species used for phenological observations and ecophysiological measurements in the dry forest of Guanacaste, Costa Rica. Species are grouped according to functional types (D_{hard}, etc.) described in Table 2.

Functional type A*	Species B	Family C	No. trees observed D	Field sites E	Figs. F
D_{hard}	*Apeiba tibourbou*	Tiliaceae	2	H_c, H_w	48B, C
	Astronium graveolens	Anacardiaceae	2	H_c	...
	Calicophyllum candidissimum	Rubiaceae	3	Sa, Ho	b
	Lonchocarpus minimifolium	Fabaceae	4	H_c, Ho	b
	Luehea candida	Tiliaceae	7	All	4A, b
	Lysiloma seemannii	Mimosaceae	4	H_c, Ho	a
	Machaereum biovulatum	Fabaceae	3	H_c	...
	Tabebuia impetigunosa	Bignoniaceae	8	H_{all}	...
	Tabebuia ochracea spp. *neochrysantha*	Bignoniaceae	14	All	a, b
D_{light}	*Bombacopsis quinatum*	Bombacaceae	3	H_c, Ho	6A
	Bursera simarouba	Burseraceae	3	H_c, Ho	...
	Cochlospermum vitifolium	Cochlospermaceae	7	H_c	...
	Enterolobium cyclocarpum	Mimosaceae	6	H_c, Ho	6B
	Spondias mombin	Anacardiaceae	2	H_c, Ho	6C
	Spondias purpurea	Anacardiaceae	5	H_c, Ho	a
D_{soft}	*Albizza guachapele*	Mimosaceae	5	Ho, Sa	5A
	Caesalpinia eriostachys	Caesalpinaceae	1	Sa	...
	Cassia emarginata	Caesalpinaceae	4	Ho, Sa, T	5C, D
	Cordia alliodora	Boraginaceae	5	7H_m, Ho	a
	Gliricidia sepium	Fabaceae	3	Ho	...
	Guazuma ulmifolia	Sterculiaceae	6	H_m, Ho	a
	Myrospermum frutescens	Fabaceae	5	Sa, Ho	5B, a
	Pterocarpus rohrii	Fabaceae	1	Ho	a
	Tabebuia rosea	Bignoniaceae	3	Ho, T	...
EV_{soft}	*Andira inermis*	Fabaceae	1	Ho	a
	Cassia grandis	Caesalpinaceae	4	Ho	7C
	Dalbergia retusa	Fabaceae	3	Ho	7B
	Hymenea courbaril	Caesalpinaceae	2	Ho	...
	Licania arborea	Chrysobalanaceae	2	Ho	a
	Pithecellobium saman	Mimosaceae	4	Ho	a
	Schoepfia schreberi	Olacaceae	1	H_m	...
	Simarouba glauca	Simaroubaceae	3	Ho, T	7D
	Thouinidium decandrum	Sapindaceae	4	H_c, Ho	7A
EV_{light}	*Eugenia salamensis*	Myrtaceae	4	Ho	6D, a
	Gmelina arborea	Verbenaceae	2	Ho	a
	Ochroma lagopus	Bombacaceae	2	Ho	...
	Psidium guajava	Myrtaceae	1	Ho	...
	Sterculia apetala	Sterculiaceae	1	Ho	...

* Columns: (A) Functional type. (B) Species. (C) Family. (D) Number of trees used in ecophysiological measurements. (E) Field sites at which experimental trees were observed. All, all sites; H_{all}, all HILL sites; H_c, very dry center of HILL forest; H_m, moist slopes on HILL; H_w, wet sites near irrigation canal; Ho, moist HOTEL sites; Sa, dry savanna sites near HILL and elsewhere; T, very dry TUFF site. (F) References to figures containing experimental data for this species: a, Borchert 1994*c*; b, Borchert 1994*a*.

nological observations during the dry season, were selected (Table 1). Riparian trees were excluded because of their large size. Species names follow Janzen and Liesner (1980), where authors and synonyms may be found. Species listed in Table 1 will be referred to by genus only, except for the genera represented by >1 species.

Phenology

Using binoculars, phenological observations were normally made every 2 wk, but weekly during periods of rapid developmental change. The following developmental stages were scored on a scale from 0 to 3 (0—none; 1—few, <20%; 2—many, 20–80%; 3—abundant, >80%): Leaves: a—old, green; b—old, yellow-brown; c—new, emerging from buds; d—new, fully expanded. Flowers: a—buds visible; b—flowers open; c—flowers fading, abscising. Fruits (mainly pods): a—very small, <2 cm; b—medium, <80% of full size, c—full size, green; d—full size, mature (brown, dry). Examples of phenological records obtained by this method are in Borchert (1992).

Measurement of tree water status

Water potential (see Table 2I, J, and Figs. 2–7) 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 bamboo scaffolding. Triplicate samples were collected every

TABLE 2. Functional tree types in the dry forest of Guanacaste at La Pacifica. Trees were grouped according to distribution at different sites, temporal pattern of development, and water status during the dry season. Species are listed for the driest site at which they occur, even though most species occur also at moister sites and may display different phenology there (see *Results*).

			Phenology (month of stage)			Wood		Water status (min values)		
Species A*	Site B	Leaf type C	Shed D	Flush E	Flower F	Density (g/cm^3) G	WC_{sat} (% DW) H	ψ_{leaf} (MPa) I	ψ_{stem} (MPa) J	SWC (%) K
Deciduous trees										
Dry upland forest (subsoil water reserves are depleted early in the dry season)										
D_{hard} Hardwood trees that are bare for several months and desiccate strongly										
Apeiba	dry	mes	1–3	5–6	6	>0.7	<64	−3.6	<−4	30
Astronium	dry	cor	irregular			1.2	19*	−3.2	−3	30
Calicophyllum	sav	mes	2–3	6	12–1	>0.9	<32		<−4	22
Lonchocarpus	dry	mes	2–4	5–6	8	0.91	31*	−3.4	<−4	42
Luehea	dry	mes	1–2	5–6	6	0.91	31*	−3.8	<−4	29
Lysiloma	dry	mic	2–4	6–7	7	0.92	30*	<−4	<−4	31
Machaereum	dry	mes	2–4	6–7	8	>0.9	<32			35
T. impetigunosa	dry	mes	1–2	5–6	[rain]	0.96	25*	−4	<−4	29
T. ochracea	dry	mes	1–2	5–6	[rain]	1.1	20	−3.9	<−4	29
Means:						0.94	32	−3.7	−3.9	31
D_{light} Lightwood trees with high stem water storage										
Bombacopsis	dry	mes	12	5–6	1–3	0.47	121	−1.5	−0.5	62
Bursera	dry	mes	12	5–6	5–6	0.47	137			64
Cochlospermum	dry	mes	12	5–6	1–3	0.19	412			63
Enterolobium	dry	mic	1–2	2–4	2–4	0.49	125	−2.3	−1.1	52
S. mombin	mst	mes	1–2	4–5		0.39	171	−0.8	−0.7	67
S. purpurea	dry	mes	12	5–6	1–2	0.37	191		−1	69
Means:						0.40	193	−1.5	−0.8	63
Dry, open savanna (small water reserves persist in the subsoil)										
D_{soft} Softwood trees that rehydrate and flower or leaf out during drought										
Albizia	sav	mes	12–1,5		1,5	high		−1.8	−0.8	47
Caesalpinia	sav	mes	12–1	2–4	1–3	0.74	57*			
C. emarginata	sav	cor	1–2	4–5	2–3	0.89	33*	−2.8	−3.7	38
Cordia	sav	mes	2–3	6	2	0.70	63	−3.7	<−4	37
Gliricidia	sav	mes	1–2	3–5	12–2	0.64	78*	−1.4	−0.9	50
Guazuma	sav	mes	1–2	4–5	3–4	0.67	71*	−2.5	−1.7	45
Myrospermum	sav	mes	12–1	4–5	1–2	>0.8	<48	−3.5	−3.6	44
Pterocarpus	mst	cor	12–1	4–5	2	0.52	114	−2	−2.2	42
T. rosea	sav	scl	1–2	4–5	1–2	0.72	60*	−2.2	−2.3	71
Means:						0.71	65	−2.5	−2.4	47
Evergreen trees										
Moist lowland sites (tree roots have access to the water table)										
EV_{soft} Evergreen softwood trees with coriaceous leaves										
Andira	mst	cor	11–1		2	>0.7	<64	−1	−0.3	44
C. grandis	mst	cor	3		3	>0.7	<64	−2.2	−2.5	46
Dalbergia	mst	cor	2–3		3	0.83	41*	−2.2	−1.5	42
Hymenea	mst	cor	1–3		3–4	0.61	94	−2.6	−1.8	47
Licania	mst	cor	irregular		1	0.59	100	−4	−0.5	50
Pithecellobioum	mst	cor	3		3	0.74	57*	−2.7	−2.4	49
Schoepfia	mst	cor	5–6			>0.7	<64	−3.8	−3	48
Simarouba	sav	cor	12–1		1–2	>0.6	<89	−1.2	−1	45
Thouinidium	dry	cor	12–1		1–2	>0.6	<89	−2.7	−1.5	42
Means:						0.67	74	−2.5	−1.6	46
EV_{light} Light- or softwood trees with mesic or sclerophyllous leaves										
Eugenia	mst	scl	3–5	4–6	3–6	>0.6	<89	−3.5	−1.5	49
Gmelina	mst	mes	irregular		12–2	0.42	167	−1.6	−0.8	54
Ochroma	mst	mes	12–2		12–2	0.32	196	−1.1	−0.5	79
Psidium	mst	scl	12–2			>0.5	<120	−2.7	−0.1	44
Sterculia	mst	mes	12–2		12–1	0.49	141	−1.2	−1.1	74
Means:						0.47	143	−2.0	−0.8	51

* Columns: (A) Species as in Table 1. (B) Site: dry = dry upland site; sav = dry, savanna; mst = moist lowland sites. (C) Leaf structure: cor = coriaceous; mes = mesomorphic; mic = microphylls; scl = sclerophyllous. (D–F) Phenology: (D) leaf shedding; (E) flushing; (F) flowering; rain = flowering after heavy rainfalls. (G) Wood density; (H) % saturation water content of wood (WC_{sat}). * Wood density obtained from Barajas-Morales (1987) and saturation water content calculated from density.

1–2 wk between the times of 0530 and 0700, placed into plastic bags immediately after cutting, stored in a cooler containing moist paper, and processed within 2 h after sampling. If variation in ψ exceeded 0.3 MPa, measurements were repeated the next day. Errors in Figs. 4–7 are thus less than ±0.15 MPa. 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 ψ_{xylem}, was obtained from leaves or leaf-bearing branch sections. 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 and discussed in more detail in Borchert (1994*c*). Once xylem tension is released by the double cut, the retention of water depends only on the tension of stem 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. Progressively lower values of ψ_{stem} indicate increasing tension of stem tissues. ψ_{stem} is independent of ψ_{leaf}; for example, parenchymatic tissues near the xylem of a rehydrating branch may become water-saturated while xylem tension is high (Fig. 7A–C). Because of the high elastic modulus 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 varies strongly with long-term tree water balance (see *Results*; Borchert 1993).

Stem water content (see Table 2K and Figs. 2–7).— Measurement of ψ_{stem} in tall forest trees is hampered by the difficulty of obtaining twigs for use in the pressure chamber. Changes in girth correlate 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). Variation in electric resistance was therefore used to monitor the water status of tree trunks (Borchert 1994*a*). Resistance to alternating current (AC) of < 1 kHz (or impedance) between electrodes 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, 10 mm apart) was driven at breast height 20 mm deep into bark and sapwood of a tree. Resistance between these electrodes was measured with a Bouyoucos soil moisture meter (Model BN-2B using AC of 480 Hz, Beckman, Cedar Grove, New Jersey). Instead of the instrument's exponential scale for electrical resistance in ohms, the linear, arbitrary scale indicating "percent available soil moisture" was used and data are given as percent stem water content (SWC), which thus constitutes a relative measure based on electric resistance of the outer 20 mm of tree trunks. Differences between duplicate measurements taken on the same trees during the 1st wk of monitoring water status never exceeded 3% SWC, and single measurements were therefore taken thereafter. Interspecific differences in the range of SWC were found to be indicative of differences in trunk water storage capacity (Figs. 2 and 3A), and intraspecific variation indicates differences in the water status of trunk tissues (Figs. 3B, 4B, C; Borchert 1994*a*).

Wood cores (5 mm diameter, 30 mm long) weighed fresh (fresh mass, FM), after soaking for 24 h (saturation mass, SM), and after oven drying (dry mass, DM) were used to determine the following variables: wood density (D, g/cm^3) = DM/volume, water content (WC, % FM) = 100 (FM − DM)/FM and saturation water content (WC$_{\text{sat}}$, % DM) = 100 (SM − DM)/DM (Table 2G, H; Fig. 2; Schulze et al. 1988). WC and WC$_{\text{sat}}$ represent the actual and potential water content of wood, respectively, and hence are measures of trunk water storage capacity. WC and WC$_{\text{sat}}$ increase with the fraction of living parenchyma cells in the wood and are negatively correlated with wood density (Fig. 2 insert; Tables 2 and 3; Schulze et al. 1988) and directly with SWC (Table 3). Cores could not be excised from most hardwood trees, because of the high density of the wood. Density of these or related species was therefore obtained from Barajas-Morales (1987), and WC$_{\text{sat}}$ was calculated as $\text{WC}_{\text{sat}} = 100\ (1 - D/1.5)/D$, where 1.5 is the mean density of wood substance. Wood density and water storage capacity of wood are known to vary widely within tropical tree species (e.g., Howe 1974).

←

Values preceded by > are estimates based on resistance of wood to nail insertion during measurements of stem water content. (I–K) Tree water status during the dry season. All data represent the lowest values observed in any experimental tree during the dry season. (I) ψ_{leaf}; (J) ψ_{stem}; (K) stem water content (SWC). Phenology and measurements of tree water status are based on the number of experimental trees given in Table 1. For calculation of means, <a and >b were treated as a and b, respectively.

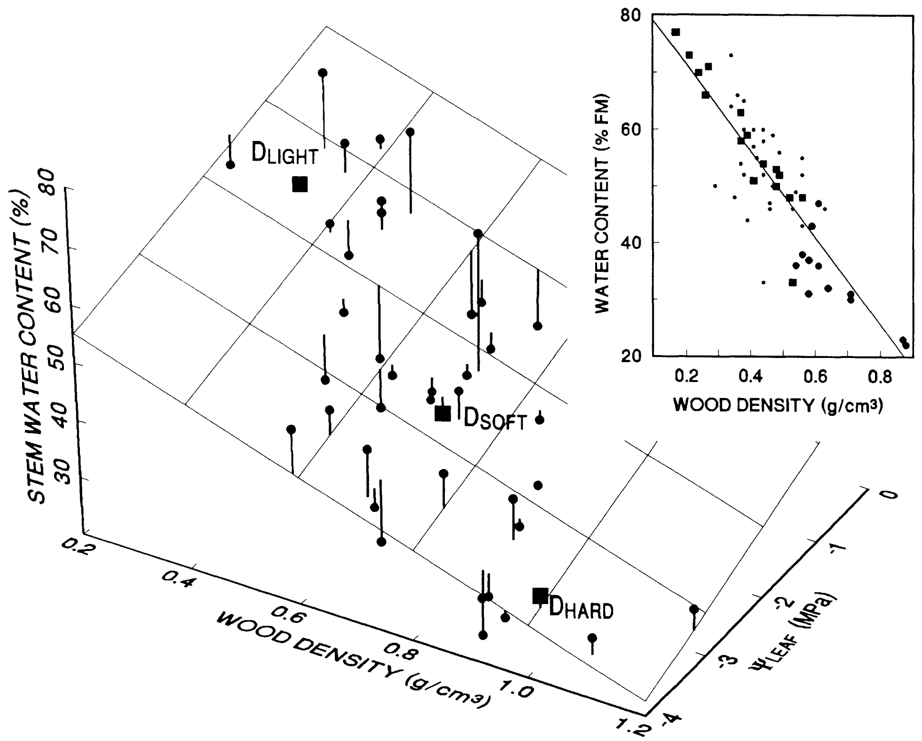

FIG. 2. Regression between wood density, minimum $\psi_{\rm leaf}$, and stem water content (SWC) for the deciduous species listed in Table 2. ■, means for functional types. Length of drop lines represents deviation from regression plane. $R^2 = 0.73$; regression coefficients ± 1 SE are −32.9 ± 7.46 for SWC vs. density and 5.08 ± 1.65 for SWC vs. minimum $\psi_{\rm leaf}$, respectively. $D_{\rm hard}$ species have high density wood and low minimum $\psi_{\rm leaf}$ and SWC; $D_{\rm light}$ species have low density wood and high minimum $\psi_{\rm leaf}$ and SWC; $D_{\rm soft}$ species have intermediate values. Insert: Correlation between wood density and water content of 32 samples of soft- and lightwood trees collected in January and February 1992. ●, $D_{\rm soft}$ species; ■, $D_{\rm light}$ species; •, $\rm EV_{light}$ species. $R^2 = 0.73$, correlation coefficient −0.85 (graphs and statistics done with AXUM software, Trimetrics, Seattle, Washington).

RESULTS

Phenology of trees during the dry season

Phenological differences among trees in the various parts of the HILL forest (Fig. 1; see *Field sites, materials, and methods*) began to appear in early January 1991, ≈1 mo after the last rainfall. Leaves of most trees in the dry center of HILL changed color and were shed during January. Trees remained bare until leaves emerged ≈2 wk after the first heavy rains in mid-May. Only a few trees of *Astronium, Schoepfia,* and *Thouinidium,* and the common understory treelet *Jacquinia pungens* kept their leaves throughout the dry season.

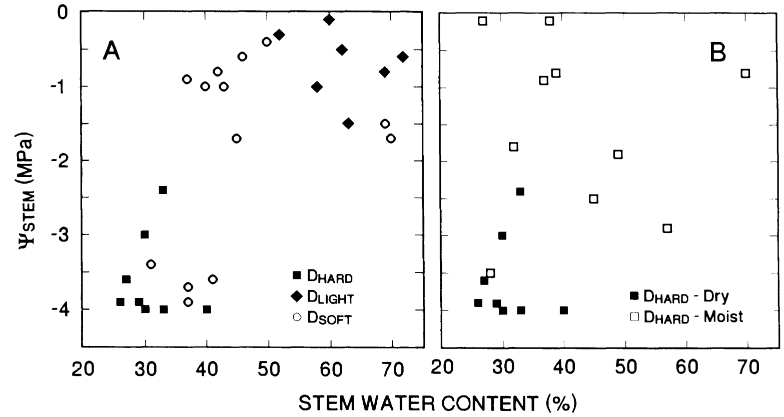

FIG. 3. (A) Relationship between minimum $\psi_{\rm stem}$ and stem water content (SWC) for three deciduous functional tree types growing at dry sites (see Table 2; Fig. 1). (B) Relationship of $\psi_{\rm stem}$ and SWC among $D_{\rm hard}$ trees growing at the dry HILL forest center or at wet sites near an irrigation canal (see Fig. 1).

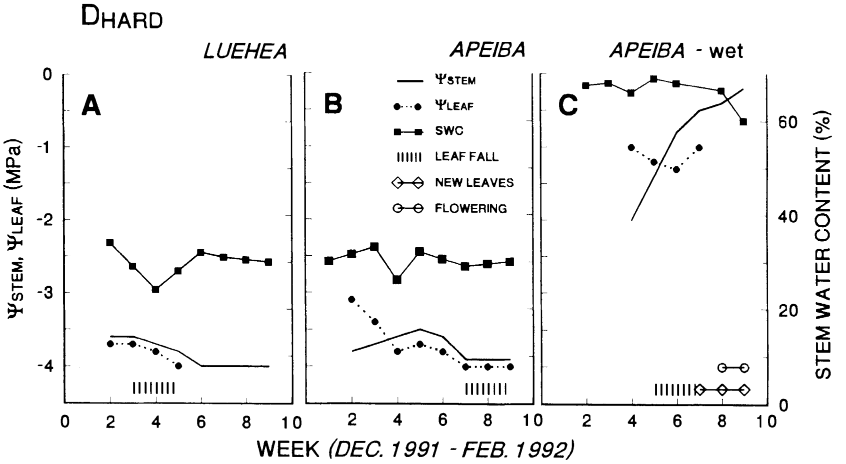

FIG. 4. Changes over time in tree water status (ψ_{leaf}, ψ_{stem}, stem water content [SWC]) and phenology (leaf fall, flushing, flowering) in individual trees of deciduous hardwood species (D_{hard}) at dry (A, B) and wet sites (C) in the tropical forest of Guanacaste, Costa Rica (Tables 1 and 2; observed between 7 December 1991 and 20 February 1992).

Most trees growing within 20 m from the irrigation ditch and along the pasture at the northwest corner of HILL retained their leaves 3–4 wk longer. By mid-February the bare forest in the center of HILL was surrounded by a "green belt" outside the boundaries shown in Fig. 1, a visual manifestation of differences in soil water availability between trees in the center and along the margins of HILL. Leaf shedding progressed gradually down the hillside towards the irrigation canal. Among trees growing within 3–5 m of the ditch, leaf shedding and the emergence of new shoots, leaves, and flowers proceeded irregularly throughout the dry season.

The only rainfall during the dry season 1990/1991 (30 mm on 3 March 1991) caused mass flowering of *Tabebuia ochracea* (known to depend on full rehydration of twigs; Borchert 1994*b*) in a strongly site-specific manner: not a single tree flowered in the dry center of HILL, but all bare trees along and outside the boundaries of the HILL center were in full flower within 6 d after the rainfall (Fig. 1). Inversely, the first heavy rains in May (>100 mm) caused heavy flowering of trees in the HILL center, but only sparse flowering among those along the margins. Bignoniaceous woody vines behaved similarly.

Phenology varied widely among different species in the HOTEL area. Throughout the dry season, some trees were shedding leaves, flowering, or flushing, and old or new leaves were present on most trees. In the riparian forest along the Corobici River, most trees exchanged leaves early in the dry season, only few trees were bare at any time, and the forest remained evergreen.

Analysis of phenological variation

The comparative and experimental analysis of inter- and intraspecific variability in tree phenology observed within the dry forest ecosystem was guided by the hypothesis that differences in water availability and hence tree water status are likely to cause the observed variation in phenology (Reich and Borchert 1982, 1984, Borchert 1991, 1992). Expansion of flower or vegetative buds during climatic drought, the phenological events to be explained, depend on the water status of stem tissues in the supporting branches (Borchert 1994*c*). Measurement of the water status of stem tissues (see *Field sites, materials, and methods*) is thus central to the analysis of phenology during seasonal drought.

Physiologically relevant structural traits, seasonal development, and variation in tree water status during the dry season were compared for all experimental species (Table 2; Figs. 2–7). In most species, variables affecting tree water status were well correlated with each other (Fig. 2; Table 2G–K; Table 3) and with the observed phenological patterns (Table 2D–E). Tree species clustered into a number of functional types sharing most of these traits (Table 2, Fig. 8). In naming these functional types two crucial determinants of tree water balance were considered: abbreviations for Deciduous and EVergreen were combined with subscripts characterizing species as hard-, soft-, or lightwood trees (Tables 1 and 2) and hence as trees with low to high

TABLE 3. Correlations among five variables affecting tree water status. Correlations were calculated from the values given in columns G–K of Table 2, treating <a and >b as a and b, respectively.

	Sat. water content	Minimum ψ_{leaf}	Minimum ψ_{stem}	Stem water content
Wood density	−0.87	−0.71	−0.79	−0.81
Sat. water content		0.61	0.64	0.7
Minimum ψ_{leaf}			0.79	0.76
Minimum ψ_{stem}				0.73

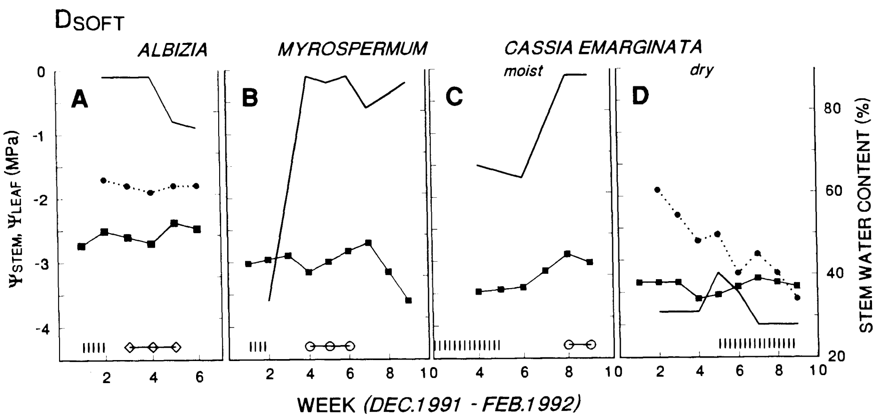

FIG. 5. Changes over time in tree water status (ψ_{leaf}, ψ_{stem}, stem water content [SWC]) and phenology (leaf fall, flushing, flowering) in individual trees of deciduous softwood species (D_{soft}) at dry (A, B, D) and moist sites (C) in the tropical dry forest of Guanacaste, Costa Rica (Tables 1 and 2; observed between 7 December 1991 and 20 February 1992). Symbols as in Fig. 4.

water storage capacity (see Fig. 2 for correlation between wood density and water content). Trees of different functional types were found to occur preferentially at certain sites along the gradient from very low to high soil moisture availability (Fig. 1) and will be described in order of decreasing drought tolerance. Microsite differences resulted in large variation in tree water status and hence phenology (Figs. 4B, C and 5B, C). Measurements given in Figs. 4–7 are therefore from individual, representative trees. Data for additional species have been published elsewhere (see Table 1F).

D_{hard}: *deciduous hardwood trees that desiccate strongly and remain bare to the end of the dry season (Table 2,* D_{hard}*; Figs. 2–4).*—Deciduous hardwood trees dominate the dry center of the HILL forest, the TUFF site, and other hilltops at La Pacifica (Fig. 1). Trees are 10–15 m tall and have high-density wood ($D = >0.8$ g/cm^3) and often a thin, hard bark. Mesomorphic leaves with moderate drought tolerance (*Tabebuia*: Olivares and Medina 1992) were shed ≈4–6 wk after the last rain, and tree growth remained arrested throughout the dry season. At the time of leaf shedding, trees had become highly desiccated ($\psi_{\mathrm{leaf}} < -3.2$ MPa; $\psi_{\mathrm{stem}} < -4$ MPa; SWC <35%; Fig. 4A, B; Table 2J, K). The absolute water depletion of such hardwood trees during the dry season is small (8–20% DM) but represents a large fraction of their very low saturation water content (Table 2H; Schulze et al. 1988). Trunks of species with thin bark shrunk very little during the dry season, i.e., strong desiccation was not correlated with significant stem shrinkage (see Figs. 1 and 2 in Reich and Borchert 1984). *Tabebuia ochracea,* with unusually thick bark and pronounced stem shrinkage during drought, is an exception (Reich and Borchert 1982). After heavy rainfall or irrigation ψ_{stem} increases to > -0.2 MPa within 48 h, and SWC saturates within 7–10 d (Borchert 1994*b*). Rehydration causes mass flowering in *Tabebuia ochracea* and rapid flushing in all species.

D_{hard} trees growing at moist sites experienced only moderate water stress; they maintained a higher SWC and shed leaves later than trees at dry sites and often flowered and flushed during the dry season (Figs. 3B and 4C).

D_{light}: *Deciduous trees with low-density wood and high stem water storage (Table 2,* D_{light}*; Figs. 2, 3A, 6A, B).*—Most species are pioneers with high light requirements occupying very dry, open, often rocky sites (Fig. 1) and sharing many traits with stem-succulent desert trees (Nilsen et al. 1990). Trees have shallow roots (*Bursera*: Olivares and Medina 1992) and relatively thick trunks with smooth, thick bark (20–35 mm) and low-density wood ($D = <0.5$ g/cm^3) containing extensive nonlignified, parenchymatous tissues (Roth 1981). Correspondingly, trunk water content is exceptionally high (Table 2G, H; Fig. 2 insert; Schulze at al. 1988). Mesomorphic leaves have little drought tolerance (*Bursera*: Olivares and Medina 1992) and are shed rapidly during the early dry season, even in trees at wet sites. Most species flower after leaf shedding for prolonged periods (Table 2F). Growth of vegetative buds often begins during the late dry season before the first rains, but full stem expansion and leaf growth occur only after resaturation of the soil by the first heavy rains (Reich and Borchert 1984, Bullock and Solis-Magallanes 1991, Bullock 1992).

During early drought bare D_{light} trees had the highest observed SWC and ψ_{stem} near saturation (Table 2K, Figs. 3A, 6A; Borchert 1994*c*). Use of stored water during dry-season flowering and possible water loss by evaporation is indicated by a moderate decline in ψ_{stem}, by stem shrinkage during and after flowering (Fig.6A; Reich and Borchert 1984), and by a relatively high water depletion during the dry season (Schulze at al. 1988). In contrast to all other species, *Enterolobium* exchanged leaves during drought while maintaining ψ_{stem} near saturation (Fig. 6B).

D_{soft}: *Deciduous softwood trees that rehydrate and flower after leaf shedding during drought (Table 2,* D_{soft}*;*

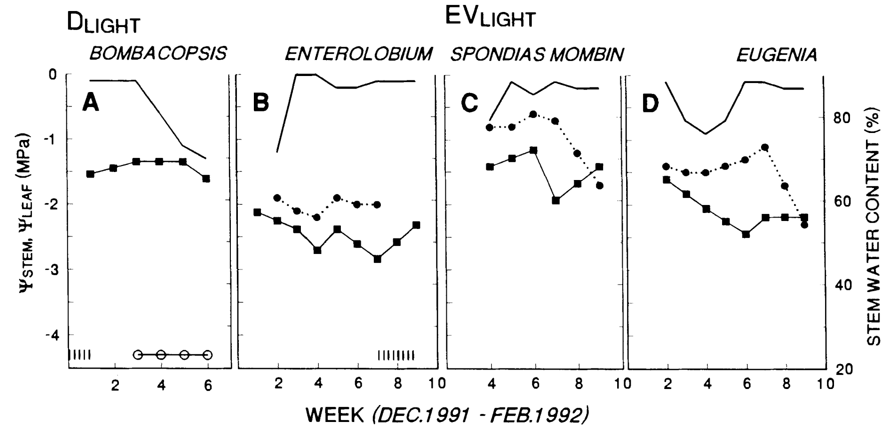

FIG. 6. Changes in tree water status (ψ_{leaf}, ψ_{stem}, stem water content) and phenology (leaf fall, flushing, flowering) in individual trees of deciduous lightwood species at dry sites (D_{light}; A, B) and evergreen lightwood species at moist sites (EV_{light}; C, D) in the tropical dry forest of Guanacaste, Costa Rica. Symbols as in Fig. 4.

Figs. 2, 3A, 5).—Deciduous softwood trees (not to be confused with temperate, coniferous "softwoods") are common at forest margins (Fig. 1) and in open woodlands, but rare within dense upland forests. Trees have wood of medium density (D = 0.5–0.8 g/cm^3) and mesic to leathery leaves, that are shed during the early to mid-dry season.

In marked contrast to D_{hard} trees, values of ψ_{stem} below −3 MPa and SWC below 40% were observed only rarely (Table 2J, K) and leaf shedding resulted in rehydration, as indicated by a rise in ψ_{stem}, followed by the emergence of flowers from buds formed during the preceding growing season (Table 2F). Bare D_{soft} trees covered with white (*Myrospermum*), yellow (*Caesalpinia, Cassia emarginata*), pink (*Gliricidia*), or orange flowers (*Pterocarpus*) stand out conspicuously in bare woodlands during the dry season. In contrast to rain-induced mass flowering in *Tabebuia ochracea,* flowering in D_{soft} trees does not depend on rainfall, and the timing of leaf fall and subsequent flowering varied widely with species and site moisture availability (Fig. 5). In *Albizia,* mesic leaves were exchanged and flowers appeared on new shoots during the 1st mo of drought; leaves persisted throughout the dry season and were replaced again after the first rains (Table 2D–F; Fig. 5A). In *Cassia emarginata* growing at dry sites, gradual shedding of the coriaceous leaves was followed by slow rehydration and sparse flowering; at moist sites rehydration after leaf shedding was fast and flowering abundant (Fig. 5C, D). In contrast to all other species, *Cordia* retained strongly desiccated leaves ($\psi_{\mathrm{leaf}} < -3$ MPa) long into the dry season and formed terminal inflorescences before leaf shedding, when ψ_{leaf} and ψ_{stem} were below −3 MPa (Table 2; Borchert 1994*c*).

EV_{soft}: Evergreen softwood trees that exchange coriaceous leaves and flower during the dry season (Table 2, EV_{soft}; Fig. 7).—Most species in this rather homogeneous group comprising many leguminous trees have wood of medium density (D = 0.6–0.8 g/cm^3) and large, long-lived, coriaceous, pinnate leaves. Trees are fac-

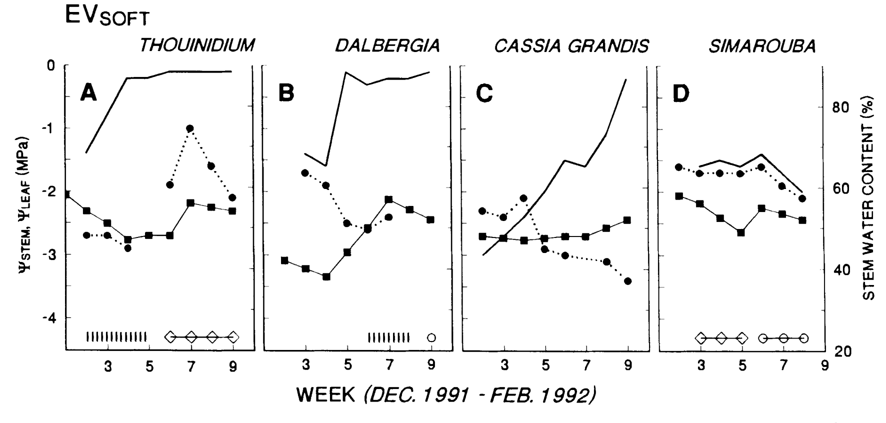

FIG. 7. Changes in tree water status (ψ_{leaf}, ψ_{stem}, stem water content) and phenology (leaf fall, flushing, flowering) in individual trees of evergreen softwood species (EV_{soft}) at dry (A, D) and moist sites (C, D) in the tropical dry forest of Guanacaste, Costa Rica. *Cassia grandis* exchanged leaves in March, shortly after the end of the observation period. Symbols as in Fig. 4.

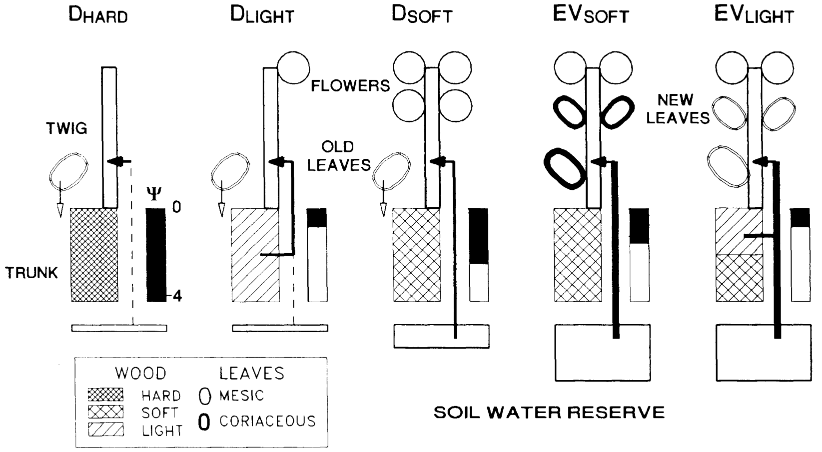

FIG. 8. Schematic showing how functional tree types (labels, top) differ in water relations and phenology during the dry season and are adapted to sites with different soil water availability in the tropical dry forest biome. Soil water reserves (bottom), trunk water storage [a function of wood structure (center left)], and leaf type (mesic or coriaceous) determine the degree of desiccation during the early dry season (gauges at center right showing ψ_{stem} in MPa) and the amount of water available for rehydration (arrows). Differences in the water status of the tree crown (TWIG) cause differences in phenology (top) such as shedding or retention of old leaves, flowering on leafless or leaf-bearing twigs, and expansion of new leaves during the dry season. For details see *Discussion: Seasonal variation in tree water status and phenology* and Table 2.

ultatively evergreen, i.e., at moist sites leaves are exchanged rapidly and new leaves emerge before old leaves have been shed completely, while at dry sites trees may stand bare for a few weeks (*Pithecellobium*: Sobrado 1991). Leaves are exchanged either very early (*Andira, Thouinidium*) or later during the dry season (Table 2D, E; Fig. 7A). Flowers may open rapidly on old wood after leaf shedding (*Cassia grandis, Dalbergia*), gradually on emerging new shoots (*Pithecellobium*), or at the end of a flush in a terminal inflorescence (*Hymenea, Simarouba, Thouinidium*; Borchert 1992). Coriaceous leaves of EV_{soft} species, like those of other evergreen tropical species (Sobrado 1986, 1991, Fanjul and Barradas 1987), are drought resistant; they maintain high assimilation rates, good stomatal control (C. Martin et al., *unpublished manuscript*) and relatively high ψ_{leaf} until shortly before shedding (Fig. 7). Emergence of new leaves was always preceded by an increase of ψ_{stem} to near saturation, but only rarely by an increase in SWC (Fig. 7A–C; Borchert 1994*c*). In marked contrast with D_{soft} species, EV_{soft} trees usually rehydrate while bearing old leaves, i.e., stem rehydration is not the result of a reduction in transpirational surface.

During the dry season, *Simarouba* stood out at the dry TUFF site as the only evergreen tree surrounded by bare D_{hard} trees. Old, thick, leathery leaves were shed slowly after flushing and flowering during the early dry season, when ψ_{stem} was as low as −2 MPa (Fig. 7D). *Thouinidium,* which exchanges leaves and then flowers during early drought, occurs occasionally in dry upland forests (Figs. 1, 7A).

EV_{light}: Evergreen, water-storing lightwood trees (Table 2; Fig. 6C, D).—In this group, bona fide lightwood species (*Gmelina, Ochroma, Sterculia*) were combined with others of intermediate characteristics between EV_{soft} and EV_{light} species in order to keep the number of functional types small. Other species occurring at wet or riparian sites, which were observed but not studied in detail, are likely to belong to this group (e.g., *Anacardium, Guarea, Sloanea, Stemmadenia, Thevetia*). These evergreen, water-storing trees maintain a positive water balance (high ψ_{stem}, ψ_{leaf}, SWC), flower and exchange leaves during the dry season. *Spondias mombin,* a D_{light} species, behaved like an EV_{light} tree at a moist site (Fig. 6C).

DISCUSSION

Seasonal variation in tree water status and phenology

Temporal correlations between ψ_{stem}, found to be a reliable measure of the water status of tree branches, and the time course of tree development during the dry season (Figs. 4–7) confirm the proposed role of water status as the principal determinant of tree phenology in tropical dry forests (Reich and Borchert 1984, Borchert 1991, 1992). With few exceptions requiring further analysis, buds remained arrested as long as ψ_{stem} was low (Fig. 4), and flowering or bud break were preceded by an increase of ψ_{stem} to saturation values (> -0.2 MPa; Figs. 4–7). The wide variation in phenology observed among trees of the dry forest biome exposed to the same regime of seasonal climatic drought should then be caused by variation among the components of the soil–plant–atmosphere continuum that determines tree water status (Fig. 8; Hinckley et al. 1991).

Whereas the upper soil layers dry out soon after the cessation of rains, the availability of subsoil moisture varies widely at different sites and determines the degree of desiccation observed in trees with low stem water storage. Low soil moisture availability is indicated by the deciduousness of almost all trees at upland sites (Fig. 8). Rate and degree of desiccation are higher in dense hill forests with high root competition than among widely spaced savanna trees (Table 2J, K; D_{hard} vs. D_{soft}). At moist lowland sites, where roots have access to the water table, trees dry out only moderately (Table 2J, K; EV_{soft}) and exchange leaves during the dry season. These site-dependent differences in soil water availability, not seasonal rainfall, are the principal environmental cause of variation in tree water status, phenology, and distribution of tree species (Table 2B–F; Figs. 1 and 8).

As fine roots in the dry top soil become nonfunctional, trees at moist sites must obtain their entire water supply from roots extending into deeper soil layers. At steep, washed-out banks along the Corobici River, many 2–4 cm thick, unbranched roots of riparian trees grow straight down for several metres towards the moist soil layer just above the water level, where they form a dense network of lateral roots. Such patterns of root distribution, as also described for the desert phreatophyte, *Prosopis* (Rundel and Nobel 1991), should be common among evergreen trees at lowland sites.

In keeping with the concept of drought-induced deciduousness, shedding of mesic leaves occurred earlier at dry than at moist sites and was preceded by a strong decline in ψ_{leaf} (Fig. 4) and photosynthetic capacity (C. Martin et al., *unpublished manuscript*). Drought stress is less likely to be the immediate cause of leaf exchange in evergreen species (Fig. 7C, D), whose coriaceous leaves maintain a less negative ψ_{leaf} (Table 2) and a high photosynthetic capacity until shortly before abscission (Sobrado 1991; C. Martin et al., *unpublished manuscript*).

The importance of stem water storage for tree water relations has been recognized for some time (Ewers and Cruiziat 1991, Hinckley et al. 1991, Holbrook and Sinclair 1992) and the water status of branch tissues is crucial for bud emergence during the dry season (Borchert 1993), but ecophysiological studies of drought tolerance in trees of the dry forest have been focused mainly on leaf characters (Sobrado 1986, 1991, Fanjul and Barradas 1987, Olivares and Medina 1992). The range in wood density (0.15–1.1 g/cm^3) and hence in stem water storage capacity among tropical trees is much greater than among temperate trees (0.4–0.8 g/cm^3). There are many tropical species with wood densities below 0.5 g/cm^3, in which high trunk water storage is indicated by a large water content and high SWC (Figs. 2 and 3; Table 2G, H, K; Barajas-Morales 1987, Schulze et al. 1988). Water storage capacity is highly correlated with the degree of leaf desiccation (minimum ψ_{leaf}; Tables 2H, I, K and 3) and with stem water status and phenology during the dry season (Tables 2 and 3; Fig. 8, D_{light}). In conjunction with leaf type, stem water storage thus appears to be a principal determinant of functional types among dry forest trees (Table 2). The role of water storage is strikingly illustrated by the "classic" differences between drought-tolerant D_{hard} species and drought-avoiding D_{light} species growing at the same dry upland sites (Table 2, Figs. 2–4, 6, 8; Ludlow 1989), but is less clear in softwood and water-storing lightwood species restricted to moist sites (Table 2, EV_{light}; Fig. 8).

After the cessation of rains, the water balance of most trees with a full crown of older leaves became negative (low ψ_{stem} during weeks 1–2 in Figs. 4, 5, 7). Reduction of water loss by leaf shedding did not enable rehydration in D_{hard} trees at dry sites (Fig. 4), but resulted in an increase in ψ_{stem} and subsequent flowering in D_{soft} trees at dry savanna sites (Figs. 5 and 8). Trees at moist sites were able to maintain a positive water balance in the presence of leaves: ψ_{stem} remained high in EV_{light} trees or increased after an earlier decline in EV_{soft} trees (Figs. 6C, D, 7C, 8). Increases in ψ_{stem} were only rarely followed by comparable changes in SWC, i.e., during drought water-storing tissues of tree trunks equilibrate very slowly with the parenchymatic tissues near the xylem (Borchert 1994*a*, *b*). High correlations between ψ_{stem} and SWC in strongly desiccated trees or water-saturated D_{light} trees (D_{hard} and D_{light} in Fig. 3A; Table 2J, K) indicate that equlibrium has been reached, while lack of equilibrium is indicated by poor correlations among D_{soft} trees (Fig. 3A).

Seasonal variation in tree water status thus results from complex interactions among a set of internal and environmental variables of which rainfall is only one (Borchert 1991: Fig. 10.5). Tree water status and phenology are strongly correlated with climatic drought only in hardwood trees at very dry sites, where neither soil water reserves nor stem water storage buffer the impact of seasonal drought (Table 2D, E; D_{hard}).

With few exceptions, rehydration causes flowering and flushing of bare trees in a highly opportunistic manner. This indicates that resting buds in most drought-stressed, bare trees are not dormant and the elimination of tree water deficits, not environmental cues, causes flowering or flushing. The timing of flowering by distinct, proximate changes in tree water status makes it unlikely that staggered flowering among trees in the dry forest ecosystem should have evolved as a result of competition for pollinators or seed dispersers (Janzen 1967, Borchert 1992, Fleming and Partridge 1984).

Functional types among dry forest trees

The prevalence of deciduous species at dry sites and of evergreen species at moist sites of the tropical dry forest biome has been long recognized (Sobrado 1986, Bullock and Solis-Magallanes 1990). Attempts to characterize differences among tropical dry forests by the degree of deciduousness and to explain them by variation in amount and seasonality of annual rainfall have been unsatisfactory (Hegner 1979, Murphy and Lugo 1986). In this study, the analysis of a relatively large set of well-correlated structural and functional traits, particularly those related to stem water storage, has revealed a set of distinct functional tree types (Table 2; Fig. 8). Even though the definition of these functional types and the assignment of several tree species are tentative, the characteristic distribution of functional tree types within the dry forest biome strongly suggests that they represent different adaptive strategies.

The secondary HILL forest (Fig. 1) has regenerated during the past 40 yr. The exclusive occurrence of D_{hard} and D_{light} species at the very dry Hill center, confinement of D_{soft} species, including the pioneers *Cordia* and *Guazuma,* to the moister forest margins, and the absence of evergreen functional types ($\mathrm{EV}_{\mathrm{soft}}$, $\mathrm{EV}_{\mathrm{light}}$) from the dry upland site indicate that tree species have sorted out during the past 40 yr according to site factors, mainly soil water availability. Given that few trees reach 15 m in height and the canopy is open and irregular, light availability is unlikely to have played a major role in the establishment of the present pattern of tree distribution.

Representation of the proposed functional tree types in the less disturbed Costa Rican lowland dry forests at Palo Verde and Santa Rosa National Parks appears to be similar to that at La Pacifica (Hartshorn 1983). In the very dry forests of Mexico and Venezuela deciduous hard- and lightwood trees are more common (Sobrado 1986, Bullock and Solis-Magallanes 1990), while evergreen species predominate in neotropical savannas and Asian moist-deciduous monsoon forests (Hegner 1979, Sarmiento et al. 1985).

ACKNOWLEDGMENTS

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 following persons, who contributed in various ways to the project: the managers of La Pacifica, P. Nett and Ing. F. Estrada, provided logistical support and permission to do field work; W. Hagnauer gave valuable logistical support and advice; J. Herrick, Ohio State University, shared his analysis of meteorological records for 1991; Dr. K. Glander, Duke University, and the Centro Ecologico La Pacifica provided keys to large sets of trees identified by Q. Jimenez, J. L. Poveda, and P. Sanchez of the Herbario Nacional de Costa Rica; D. Smith evaluated rock samples from field sites, and C. Martin, University of Kansas, shared his references on tropical ecology. Special thanks are due to the reviewers and subeditor of this paper for valuable suggestions for improvement.

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