Modification of vegetative phenology in a tropical semideciduous forest by abnormal drought and rain [1]

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ABSTRACT
The control of vegetative phenology in tropical trees is not well understood. In dry forest trees leaf abscission may be enhanced by advanced leaf age, increasing water stress or declining photoperiod. Normally it is impossible to dissect the effects of each of these variables, because most leaves are shed during the early dry season when daylength is near its minimum and leaves are relatively old. The 1997 El-Niño Southern Oscillation caused a 10-wk long, severe abnormal drought from June to August in the semideciduous forests of Guanacaste, Costa Rica. We monitored the effect of this drought on phenology and water status of trees with young leaves and compared modifications of phenology in trees of different functional types with the pattern observed during the regular dry season. Although deciduous trees at dry sites were severely water-stressed ($\Psi_{STEM} < -7MPa$) and their mesic leaves remained wilted for > 2 months, these and all other trees retained all leaves during the abnormal drought. Many trees exchanged leaves 3-4 months earlier than normal during the wet period after the abnormal drought and shed leaves again during the regular dry season. Irrigation and an exceptional 70-mm rainfall during the mid dry season 1998/99 caused bud break and flushing in all leafless trees except dormant stem succulents. The complex interactions between leaf age and water stress, the principal determinants of leaf abscission, were found to vary widely among trees of different functional types.

Keywords: Abnormal drought - El-Niño Southern Oscillation - leaf abscission - phenology - tropical trees

Tropical dry forests occupy tropical regions with a severe dry season lasting several months. In the semideciduous forests of Guanacaste, Costa Rica, less than 5% of annual precipitation is received during the 5-6 mo long dry season. Tree species of different functional types have evolved under these climatic conditions. They range from deciduous hardwood trees and water-storing stem- succulent trees, which dominate dry upland forests, to brevideciduous and leaf-exchanging evergreen trees confined to moist microsites with good soil water reserves (Borchert 1994a). Patterns of leaf abscission during the dry season range from rapid shedding of short-lived, mesic leaves in deciduous species to irregular leaf exchange of long-lived, coriaceous leaves in evergreen and brevideciduous species.

Water stress appears to be the main cause for leaf shedding, and leaves are retained longest in deep-rooted species remaining well hydrated throughout the dry season. There are no answers to more specific questions such as the following: Is leaf abscission induced, when leaf water potential (Ψ_L) declines below a threshold value? What are the threshold values in trees of different functional types? Are leaves in late-shedding species retained longer because they are less water-stressed or because they are more drought-tolerant? How does leaf age affect responses to drought?

Drought does not always cause leaf abscission, and leaves may abscise without being water-stressed. For example, leaves are usually not shed during the short dry season in July/August, but leaves of stem succulent trees abscise rapidly during the early dry season without being water-stressed (Borchert and Rivera 2001). Some species have two annual leaf exchanges, including one during the rainy season (e.g., *Albizia guachapele; Erythrina poeppigiana,* Borchert 1980). To explain such observations, increasing leaf age and changes in daylength have been proposed to affect leaf abscission (Reich and Borchert 1988, Addicott 1991, Holbrook et al. 1995).
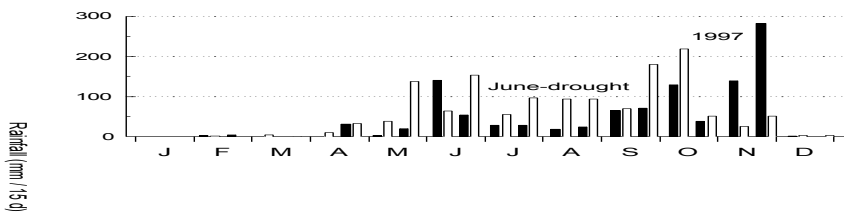

FIGURE 1. Rainfall at Hacienda La Pacifica, Guanacaste, Costa Rica, for 1997 (*filled bars*) and 1991-1996 (*empty bars*).

During the early dry season in Guanacaste, Costa Rica (Nov/Dec), the three variables potentially affecting leaf abscission change in parallel: soil and tree water deficits increase, daylength approaches its minimum at the winter solstice, and most leaves are relatively old. In 1997, the El-Niño Southern Oscillation (ENSO) caused a 10-wk long, severe, abnormal drought starting during the early rainy season in mid-June (June-drought; Fig. 1). The drought began soon after deciduous trees had leafed out in response to the first heavy rains and when day-length was near its maximum. Being alerted to the approaching ENSO event by the forecasts of the Experimental Climate Forecast Division, Scripps Institution of Oceanography, San Diego, we were ready to monitor phenology and water relations during the June-drought and the following regular dry season in trees of several functional types at sites with moderate and low soil water storage known from earlier field studies (Borchert 1994a). As a unique, large-scale natural experiment, the June-drought modified the normal pattern of vegetative phenology in many trees and thus permitted dissecting the effects of water stress, leaf age and photoperiod on leaf abscission. Later, abnormal flushing of leafless trees was induced by irrigation and an exceptional 70-mm rainfall in the middle of the 1998/99 dry season. In this study, we compare normal phenological patterns with the modifications of vegetative phenology caused by the ENSO-induced June-drought and by abnormal rain or irrigation during the dry season.

MATERIALS AND METHODS

EXPERIMENTAL TREE SPECIES. -- Most of the species analyzed were grouped earlier into functional types based on their phenology, seasonal variation in tree water status and other variables (Borchert 1994a). Phenological observations and measurements of tree water status were made in 39 trees of 27 species representing all functional types. Functional types and observed species are listed in Table 1. Species names follow Janzen and Liesner (1980), where authorities and synonyms may be found. In the text, species are referred to by genus name only, except when several congeneric species are discussed.

FIELD SITES AND CLIMATE.-- Field observations were made at Hacienda La Pacifica, Cañas, Guanacaste, Costa Rica, the site of earlier studies of phenology and ecophysiology of neotropical dry forest trees (Frankie et al. 1974, Reich and Borchert 1984, Borchert 1994a, Rivera and Borchert 2001). Throughout the observation period, daily rainfall was recorded at Finca Las Pumas, ~3 km from our field sites. Monthly mean temperature is 28 ± 1° C throughout the year. Means of rainfall/15 d for 1991-1996 are given in Fig. 1. Normally, precipitation exceeds evaporation during most of the wet season from late May to Nov. After the cessation of rainfall in Nov/Dec, high evapotranspiration caused by declining relative humidity and strong winds results in rapid drying of the upper soil layers (Gerhardt 1996).

Trees at sites with moderate or low soil water storage are most affected by abnormal drought. Phenological observations and measurements of tree water status were therefore done at upland sites more than 1 km from the nearest river and well above the ground water table. The Tuff site, located ~150 m N of the Pan-American Highway (10º 27' 50" N, 85º 9' 39" W), consists of a dome-shaped outcropping of volcanic tuff (rhyolite) covered by a shallow layer of soil and is one of the driest sites in the research area. It is dominated by drought-deciduous species, but has also some brevideciduous and leaf-exchanging trees

TABLE 1. Tree species of four functional types, whose phenology and water relations were analyzed between 1997 and 1999 in the semideciduous forest of Guanacaste, Costa Rica. Some species occurred at very dry sites with shallow soil (D), others were restricted to upland sites with deep soil and moderate soil water storage (M). Figure numbers refer to analyses of tree water relations.

Species	Family	Site	Figure
A. DECIDUOUS SPECIES			

Leaves expand during the early rainy season and are shed during the early dry season.

Species	Family	Site	Figure
Chomelia spinosa	Rubiaceae	D	1B
Cordia alliodora	Boraginaceae	M	
Luehea candida	Tiliaceae	D	2A, 4C
Randia sp.	Rubiaceae	D	4B
Tabebuia ochracea	Bignoniaceae	D	4C
Tabebuia rosea	Bignoniaceae	M	

B. LEAF EXCHANGING SPECIES

Young leaves emerge immediately after leaf shedding during the dry season

Species	Family	Site	Figure
Albizia guachapele	Caesalpinaceae	M	
Astronium graveolens	Anacardiaceae	M	5D
Hymenaea courbaril	Caesalpinaceae	M	2B, 5C
Licania arborea	Chrysobalanaceae	M	5D
Samanea saman	Mimosaceae	M	
Sideroxylon tempisque	Sapotaceae	D	
Simarouba glauca	Simaroubaceae	D	5E
Swietenia macrophylla	Meliaceae	M	
Thouinidium pentandrum	Sapindaceae	M	5B

C. BREVIDECIDUOUS, SPRING-FLUSHING SPECIES

After a brief leafless period, bud break is induced in Mar/April by increasing photoperiod

Species	Family	Site	Figure
Cassia emarginata	Caesalpinaceae	M	6B
Chlorophora tinctoria	Moraceae	M	
Dalbergia retusa	Fabaceae	M	6C
Diospyros nicaraguensis	Ebenaceae	D	6D
Guazuma ulmifolia	Sterculiaceae	D	2C, 6D
Lonchocarpus minimiflorum	Fabaceae	D	6B
Myrospermum frutescens	Fabaceae	M	
Piscidia carthaginensis	Fabaceae	D	6C

D. DECIDUOUS STEM SUCCULENT SPECIES

Leaves abscise in Dec; bud break is induced in April by increasing photoperiod

Species	Family	Site	Figure
Bombacopsis quinatum	Bombacaceae	M	7B
Bursera simaruba	Burseraceae	D	7B
Cochlospermum vitifolium	Cochlospermaceae	D	
Plumeria rubra	Apocynaceae	D	
Spondias purpurea	Anacardiaceae	M	

(Table 1, D in *Site* column). At the margins of the outcropping soil depth increases to 1 - 1.5 m and species composition changes rapidly. Most species observed at the margins of Tuff and two similar sites 1-2 km N (Table 1, M in *Site* column; Corral: 10º 28' 22" N, 85º 9' 20" W**;** Tenorito: 10º 28' 49"N, 85º 9' 14" W) are brevideciduous or leaf-exchanging, i.e., they form new leaves during the dry season. The La Rana site (10º 27' 28" N, 85º 8' 12" W), used only for an irrigation experiment (see below), was described earlier (Borchert 1994a).

PHENOLOGY. -- With some interruptions of a few weeks, leaf phenology was recorded for the 39 experimental trees and > 50 additional trees every 10-14 d from late June 1997 to mid-Apr 1998 and from Oct 1998 to June 1999 as shown in Fig. 2. Quantification of leaf phenology using scores from 1 to 3 provides an adequate description of the temporal pattern of leaf phenology that characterizes each functional type. Because of the complexity of the developmental patterns, the large variation inherent in phenology scores and the low observation frequency relative to the rate of the observed developmental changes (Fig. 2), statistical treatment of the developmental patterns is not justified

To facilitate comparison between different patterns of seasonal vegetative development, The following rules were used to construct schematic curves describing leaf phenology as percent leaf cover from phenology scores. The period from the beginning to the end of flushing, as defined in Fig. 2, is described by a sigmoid increase in leaf cover from 0 to 100 %. In species with regular recurrent flushing during Sep/Oct leaf cover was increased to 80 and 100% during the first and second flush, respectively (Fig. 2C),. The period from the beginning leaf senescence to deciduousness is shown as a sigmoid decline in leaf cover. For some species, rapid, abnormal leaf exchange during Sep 1997 was not observed but deduced from the presence of leaf litter and new foliage in mid-October (Fig. 2B). To show a complete cycle of vegetative phenology for 1997, data from later years were used to draw changes in leaf cover between April and June 1997.

Patterns of seasonal development were similar for all trees of each functional type. Flushing induced by rainfall (Fig. 2A, June) or increasing daylength (Fig. 2C, Mar/Apr) was highly synchronous among all deciduous or spring-flushing trees, respectively, but he timing of leaf exchange varied by a few weeks, because the rate of leaf abscission varies among conspecific trees with soil water availability (Fig. 2B, Jan/Feb). For each functional type, vegetative phenology will be therefore represented by leaf phenology curves of one or two representative trees.

TREE WATER STATUS. -- During drought periods water potential of leaves (Ψ_L) and leafless terminal twigs (Ψ_S) was measured with a pressure chamber (Model 1000, PMS Instruments, Corvallis, USA; Borchert 1994a,b) in samples collected at dawn (*predawn*) and in the early afternoon (*midday*). For species with more than one observed trees, seasonal variation in water status and leaf phenology are given for trees at the driest sites, which are most responsive to seasonal drought. Only predawn Ψ_S (pΨ_S) and mid-day Ψ_L (mΨ_L) were used in the following analyses for the reasons given below.

For measurement of pΨ_S, leaves or leaflets were removed from terminal twigs or petioles, respectively, immediately before triplicate samples were cut and placed into sealed plastic bags stored in a moist container until measurement at most 1-2 h later. Variation in Ψ_S among samples rarely exceeded 0.2 MPa and means of 2 or 3 samples are given in the graphs. If variation exceeded 0.3 MPa, measurements were repeated the next day. The Ψ of stem tissues sampled in this way is in equilibrium with Ψ_{SOIL} and constitutes a reliable indicator of soil water

FIGURE 2. Representative phenological records for individual trees of three functional types from June 1997 to April 1998. Left - Observed stages of leaf phenology: Y - young, light-green; M - mature, dark-green; S - senescent, brown or yellow; A - abscised leaves. Center - Phenology scores: 1 - <30%; 2 - 30-80%; 3 - >80% of leaves. Filled boxes: start and end of flushing; empty boxes: start and end of leaf senescence and abscission.   Abnormal leaf shedding and flushing due to the 1997 June-drought are indicated by bold phenology scores.
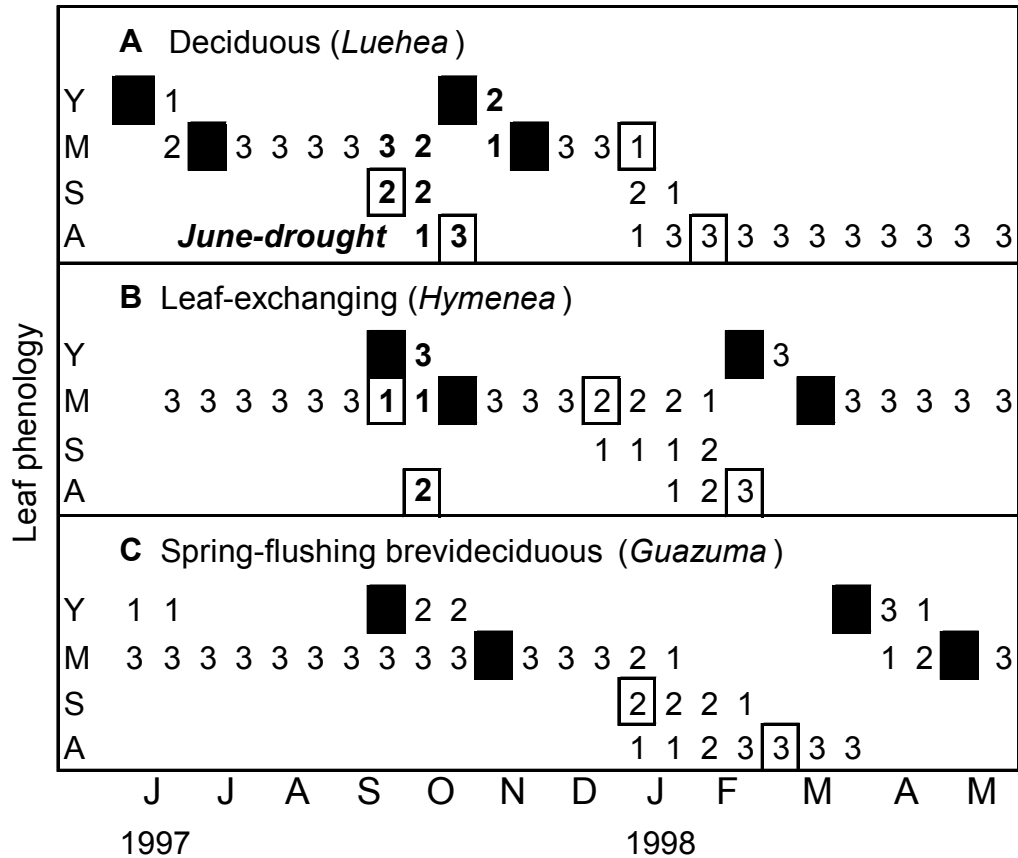
available to the tree (PAW - plant available water; Hinckley et al. 1991, Borchert 1994a,b). At our experimental sites, where excavation revealed many roots penetrating deep into fissures of the underlying volcanic tuff, use of $p\Psi_S$ as a gauge for PAW is the only suitable method.

Mid-day Ψ_L , the minimum Ψ_L attained during the day, was used as a measure of leaf water stress during drought. The difference between $p\Psi_S$ and $m\Psi_L$ represents the maximum soil-leaf Ψ -gradient established during the day by transpirational water loss. Seasonal variation of this gradient is a valuable indicator of tree responses to seasonal drought and crucial for comparing the responses of different functional types to June vs. normal drought. For example, a decline in predawn Ψ_L and $m\Psi_L$ in the presence of high PAW (high $p\Psi_S$) indicates loss of stomatal control in old leaves (Reich and Borchert 1988). Predawn Ψ_L , frequently used in field studies, is therefore not a suitable indicator of PAW (Holbrook et al. 1995).

Seasonal variation in tree water status varies strongly with PAW. It is therefore characteristic for each tree and cannot be averaged for all trees of a functional group. As a measure of water stress during the June-drought and during the regular dry season, means and standard deviations for the minima of Ψ_S and Ψ_L in all observed trees of the different functional groups are given in Fig. 3.

IRRIGATION. -- From late Feb to May 1998 a 10x15 m area with very shallow topsoil at the Tuff site was irrigated every 2 wk with 20-30 L / m^2 (20-30 mm) water pumped from a nearby irrigation canal. Control trees were separated from irrigated trees by two parallel, 50 cm-deep trenches dug into the underlying tuff with a backhoe to severe all roots between the two adjacent lots and prevent rehydration and bud break of the control trees. Simultaneously, a similar area with > 1 m topsoil was irrigated at the Bosque La Rana site.

RESULTS

The 1997 El-niño and 1998 La-niña events caused significant deviations from the normal climatic pattern during three different periods. Rainfall was well below the estimated evaporation of >150 mm/mo from mid-June to August 1997 (June-drought; Fig. 1). For all functional types, minima of pΨ_S measured in Jul/Aug were similar to those in Dec/Feb   (Fig. 3), indicating that during the June-drought water stress was similar to that of the following regular dry season. Heavy rains from Sep to Nov 1997 resaturated soils before the regular dry season, as indicated by pΨ_S >-1MP from Sep to Dec (Figs. 4-6). The La-niña event delayed the onset of the 1998/99 dry season (30 mm rain on Dec. 20, 1998). With lower than normal temperature and wind speeds, the deciduous La Rana forest became leafless 2-3 mo later than in 1991 (Borchert 1994a). For the first time in 45 years, 72 mm rain fell in the middle of the dry season, on Feb. 15/16, 1999 (W. Hagnauer, pers. obs.). These modifications of climate constitute large-scale, natural experiments, which changed environmental inputs for all trees at our field sites.
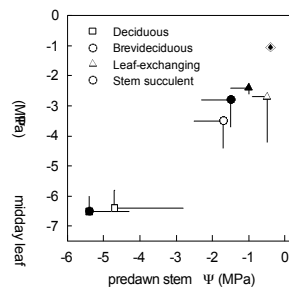

FIGURE 3.   Water relations in trees of different functional groups during the 1997 June-drought (*filled symbols)* and the normal dry season 1997/*98 (empty symbols*). Means and standard deviations were calculated for the lowest observed values of $_{STEM}$ and Ψ_{LEAF} for deciduous (n=9; 5 species), brevideciduous (n =12; 10 species), leaf-exchanging (n=4; 4 species) and stem succulent trees (n=2; 1 species) growing at relatively dry upland sites.

Minima of pΨ_S observed during the two dry periods of 1997/98 (Fig. 3) and the phenological responses to abnormal drought and rain varied widely between trees of different functional types, but were similar among trees of the same functional type. Earlier definitions of functional types (Borchert 1994a,b) were modified based on our improved understanding of the interactions between environmental and endogenous controls, which resulted from this and other

recent studies (Borchert and Rivera 2001; G. Rivera at al., pers. obs.). For each functional type, a brief description of the normal vegetative phenology will be followed by the observed responses to abnormal climatic inputs during 1997-99.

DECIDUOUS HARDWOOD SPECIES -- *Mesic leaves expand rapidly after the first rains of the rainy season and leaves are shed during the early dry season* (Figs.2A, 4A; Table 1A). During the 1997 June-drought, leaves formed after the first rains at the very dry Tuff site were severely wilted by early July, and terminal flower buds of *Luehea* abscised before expanding. Both $m\Psi_L$ and $p\Psi_S$ declined to extremely low values in trees with wilted leaves, indicating that the shallow top soil containing the trees' roots had dried out completely (Fig. 4B,C, Jul/Aug). The sensitivity of $p\Psi_S$ to variations in PAW is illustrated by the response to a single 15-mm rain shower on Aug.14, 1997, which caused a sharp temporary rise in $p\Psi_S$ of strongly desiccated, shallow-rooted species (Fig. 4C, Aug) and a smaller increase in many deep-rooted trees (Figs.5 B, C; 6B).

Severely wilted leaves did not begin to abscise before mid-August. Leaves rehydrated after the first major rainfalls were shed and immediately replaced by a new set of leaves in Sep/Oct (Figs. 2A; 4A, Sep *circles*). These leaves abscised during the early dry season, when $m\Psi_L$ declined rapidly (Figs. 2A; 4A, Dec/Jan 1998). Precocious, drought-induced shedding of early leaves thus resulted in an abnormal leaf exchange during Sep.

Leaves of deciduous trees are normally shed in Dec/Jan, when 7-8 mo old (Table 2A). In 1997, leaves formed in June and Oct were shed in Sep and Jan, respectively, when only 4 mo old (Table 2 B,C). Exposure of relatively young leaves to severe drought thus strongly reduced the life span of both sets of leaves as compared to the normal life span. To test whether lack of exposure to severe water stress might increase leaf life span, flushing of leafless trees was induced in early March 1998 by irrigating part of the Tuff site. With biweekly irrigation all trees formed a full crown of leaves and maintained a high $m\Psi_L$ and $p\Psi_S$ for the remainder of the dry season (Fig. 4, Mar 98, *squares*). These leaves were 3 mo older than those formed by the control trees in June 1998 (Fig. 4A, Mar-June '98; Table 2D,E). Due to late shedding during the 1998/99 dry season (see above), leaves of irrigated trees attained a maximum age of 11-12 mo, 3 mo more than the controls (Table 2 D, E). Similar results were obtained in a parallel irrigation experiment at the La Rana upland forest site. Deciduous trees growing at moist sites often flush during the dry season soon after leaf abscission, 2-4 mo earlier than conspecific trees at dry sites, but shed their leaves together with trees at dry sites during the early dry season.

Rainfall in Feb 1999 caused rapid rehydration in all trees (compare Borchert 1994c), which was followed by a rapid decline in $p\Psi_S$ to very low values as the top soil dried out again (Fig. 4B,C Mar, *triangles*). Thus, $p\Psi_S$ remained in the range permitting plant growth (>-1 MPa) for at most 2-3 wk. During this period new leaves emerged throughout the crown of leafless trees, but in trees retaining old foliage bud break was confined to leafless twigs. A full set of leaves was formed in species with buds containing preformed leaves (*T. ochracea)*, but

FIGURE 4. Modification of the phenology of deciduous hardwood species at very dry microsites by the 1997 June-drought, irrigation and abnormal rain. A – Seasonal variation in rainfall (*bars*) and leaf phenology (*simple line*) in 1997/1998. *Circles*: abnormal leaf exchange induced by the June-drought; *squares*: flushing during irrigation in 1998; *triangles*: flushing induced by rain in Feb 1999. B, C – Seasonal variation in tree water status during seasonal drought (*circles*) and after irrigation (*squares*) and abnormal rain (*triangles*). B - *Chomelia spinosa, [Randia sp.];* C - *Luehea candida,[Tabebuia ochracea].* Phenology and seasonal variation in Ψ for the species in brackets were very similar to those shown.
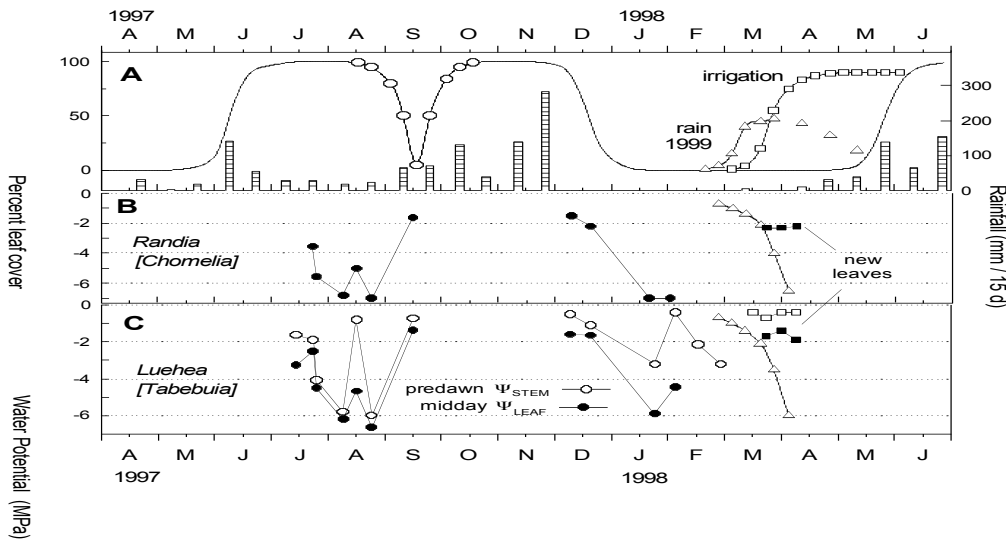

TABLE 2. Modification of leaf phenology in deciduous hardwood species (*Luehea candida, Tabebuia ochracea*) by drought and irrigation.

	Observation period.	Flushing	Shedding	Max. leaf age
A	Normal year	May/June	Dec/Jan	7- 8 mo
B	During 1997 June drought	June '97	Sep/Oct '97	4 mo
C	After 1997 leaf exchange	Oct '97	Dec '97/Jan '98	4 mo
D	1998 controls	May/June'98	Jan/Feb '99	8-9 mo
E	1998 after irrigation	Mar '98	Jan/Feb '99	11-12 mo

only a few leaves expanded in other species (*Chomelia*, *Luehea*). As observed earlier after a single irrigation during the dry season (Borchert 1994c), all leaves wilted before being fully expanded, many abscised before the end of the dry season (Fig. 4A Apr/May, *triangles*), and trees flushed again during the early wet season. For wide-spaced seedlings *of T. ochracea* growing in open areas without trees, the top soil volume rehydrated by the Feb. 15 rain was large relative to the seedlings' water consumption. Seven wk after the rain pΨ_S therefore remained as high as -1.5 MPa, shoot growth lasted much longer than in large trees, and new leaves did not wilt.
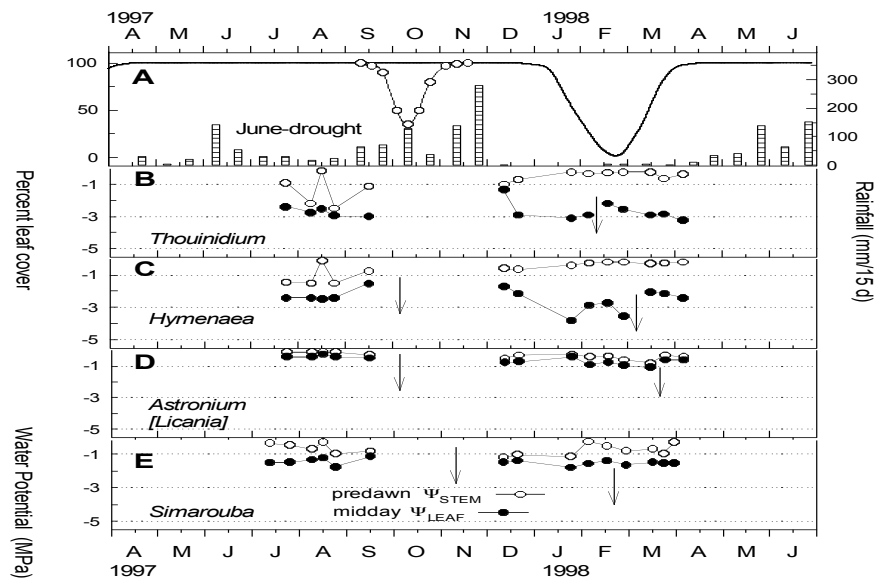

FIGURE 5. Modification of the phenology of leaf exchanging and evergreen species by the 1997 June-drought. A – Rainfall (bars) and leaf phenology in 1997/98 without (*simple line*; species in B) and with abnormal leaf exchange induced by the June-drought (*circles*; species in C and D). B - E   - Seasonal variation in tree water relations. Arrows indicate leaf exchange. B - *Thouinidium pentandrum*; C - *Hymenaea courbaril*; D - *Astronium graveolens, [Licania arborea]*;   E - Evergreen species *Simarouba glauca*.

LEAF EXCHANGING, EVERGREEN SPECIES -- *Young leaves emerge during or immediately after leaf shedding during the dry season* (Figs. 2B; 5A, Jan-Mar; Table 1B). *Some species flush again during the wet season* (recurrent flushing). In Oct 1997 many evergreen trees exchanged part or all of their leaves precociously after maintaining a relatively high Ψ during the June drought (Figs. 2B; 5, Sep-Oct, *arrows*) and recurrent flushes were delayed until Sep/Oct (e.g., *Samanea saman*). Both old and new leaves were exchanged for new leaves during the dry season (Figs. 2B; 5, Jan-Mar *arrows*). Whereas $p\Psi_S$ generally remained high throughout the dry season, $m\Psi_L$ declined in many trees before leaf shedding (Fig. 5B,C, Dec/Jan). At very dry sites with thin topsoil *Simarouba* often stands out during the dry season as one of the few species retaining thick and leathery leaves when most other trees are deciduous. Throughout the year, trees remained well hydrated and, at irregular intervals, flushed new leaves before old leaves were shed, i.e., the species is truly evergreen (Fig. 5 E). *Albizia* regularly exchanges its mesic leaves twice a year, once during the early wet season and once during the early dry season. During leaf exchange all leaves in a tree's crown abscise within less than a week and new leaves emerge immediately thereafter. The 1997 June-drought did not notably affect this pattern.

BREVIDECIDUOUS, SPRING-FLUSHING SPECIES. -- *Leaves are shed gradually during the mid dry season. After a brief leafless period, vegetative bud break is induced in Mar/Apr by increasing day-length* (spring-flushing; Figs. 2C; 6A; Table 1C; Borchert 2000; G. Rivera et al., pers.obs.). *Some species (e.g., Diospyros, Guazuma) regularly form recurrent flushes during periods of high precipitation in Sep/Oct* (Figs. 2C; 6A). In most brevideciduous species $p\Psi_S$ declined only moderately during the 1997 June-drought (Fig. 6B,C) and leaf phenology was not affected except for the shedding of some leaves in Sep. During the mid dry season $m\Psi_L$ of 10-11 mo old leaves often declined to values distinctly lower than those measured during the June-drought (Figs. 3, errors for minima of $m\Psi_L$; 6B,C, Feb/Mar) and all leaves abscised (Fig. 6A, Feb-Mar). During or after leaf shedding $p\Psi_S$ increased to high values (Borchert 1994a,b) and after a short leafless period trees flushed synchronously in late Mar/Apr, weeks before the first heavy rains (Figs. 2C; 6A, Apr; Borchert 2000; G. Rivera et al., pers. obs.). Rainfall in Feb 1999 induced rapid flushing in leafless trees, but not in trees retaining old foliage. In contrast to deciduous species, $p\Psi_S$ declined slowly during flushing and most trees formed a full crown of leaves (Fig. 6 A,D, Mar-Apr, *triangles*).

DECIDUOUS STEM-SUCCULENT SPECIES.-- *Leaves abscise rapidly during the early dry season. During the late dry season formation of small shoots is induced by increasing daylength, but leaves expand only after the first rains* (Fig. 7A; Table 1D; Borchert and Rivera 2001). Water status and vegetative phenology of *Bombacopsis* (Fig. 7B) and most other stem-succulent species (e.g., *Bursera, Plumeria, Spondias*) were not notably affected by the June-drought, and the abnormal rain did not induce flushing in leafless trees.
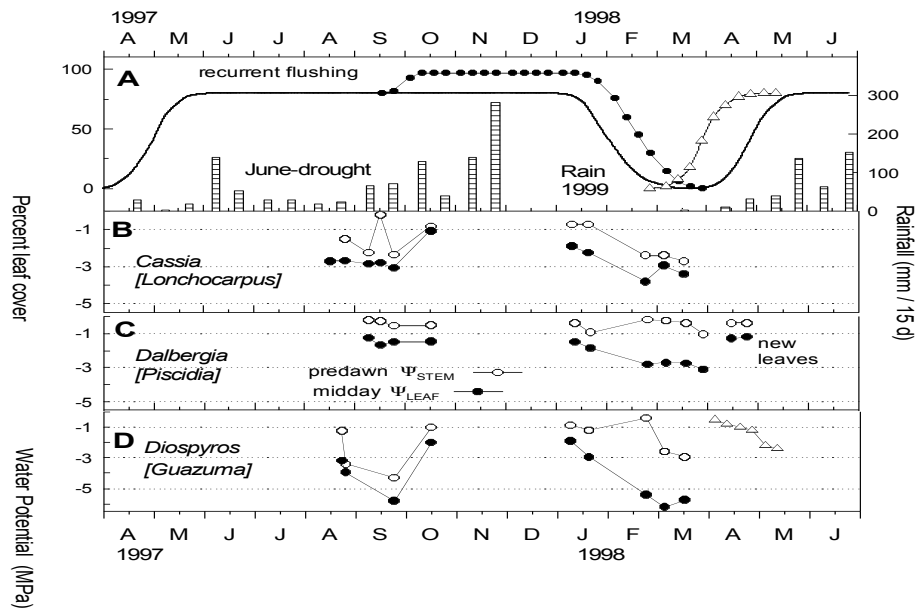
FIGURE 6. Phenology of brevideciduous species in 1997/98 and the effect of abnormal rain in 1999 . A –Rainfall (*bars*) and leaf phenology with a single annual flush of leaf growth (*simple line*; species in B,C) or with regular recurrent flushing (*dotted line*; species in D). *Triangles*: flushing induced in leafless trees by the Feb 1999 rain. B-D - Seasonal variation in tree water relations; B – *Cassia emarginata, [Lonchocarpus minimiflorus]*; C – *Dalbergia retusa, [Piscidia cartha-ginensis]*; D - *Diospyros nicaraguensis, [Guazuma ulmifolia]. Triangles:* water relations of rain-induced shoots.

FIGURE 7. Phenology and water relations of deciduous stem succulent species in 1997/98. A – 1997 rainfall (*bars*) and leaf phenology of *Bursera simaruba* (*line*). Formation of small, arrested shoots in April is followed by full shoot and leaf expansion after the first heavy rains. B – Seasonal variation in water relations of *Bombacopsis quinatum [Bursera simaruba].*

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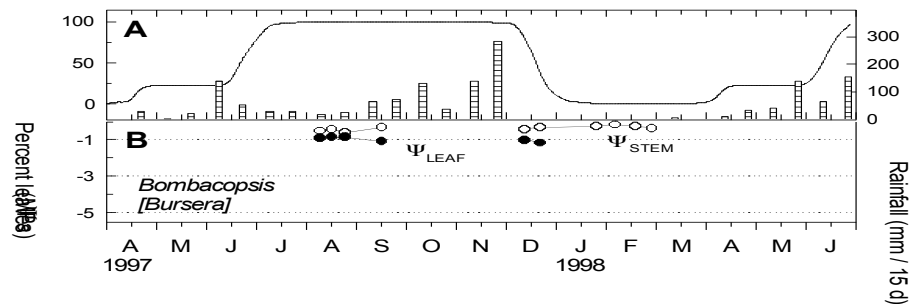
DISCUSSION

ENVIRONMENTAL AND INTERNAL CONTROLS OF LEAF ABSCISSION

LEAF AGE. -- As indicated by the observed minima of $p\Psi_S$, in 1997 soil water availability and water stress were similar during the June-drought and the following dry season among trees of different functional types (Fig. 3). However, all foliage was retained during the June-drought, when leaves were young, and most leaves abscised during the first 2-3 mo of the dry season, when leaves were older (Figs. 2, 4-7). These observations confirm the important role of leaf age in the onset of leaf senescence and abscission (Reich and Borchert 1988, Borchert 1994a, Holbrook et al. 1995) and reveal the following age-dependent responses of leaves to drought.

Very young leaves of deciduous trees (<2-3 mo old) did not abscise during the June-drought, even though they were severely water-stressed for >8 wk and their $m\Psi_L$ declined below the turgor loss point, as indicated by wilting. Similarly, leaves of *Tabebuia impetiginosa* formed after a single irrigation in mid-dry season remained wilted, but did not abscise, during 2 mo of severe drought (Borchert 1994c). Severe water stress therefore does not induce abscission in very young leaves as it does in older leaves. However, during the rainy period following the June-drought, rehydrated leaves abscised in all deciduous and most leaf-exchanging species (Figs. 4; 5B,C). As abscission is normally delayed in well-hydrated older leaves (see below), the timing of this leaf exchange is unusual and suggests that exposure of young leaves to severe water stress triggered unknown functional changes, which eventually resulted in leaf shedding. In many leaf-exchanging and brevideciduous species $m\Psi_L$ declined markedly before leaf abscission during the dry season, but $p\Psi_S$ remained high. This indicates that age-dependent loss of stomatal control in old leaves coincided with the large increase in evaporative demand and tree roots had access to subsoil water reserves (Figs. 5, 6 Dec-Jan).

As in *Erythrina poeppigiana* (Borchert 1980), the two annual leaf exchanges of *Albizia* are asynchronous among conspecific trees and occur under opposite environmental conditions. This rules out control of abscission by seasonal variation in tree water status and indicates that leaf senescence is triggered by unknown internal causes once leaves approach the end of their relatively short life span.

WATER STRESS. – Drought-induced water stress, well established as a major cause of leaf abscission (Addicott 1991; Borchert 1994a; Holbrook et al. 1995), varied widely among trees of different functional types (Fig. 3). In deciduous species, a decline in Ψ_L to very low values induced abscission in all leaves older than about 2-3 mo and abscission of older leaves was delayed during rainy periods. Life span of leaves therefore varied from 4-12 mo (Table 2). Leaf-exchanging and brevideciduous species were exposed to the same range of moderate water stress during both drought periods (Fig. 3), yet their responses were quite different. Brevideciduous trees shed at most a few leaves after the June-drought, and the marked decline in $m\Psi_L$ before leaf shedding during the regular dry season suggests that low Ψ_L is the immediate cause of abscission in older leaves (Fig. 6B-D). In leaf-exchanging species the timing of leaf abscission after the June drought and during the early dry season indicates that it is induced by seasonal drought, even though water stress was moderate and leaf shedding was generally not preceded – and hence directly caused - by a distinct decline in Ψ_L (Fig. 5B-E).

DECREASING DAYLENGTH. -- In stem succulent species 6-mo-old leaves with a high $m\Psi_L$ regularly become senescent and are shed rapidly in Dec (Fig. 7; Nilsen et al. 1990, Borchert and Rivera 2001), but none of these species was affected by the 1997 June-drought. These observations rule out induction of leaf abscission by water stress and suggest a role of

decreasing daylength in conjunction with advancing leaf age (Murashige 1966, Borchert and Rivera 2001).

CONTROL OF BUD BREAK

In trees of all functional types, rehydration of stem tissues (pΨ_S > -0.5 MPa) and elimination of correlative inhibition by old leaves are prerequisites for bud break (Borchert 1994a,b, 2000). In deciduous and leaf-exchanging species bud break occurs as soon as these conditions are met (Figs. 4, Sep/Oct, May/June; 5, Sep/Oct, Jan-Mar). Abnormal rainfall caused bud break in leafless trees (Figs. 4A, 6A, Mar), but not in trees retaining old foliage. Similarly, irrigation during the dry season did not result in earlier than normal flushing in leaf-bearing evergreen and brevideciduous trees in Panama and Northern Australia (Wright and Cornejo, 1990; Myers et al. 1998).

Bud break in well hydrated, leafless trees of spring-flushing stem succulent and brevideciduous species is induced in the absence of rain by increasing photoperiod in late March/April (Figs. 2C, 6A, 7A, Mar-Apr; Borchert and Rivera 2001; G. Rivera et al., pers.obs.). Heavy rain in Feb '99 did not induce bud break in leafless stem succulents, which are dormant during the dry season (Borchert and Rivera 2001), but caused earlier than normal flushing of leafless brevideciduous trees (Fig. 6A, Mar, *Rain 1999*). In these species, bud break is apparently induced by heavy rain or increasing photoperiod, whichever comes first (Borchert 2000; G. Rivera et al., pers. obs.).

DIFFERENCES BETWEEN FUNCTIONAL TYPES

Before recent deforestation, semideciduous forests in Guanacaste received amounts of annual rainfall that support evergreen forests elsewhere (mean 1920-1940: 1871 mm; Borchert 1998). The climate of these forests differs from that of seasonally dry evergreen forests in the extreme inter-annual variation in rainfall (800 - 2400 mm; Borchert, 1998: Fig. 4) and the 5-6 mo long dry season receiving < 5% of annual precipitation. ENSO events may cause exceptionally long dry seasons (e.g., > 6 mo with a total of < 50 mm precipitation in 1987, 1991, 1996) and abnormal 10-12 wk long dry periods during the rainy season (1990, 1994, 1997; Hagnauer, pers. obs.). Under this harsh, unpredictable climate, tree species of different functional types have evolved sets of functional and structural traits, which clearly set them apart from each other and fall into two major categories (Table 3; Borchert 1994a). Deciduous species tolerate very low levels of PAW and are dominant at dry upland sites of semideciduous forests (Table 1A,D; Borchert 1994a) and in deciduous neotropical forests (Mexico: Bullock and Solis-Magallanes, 1990), but uncommon in wet forests. Leaf-exchanging and brevideciduous species are confined to moist microsites of semideciduous forests (Table 1B,C) and predominate in seasonally dry, evergreen forests (Panama: Wright and Cornejo 1991; Eastern Amazonia: Nepstad et al 1994) and tropical savannas (Williams et al. 1997).

Deciduous hardwood species are the only tropical trees whose tissues tolerate desiccation to very low water potentials ((Table 3A; R. Borchert, pers.obs.). During seasonal drought, Ψ_S and Ψ_L decline to values far lower than those observed in other functional types (Figs. 3, 4). Their opportunistic vegetative phenology is mainly determined by seasonal variation in soil water availability, which results in large seasonal variations in trunk diameter (Daubenmire 1972, Reich and Borchert 1984) and formation of distinct annual rings (Worbes 1995, Borchert 1999). Accordingly, the phenology of deciduous species was most affected by abnormal drought and rain during the dry season (Fig. 4).

Trees of all other functional types maintain a relatively high Ψ_S during seasonal drought (Fig. 3) by tapping subsoil water reserves with their deep roots (Figs. 5, 6; Borchert 1994a, Nepstad et al. 1994) or storing water in the low-density wood of their trunks (Fig. 7; Borchert 1994b). Trunks of these drought-avoiding trees do not shrink during drought and distinct annual rings are rare (Table 3 B-D). Accordingly, the phenology of many of these drought-avoiding species was little affected by abnormal drought or rain.

TABLE 3. Characteristics of functional types among tree species of the tropical semideciduous forest in Guanacaste, Costa Rica. For each functional type a reference to the original definition is followed by a revised list of characteristic properties.

SPECIES TOLERANT OF VERY LOW SOIL WATER AVAILABILITY
A. DECIDUOUS SPECIES (Fig. 4; Borchert 1994a: Table 2)
  - extremely low values of Ψ_S and Ψ_L during drought (Figs. 3, 4);
  - leaf abscission caused by strong desiccation during the early dry season;
  - flushing after rehydration of top soil during the early rainy season;
  - at moist sites leaf exchange during dry season (Borchert 1994a,c);
  - large variation in trunk diameter with seasonal variation in water status (Daubenmire 1972);
  - wood with distinct annual rings (Borchert 1999; Worbes 1995).
  - mesic leaves with low specific weight and water content;
  - generally high wood density (Borchert 1994a);
B. DECIDUOUS STEM SUCCULENT SPECIES (Fig. 7; Borchert 1994a: Table 2).
  - Water storage in parenchyma of low-density wood;
  - very high values of Ψ_S and Ψ_L maintained during drought (Fig. 3, 7);
  - leaves with high Ψ_L abscise rapidly during the early dry season;
  - vegetative buds dormant during the dry season (Borchert and Rivera 2001);
  - bud break induced by increasing photoperiod (Borchert and Rivera 2001);
  - trunks shrink during bud break and expand after the first rains (Daubenmire 1972);
  - wood without tree rings (Borchert 1999).

SPECIES CONFINED TO MOIST MICROSITES IN DRY FORESTS
C. LEAF EXCHANGING SPECIES (Fig. 4; Borchert 1994a: Table 2)
  - Species restricted to sites with good subsoil water storage;
  - high values of Ψ_S maintained during the dry season (Figs. 3, 5);
  - trunks may expand during the dry season (Daubenmire 1972)
  - young leaves emerge immediately after abscission of old leaves;
  - long-lived leaves with high specific weight and water content;.
  - indistinct or non-annual tree rings (Borchert 1999; Worbes 1995).
D. BREVIDECIDUOUS, SPRING FLUSHING SPECIES (Fig. 6; Borchert 1994a: Table 2)
  - deciduous for short, variable periods during the late dry season;
  - rehydration during the dry season during or after leaf shedding (Fig. 6);
  - flushing induced by increasing daylength or dry-season rainshowers
      (Borchert 2000; G. Rivera et al., pers. obs.);
  - trunks do not shrink during dry season (Daubenmire 1972);
    - incomplete, non-annual tree rings common (Borchert 1999; Worbes 1995).

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