

Leaf age and the timing of leaf abscission in two tropical dry forest trees

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Abstract We used experimental defoliations to examine the effect of leaf age on the timing of leaf shedding in two tropical dry forest trees. Trees of the deciduous *Bombacopsis quinata* (bombacaceae, a.k.a. *Pachira quinata*) and the brevi-deciduous *Astronium graveolens* (anacardiaceae) were manually defoliated for three times during the rainy season. All trees started to produce a new crown of leaves 2 weeks after defoliation, and continued expanding leaves throughout the rainy season. At the transition to the dry season, the experimental groups consisted of trees with known differences in maximum leaf age. Defoliations resulted in declines in stem growth but did not affect the mineral content or water relations of the leaves subsequently produced. There was no effect of leaf age on the timing of leaf abscission in *B. quinata*. In *A. graveolens*, the initiation of leaf shedding followed in rank order, the maximum leaf age of the four treatments, but there was substantial coherence among treatments in the major period of leaf abscission such that trees completed leaf

shedding at the same time. In the two species, leaf water potential (Ψ_L) and stomatal conductance (g_s) declined with the onset of the dry season, reaching minimum values of -0.9 MPa in *P. quinata* and <-2.0 MPa in *A. graveolens*. Within each species, leaves of different age exhibited similar Ψ_L and g_s at the onset of drought, and then decreased at a similar rate as the dry season progressed. Overall, our study suggests that the environmental factors were more important than leaf age in controlling the timing of leaf shedding.

Keywords *Astronium graveolens* · *Bombacopsis quinata* · Phenology · Tropical dry forest · Water relations

Introduction

Neo-tropical dry forests are characterized by the occurrence of a long and severe seasonal drought during which a large fraction of tree species experience a period of deciduousness of variable length (Daubenmire 1972; Frankie et al. 1974; Holbrook et al. 1995; Eamus and Prior 2001). Despite the marked seasonality in rainfall, and in contrast to temperate trees, the correlation between the annual climatic cycle and seasonal development is poor among tropical dry forest tree species and the synchrony in the timing of phenological events such as leaf fall and bud break is low among conspecific trees (Reich 1995; Borchert 1994). This diversity in phenological patterns raises the question of what factors are responsible for triggering major transitions such as leaf abscission and bud break. A number of environmental variables, including soil (Reich and Borchert 1988) and atmospheric moisture (Wright and Cornejo 1990; Meinzer et al. 1999), radiation intensity

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(van Schaik et al. 1993; Yeang 2007) and day-length (Nielsen and Muller 1981; Bullock and Solís-Magallanes 1990; Borchert and Rivera 2001; Borchert et al. 2005) have been proposed as important cues regulating the meristematic activity of tropical dry forest trees.

Temporal and spatial patterns of leaf abscission, however, cannot be easily attributed to the action of external factors alone (van Schaik et al. 1993; Borchert 1994; Reich 1995), suggesting that the internal water status of the plant may play a critical role in transducing these signals (Holbrook et al. 1995). The role of leaf age as a determinant of the timing of leaf abscission and asynchrony in phenology among conspecific trees has been a long-standing issue (Borchert 1994; Borchert et al. 2002). This is based on the idea that older leaves exhibit increased sensitivity to water deficits (Reich 1984; Reich and Borchert 1988). As leaves age, they experience major structural, chemical and functional changes such as decreases in nutrient content (Aerts 1996; Killingbeck 1996; Lim et al. 2007) and xylem hydraulic capacity (Brodribb et al. 2002) that contribute to the well-known decline in both photosynthesis and transpiration (Martin et al. 1994; Sobrado 1994; Kitajima et al. 1997; Brodribb et al. 2003). Thus, older leaves could be more sensitive to decreases in tree water status due to their reduced hydraulic capacity as well as their lower margins for carbon gain. It has also been suggested that leaves lose their ability to control water loss, perhaps due to an inability to prevent water loss at night (Reich 1984; Reich and Borchert 1988; Martin et al. 1994).

Borchert et al. (2002) took advantage of unusual climatic patterns occurring as a consequence of an El Niño year and abnormal dry-season rains to address whether leaf abscission is controlled by leaf age. Their results demonstrate that leaf age does not, by itself, dictate the timing of leaf abscission. However, their observational study does not address the possible interactions between leaf age and environmental factors that may play a significant role in determining the timing of leaf abscission in tropical dry forest trees.

Our study examines experimentally, the role of leaf age in controlling the timing of leaf shedding in two dry forest tree species with contrasting phenology, one deciduous and one brevi-deciduous. We used experimental defoliations of plantation-grown trees to produce individuals that differed in the maximum leaf age at the start of the dry season, which allowed us to separate the effects of leaf age from climatic factors. Our experiment was designed to determine: (1) if leaf abscission in trees with younger cohorts of leaves is delayed relative to the timing of leaf fall in trees with older cohorts of leaves, and (2) the water stress thresholds required to trigger leaf abscission in tropical dry forest trees with contrasting phenology.

Materials and methods

Experimental site and plant material

Measurements were carried out near Cañas, Guanacaste (latitude 10°26', longitude 85°04', elevation 100 m) at the dry forest-basal pre-montane wet forest life zones transition (Holdridge 1967). The site receives an average of 1,500–1,950 mm of rain annually with a pronounced dry season that spans from mid-November to mid-May. Mean air temperature at the field site was 27°C with little annual variation (Fig. 1). The experiment was conducted from January 1998 to March 1999 in two 5-year-old plantations, in which, the trees were planted at a spacing of 3 × 3 m. At the start of the experiment, tree diameter at breast height (dbh) varied between 27.5 and 77.5 mm and between 18.3 and 75.1 mm, and height varied between 2.7 and 5.2 m and between 2.5 and 6.5 m in *B. quinata* and in *A. graveolens* trees, respectively.

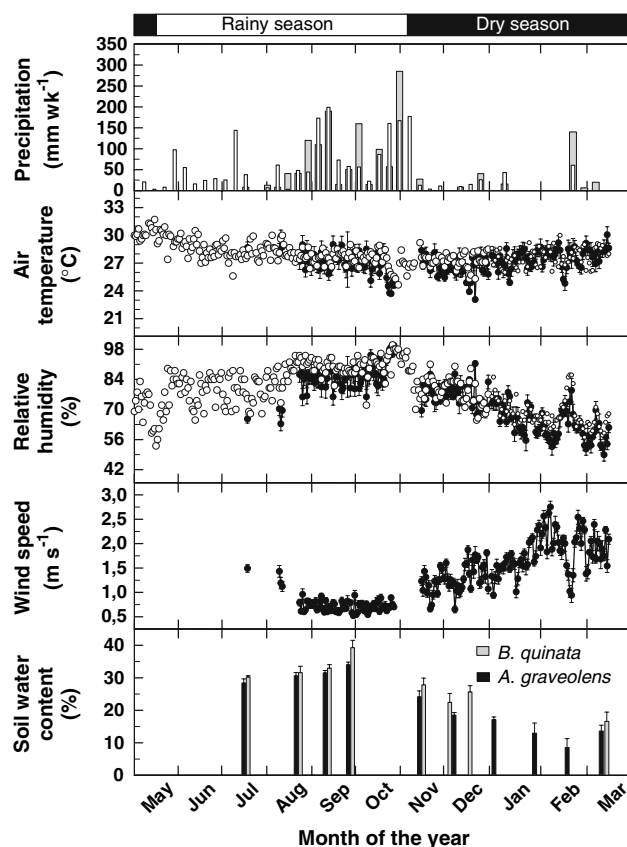


Fig. 1 Climatic conditions at the field site during the study period, from July 1998 to March 1999. Closed symbols and bars indicate measurements recorded by a weather station located ca.100 m North from the experimental plots. Data points with error bars are means (\pm SE). Open symbols are daily data collected by a nearby (\sim 2 km) meteorological station (10°22'N, 85°12'W)

Environmental conditions at the field site were monitored using a meteorological station located in an open field ca.100 m North from the field site. The station was operated under the control of a datalogger (model 21X Campbell Scientific, Logan, UT, USA) programmed to obtain hourly averages of air temperature and relative humidity, and wind speed. Rainfall was measured weekly by a rain gauge.

The soil was classified as an inceptisol of alluvial origin. Soil water content was measured gravimetrically at monthly intervals on soil samples of approximately 90 cm³ obtained from the upper 20 cm and placed in hermetically sealed containers until processing. Gravimetric soil water content was determined in an analytical balance by obtaining fresh and dry weight of soil samples; dry weight was obtained after drying the samples for 48 h at 70°C.

Two tree species with contrasting phenology were studied: *Bombacopsis quinata* Jacq. Dugand (recently, *Pachira quinata* (Jacq.), Alverson 1994) (bombacaceae) and *Astronium graveolens* Jacq. (anacardiaceae). *B. quinata* is a deciduous species that remains leafless for a substantial part of the dry season (November–May). *A. graveolens* is a brevi-deciduous species that bears leaves during most of the year, except for brief periods of leaf exchange. *B. quinata* is a stem-succulent tree (wood density = 0.38–0.43 g cm⁻³) native from Nicaragua to Venezuela and Colombia. *A. graveolens* is a hardwood (0.85–1.28 g cm⁻³) species native from Southern México to Bolivia.

Experimental control of leaf age

Leaf age was controlled experimentally by defoliating trees during the rainy season. Control trees consisted of

individuals that flushed naturally at the onset of the rains in *B. quinata* (mid-May) and during the late dry season in *A. graveolens* (early March). At three times during the rainy season, five trees per species were defoliated using hand scissors (Fig. 2). Treatments were assigned at random. A total of 20 trees of each species were studied.

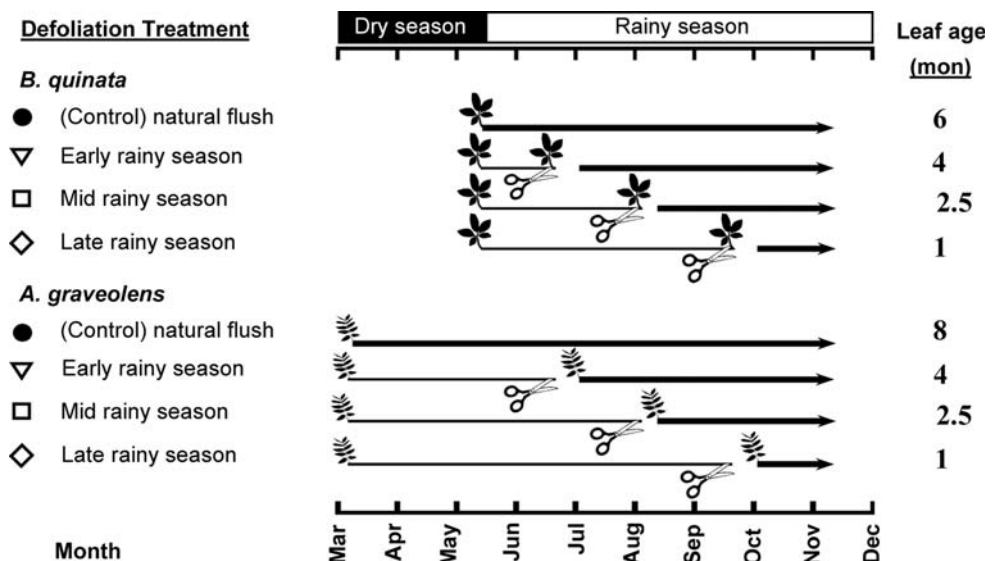
Within 2 weeks after defoliation, the trees flushed and continued producing leaves during the rainy season, so that at the onset of the subsequent dry season (mid-November), the oldest leaves in trees belonging to the four treatments were approximately 6, 4, 2.5 and 1-month-old in *B. quinata*, and 8, 4, 2.5 and 1-month-old in *A. graveolens* (Fig. 2). The defoliation treatment performed in the mid-rainy season coincided with a short dry spell during which very low rainfall was recorded for a period of approximately 3 weeks following defoliation (Fig. 2).

Leaf N, P and K contents were measured in four young, fully expanded leaves collected from each of five trees per treatment at intervals of 1.5 month following flushing. Leaves from each sampling date were bulked by treatment and processed at the Nutrient Analysis Lab., Centro de Investigaciones Agronómicas, Universidad de Costa Rica.

Tree growth and phenology

Stem diameter measured at 1.3 m and tree height were recorded monthly using a diameter tape and an extension pole, respectively. Leaf flushing and shedding were evaluated every 2 weeks using a semi-quantitative method (Fournier 1974), in which, the intensity of the phenological event is recorded according to a scale that varies from 0 to 4. In this method, 0 represents the

Fig. 2 Production of trees with canopies of different ages in Cañas, Costa Rica. Natural flushing occurred in mid-May in *B. quinata* and in early March 1998 in *A. graveolens*. Experimental defoliations took place on June 26 (early rainy season), August 7 (mid-rainy season) and September 26 (late rainy season). All trees resumed flushing approximately 2 weeks after defoliation



absence of the phenological phenomenon, 1 represents the occurrence of the phenomenon in 1–25% of the tree crown, and 2, 3 and 4 represent the occurrence of the phenomenon in 26–50, 51–75 and 76–100% of the tree crown, respectively.

Leaf water relations

Stomatal conductance (g_s), and pre-dawn (6 AM) and mid-day (12 noon) leaf water potential (Ψ_L) were measured every 2 weeks throughout the rainy season on five trees belonging to the natural flush (control) treatment. Leaf g_s was measured four times throughout the day, typically from 7 AM to 4 PM, using a steady-state porometer (model LI-1600, Li-Cor) on four fully expanded leaves per tree. Ψ_L was measured on leaves of the same age and exposure using a pressure chamber (model PMS-100, PMS, Corvallis, OR, USA). Leaves sampled for Ψ_L measurements were enclosed in plastic bags upon excision and transferred to a sealed cooler and their Ψ_L determined within 1 h.

At the onset of the dry season, Ψ_L and g_s measurements were extended to include leaves obtained from all experimentally-created canopies, because altered stomatal behavior (Reich 1984) and differential drought sensitivity of leaves of different ages (Reich and Borchert 1988) is the basis for postulating a role for leaf age in the timing of leaf abscission in response to drought. Measurements on leaves from three locations along the same branch: youngest fully expanded, oldest (most proximal) and midway between these two were included. Thus, at each sampling time, 12 leaves were measured from each tree (four per position along the branch). The oldest leaves produced by natural flushing were 6- and 8-month-old in *B. quinata* and *A. graveolens*, respectively, while the youngest fully expanded leaves were initiated on approximately October 15 and thus were ~1 month in age at the beginning of the dry season. The age of the middle leaves is unknown, but thought to be approximately halfway between the two extremes.

Data analysis

Statistical analyses were performed using SAS v.7 for Windows (SAS Institute Inc., 1998, NC, USA). Repeated-measurements ANOVA was used to compare treatments, after testing to ensure that assumptions of normality and homogeneity of variance were met. Post hoc comparisons of means were performed using the cluster-based analysis outlined in Bautista et al. (1997).

Results

Microclimatic conditions and soil water

The rainy season of 1998 started in mid-May and continued through early November, although most of the rain fall was during the last 3 months of the rainy season (Fig. 1). Mean air temperature and relative humidity were 27°C and 85%, respectively, and mean wind speed during the daytime was $7.5 \pm 0.02 \text{ m s}^{-1}$. Soil water content remained high throughout the rainy season, 33.5 and 31.1% in the *B. quinata* and *A. graveolens* plots, respectively. Weather changed substantially in early November during the transition to the dry season, after a storm at the end of October that interrupted the collection of climatic data at the field site. The dry season was characterized by lower relative humidity (69%), and higher wind speeds (16.1 m s^{-1}). Mean air temperature varied a little (27°C), and soil water content decreased to 23.1 ± 1.5 and $15.8 \pm 1\%$ in the *B. quinata* and *A. graveolens* plots, respectively (Fig. 1).

Tree growth, phenology, and the timing of leaf abscission

Increments in diameter at breast height of control trees of both species were similar (20–25 mm) (Fig. 3). Stem growth occurred only during the rainy season in *B. quinata*, but continued throughout the length of the study (i.e. into the dry season) in *A. graveolens*. Defoliation led to reductions in stem diameter growth in all treatments (Fig. 3). At the end of the experiment, defoliation during the early, middle and late rainy season resulted in stem growth reductions of 40, 72 and 33% in *B. quinata*, and of 36, 67 and 41% in *A. graveolens*, respectively. There was no change in leaf nutrient content with time for any of the treatments ($p < 0.05$; data not shown). Leaf N and P contents were similar in both species, but *B. quinata* leaf tissue contained less K than *A. graveolens* leaves (data not shown). This is consistent with other studies that show no major effect of removal of mature leaves on nutrient supply to young leaves of several species (Jonasson 1989).

In experimentally defoliated trees, flushing re-started approximately 2 weeks after defoliation in both species. Control and manipulated *B. quinata* trees continued producing leaves throughout the remainder of the rainy season (Fig. 4). Leaf production continued during the transition to the dry season, although at a lower intensity (<50%). Many of these leaves were shed before reaching full size (Fig. 4). Flushing of *A. graveolens* was intermittent, remaining at an intensity of 50% from the time of natural flushing at the beginning of March through the beginning of the dry season (Fig. 4). Leaf production declined during the early dry

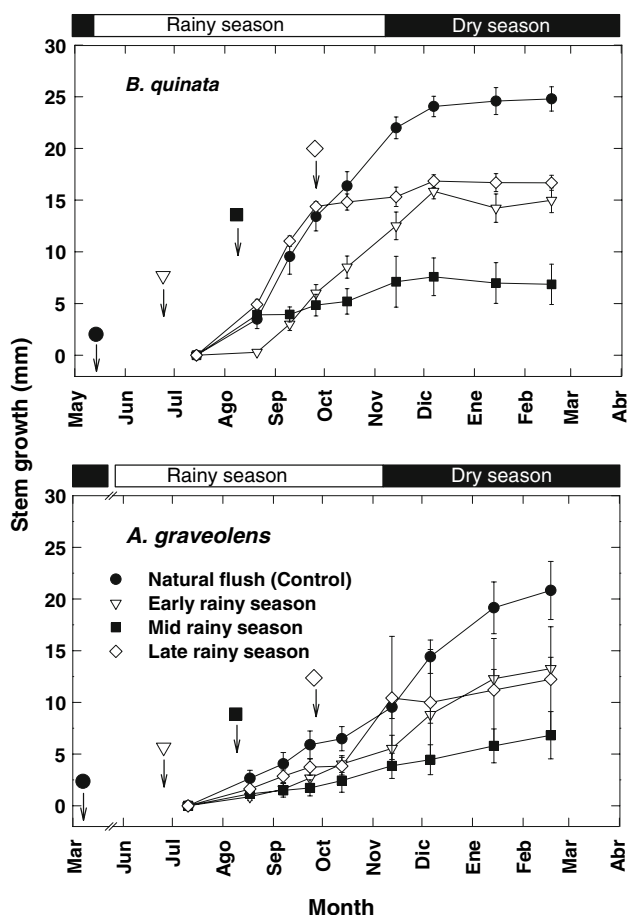


Fig. 3 Stem growth of *B. quinata* and *A. graveolens* trees subjected to defoliation treatments at three different times during the rainy season, as compared to control trees. Vertical arrows indicate the time of each defoliation treatment. Each point is the mean (\pm SE) of five trees

season and remained at low intensity (<25%) from mid-November through the end of February. Several minor flushing events were observed, the most important of which was observed in mid-December in trees that experienced the latest defoliation. These trees continued producing leaves for a period of approximately 2.5 month.

Leaf shedding in *B. quinata* began in mid-November in all treatments, continued throughout the first 2 months of the dry season, and was complete by mid-January (Fig. 4). There were significant differences among treatments in the time to achieve different degrees of leaf shedding ($p < 0.05$). However, the interaction between leaf age and leaf shedding was not significant ($p < 0.05$). Cluster-based analyses of mean separation (Bautista et al. 1997) demonstrated that there were no differences in the timing of leaf-fall among control trees and those defoliated during early or late rainy season ($p < 0.05$; Fig. 5). Trees subjected to mid-rainy season defoliation (maximum leaf age of 2.5 month) shed leaves more rapidly than trees in the

other three treatments ($p < 0.05$) and showed poor stem growth, perhaps as a result of low rainfall during leaf expansion.

In *A. graveolens*, there was a significant difference among treatments in the time to achieve different degrees of leaf shedding ($p < 0.001$; Fig. 5). Most of these differences appeared to be due to differences in the date of initiation of leaf shedding. Control trees experienced 1–25% leaf abscission approximately 20 days before the onset of the dry season, whereas trees subjected to manual defoliations during the rainy season required 10, 50 and 63 days into the dry season to achieve the same degree of leaf loss. In contrast, differences in the time required to achieve greater degrees of leaf abscission (>50%) were small.

Leaf water potential and stomatal conductance

Leaf Ψ_L measured during the rainy season was similar for the two species. For both *B. quinata* and *A. graveolens*, there were no systematic differences ($p < 0.001$) in Ψ_L associated with either the experimental defoliation treatments or the location of the sampled leaves along the branch (Fig. 6). Control (non-defoliated) trees of *B. quinata* had mean pre-dawn and mid-day Ψ_L values of -0.3 ± 0.01 and -0.7 ± 0.02 MPa, respectively, which declined to -0.7 ± 0.03 and -0.9 ± 0.03 MPa, early in the dry season. Control trees of *A. graveolens* had mean pre-dawn and mid-day Ψ_L values of -0.3 ± 0.02 and -0.9 ± 0.04 MPa, respectively. Mean pre-dawn and mid-day Ψ_L values in *A. graveolens* leaves measured during the dry season (-1.0 ± 0.11 and -1.7 ± 0.15 MPa) were significantly lower than that in *B. quinata*. However, dry season Ψ_L values in *A. graveolens* were quite variable and appeared to respond to episodic rainfall events (Fig. 6).

Values of g_S remained relatively constant throughout the day in both species, so that g_S values obtained during the course of a day were combined to produce a daily average for each leaf age examined. Leaf g_S of *B. quinata* control trees increased from ca. $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ in young leaves to a maximum of $450 \text{ mmol m}^{-2} \text{ s}^{-1}$ in October (Pacheco 2001), and then declined in response to increasing drought to $<75 \text{ mmol m}^{-2} \text{ s}^{-1}$ shortly before leaf abscission (Fig. 7). With the exception of leaves produced after the mid-rainy season defoliation, which had a very low g_S , when first measured at the end of the rainy season, g_S in the two other defoliation treatments (maximum leaf ages of 4 months and 1 month) was similar to the control trees (maximum leaf age of 6 months). There was some variation, as a function of position along the branch, but no systematic effect separated the maximum aged leaves from those produced at the end of the rainy season ($p < 0.01$).

Fig. 4 Phenology of **a** *B. quinata* and **b** *A. graveolens* measured using a semi-quantitative scale in which phenological scores represent the intensity of the phenological phenomenon evaluated (Fournier 1974). Each point is the mean (\pm SE) of five trees. Vertical arrows indicate the time of each defoliation treatment

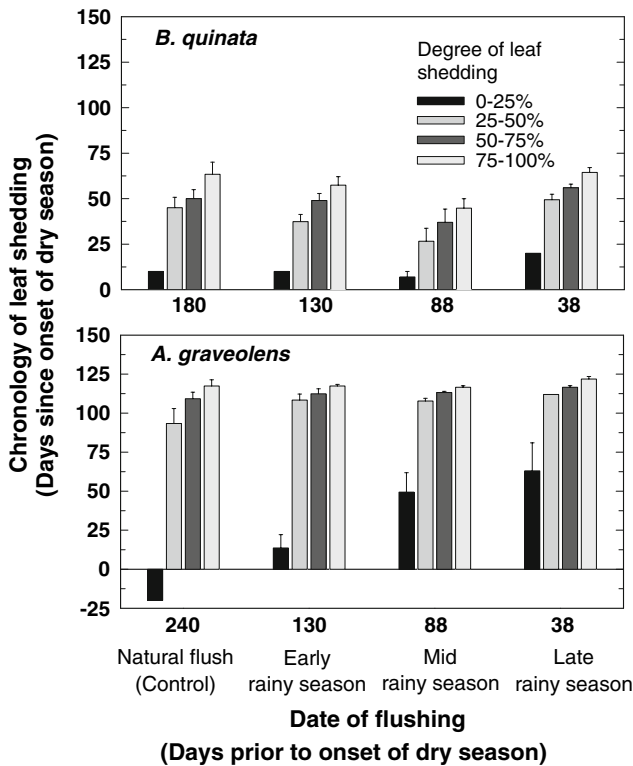
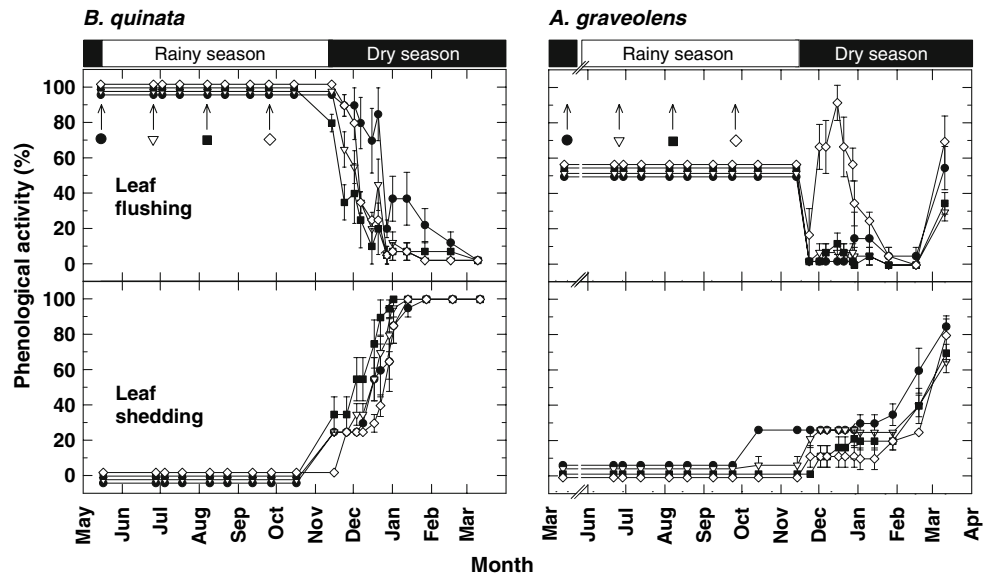


Fig. 5 Chronology of leaf shedding in *B. quinata* and *A. graveolens*, as a function of the date of flushing, and expressed as days prior to the onset of seasonal drought. The intensity of leaf shedding was recorded according to the semi-quantitative scale developed by Fournier (1974). Vertical bars are means (\pm SE) of five trees

Leaf g_s of control *A. graveolens* trees was relatively constant throughout the rainy season (250–350 $\text{mmol m}^{-2} \text{s}^{-1}$, Pacheco 2001), and progressively declined during the dry season (Fig. 7). At the beginning of the dry season, g_s of oldest leaves on the control and early-season defoliated trees

was significantly lower than the g_s of younger leaves on the same trees and of leaves of all ages in the mid- and late-rainy season defoliated trees ($p < 0.01$). These differences diminished as the dry season progressed, and all leaf age classes reached mean g_s values $< 100 \text{ mmol m}^{-2} \text{ s}^{-1}$, shortly before leaf abscission (Fig. 7).

Discussion

One major goal of this study was to examine the role of leaf age in the phenology of tropical dry forest trees, using manual defoliation as a mean to create trees with leaf cohorts of different ages at the onset of the dry season. There was no effect of leaf age on temporal patterns of leaf shedding in *B. quinata* trees or in *A. graveolens* trees in terms of the time required to achieve $>25\%$ leaf loss (Fig. 5). However, the onset of leaf senescence ($<25\%$ leaf loss) in *A. graveolens* followed in rank order the age of the oldest cohort of leaves (Fig. 5).

There were substantial differences in growth and leaf production between the two species studied. Growth in the deciduous *B. quinata* was seasonal, occurring exclusively during the rainy season. In contrast, growth of *A. graveolens*, a brevideciduous species, continued during the dry season, and in control trees was actually higher than during the rainy season. Flushing activity in of *A. graveolens* was highly responsive to water pulses during the dry season, and g_s was substantial in leaves of different ages during most of the year. Contrasting reports on the phenology of this species (Borchert 1994) may be due to this opportunistic behavior.

Leaf senescence is a genetically programmed, highly coordinated process (Lim et al. 2007) that culminates with

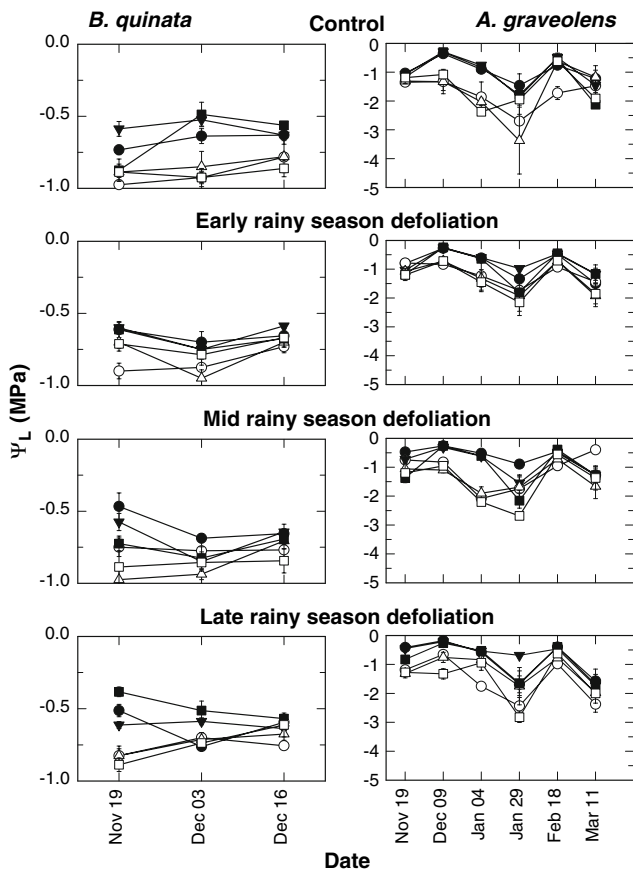


Fig. 6 Water potential (Ψ_L) of leaves of different ages during the transition to the dry season in *B. quinata* and *A. graveolens*. Solid and open symbols are pre-dawn and mid-day Ψ_L values, respectively. Note different y-axis scales and sampling dates for the two species. Symbols are as follows: filled circle and open circle more proximal leaves on each branch produced immediately following the experimental defoliation. In the case of the control trees, following the previous dry season; filled square and open square most distal fully expanded leaves on the same branch, which were approximately 0.5-month-old at the beginning of the dry season and filled inverted triangle and open inverted triangle leaves midway along these branches assumed to be intermediate in age. Four leaves per category were sampled on each tree and the mean value of these measurements used as representative of that tree

the activation of pre-existent abscission layers that triggers leaf shedding. Leaf abscission in some dry forest trees is accompanied by declines in the water transport capacity of leaf-bearing branches, but the question remains as to whether cavitation is caused by or precedes leaf abscission (Brodribb et al. 2002; Brodribb and Holbrook 2003a). However, in other dry forest species, leaf abscission occurs without the loss of transport capacity in branch xylem (Brodribb et al. 2002). In these species, phenology may be more affected by photoperiod (Borchert and Rivera 2001; Borchert et al. 2005) or atmospheric humidity (Meinzer et al. 1999) than by soil water (Wright and Cornejo 1990).

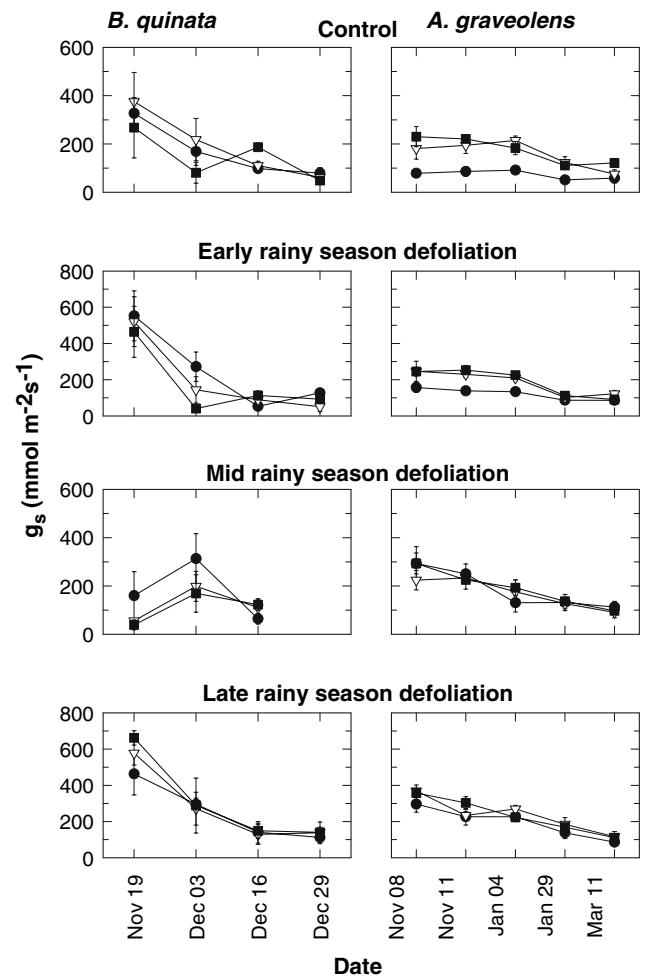


Fig. 7 Stomatal conductance (g_s) of leaves of different ages during the transition to the dry season in *B. quinata* and *A. graveolens*. Each point is the mean (\pm SE) of five trees per treatment. Symbols are as follows: filled circle more proximal leaves on each branch produced immediately following the experimental defoliation. In the case of the control trees, following the previous dry season; filled square most distal fully expanded leaves on the same branch, which were approximately 0.5-month-old at the beginning of the dry season and open inverted triangle leaves midway along these branches assumed to be intermediate in age. Four leaves per category were sampled on each tree and the mean value of these measurements used as representative of that tree

A number of authors have proposed that the leaf age might influence the timing of leaf abscission through a reduced ability of older leaves to control the water loss, especially at night (Reich 1984), increasing their sensitivity to water stress (Borchert 1994; Martin et al. 1994). In contrast, our results indicate that within each species, drought had similar physiological effects on leaves of all ages. The species examined produced leaves continuously (*B. quinata*) or intermittently (*A. graveolens*) throughout the rainy season, and later shed leaves of a wide range of ages with a high degree of synchrony, further supporting the conclusion that leaf age does not play a determinant

role in controlling the timing of leaf fall in this environment. Indeed, there was no difference in Ψ_L during drought as a function of leaf age (Fig. 6), and older leaves had similar and even lower g_S than their younger counterparts (Fig. 7).

Another goal of this study was to measure the degree of water stress associated with leaf abscission in tropical dry forest trees with contrasting phenology. In both species, g_S and Ψ_L declined during the dry season, with the majority of leaves being shed when pre-dawn and midday Ψ_L values became roughly equal. Within each species, g_S seemed to respond synchronously to a relatively narrow range of Ψ_L measured in leaves of different ages (see also Brodribb et al. 2003b), which suggests that restrictions imposed by soil and atmospheric drought on gas exchange and carbon gain of all leaf ages dominated the abscission of these leaves during drought. Stomatal closure has been found to be primarily coordinated with leaf hydraulic conductance in a number of dry forest tree species (Brodribb and Holbrook 2003b), although considerable plasticity in this relationship has been observed (Brodribb et al. 2003a). This plasticity probably arises from differential ability of leaf tissues of different species to adjust to changes in water availability by altered stomatal responses and osmotic adjustment (see Bucci et al. 2003). Such a strong coordination between hydraulic conductance of the leaf vascular system and the photosynthetic capacity of leaves has led some authors to suggest that control over photosynthesis and productivity may be dominated by changes in plant hydraulic properties (Brodribb and Holbrook 2003a), and to associate reduced hydraulic capacity, Ψ_L , and vulnerability to cavitation to longer leaf-life span in two dry forest evergreen trees (Brodribb and Holbrook 2005). Regular and reversible diurnal variations in hydraulic conductance may also be the features of long-lived leaves (Brodribb and Holbrook 2005) in contrast to deciduous trees, which experience stomatal closure, loss of leaf turgor, and xylem cavitation at Ψ_L values significantly higher than brevi-deciduous species and evergreen species.

Our results show a high similarity in the response of g_S to decreasing Ψ_L across a wide range of leaf ages within each species. Similar to other stem-succulent trees with high vulnerability to cavitation (Olivares and Medina 1992; Brodribb et al. 2003a), leaves of the deciduous *B. quinata* abscised when mid-day Ψ_L was lower than -0.9 MPa. In contrast, the leaves of the brevi-deciduous *A. graveolens* of longer life span tolerated drought (-2 MPa) and apparently maintained high xylem water transport capacity and intermittent leaf production during the dry season. Stem-succulent trees like *B. quinata* are perhaps more affected by atmospheric drought, as the transition to the dry season was characterized by increasing wind speed and sharp

drops in atmospheric moisture. It has also been suggested that day-length may play an important role in determining the timing of phenological events among tropical dry forest trees (Lawton and Akpan 1968; Borchert and Rivera 2001).

The complex interactions between leaf age and environmental factors that apparently control the timing of leaf shedding at the onset of seasonal drought preclude the separation of the effects of leaf age and environmental factors on leaf abscission (Reich and Borchert 1988; Borchert et al. 2002). The experimental approach employed in this study allowed us to conclude that environmental factors are more important than leaf age in controlling the timing of leaf abscission in tropical dry forest trees with contrasting phenology. Our study does not separate photoperiod from other environmental factors; further experimental manipulations will be needed to quantify the relative contribution of water availability versus photoperiod in leaf abscission.

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References

- Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *J Ecol* 84:597–608
- Alverson WS (1994) *Pachira quinata* (Jacq.) W.S. Albers. *Novon* 4:7
- Bautista MG, Smith DW, Steiner RL (1997) A cluster based approach to mean separation. *J Agric Biol Environ Stat* 2:179–197
- Borchert R (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449
- Borchert R, Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiol* 21:213–221
- Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34:27–39
- Borchert R, Renner SS, Calle Z, Navarrete D, Tye A, Gautier L, Spichlger R, von Hildebrand P (2005) Photoperiodic induction of synchronous flowering near the equator. *Nature* 433:627–629
- Brodribb TJ, Holbrook NM (2003a) Changes in leaf hydraulic conductance during leaf shedding in seasonally dry forest trees. *New Phytol* 158:295–303
- Brodribb TJ, Holbrook NM (2003b) Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiol* 132:2166–2173
- Brodribb TJ, Holbrook NM (2005) Leaf physiology does not predict leaf habit; examples from tropical dry forest. *Trees* 19:290–295
- Brodribb TJ, Holbrook NM, Gutiérrez MV (2002) Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant Cell Environ* 25:1435–1444
- Brodribb TJ, Holbrook NM, Edwards EJ, Gutiérrez MV (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant Cell Environ* 26:443–450

- Bucci S, Scholz FG, Goldstein G, Meinzer FC, Sternberg da SL (2003) Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: factors and mechanisms contributing to the refilling of embolized vessels. *Plant Cell Environ* 26:1633–1645
- Bullock SH, Solís-Magallanes A (1990) Phenology of canopy trees of a tropical deciduous forest in México. *Biotropica* 22:22–35
- Daubenmire R (1972) Phenology and other characteristics of tropical semi-deciduous forests in northwestern Costa Rica. *J Ecol* 60:147–170
- Eamus D, Prior L (2001) Ecophysiology of trees of seasonally dry tropics: comparison among phenologies. *Adv Ecol Res* 32:113–197
- Fournier L (1974) Un método cuantitativo para la medición de las características fenológicas en árboles. *Turrialba* 24:422–423
- Frankie G, Baker H, Opler P (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J Ecol* 62:881–919
- Holbrook NM, Whitbeck J, Mooney H (1995) Drought responses of neo-tropical dry forest trees. In: Bullock SH, Mooney HA, Medina E (eds) *Seasonally dry tropical forest*. Cambridge University Press, New York, pp 243–276
- Holdridge LR (1967) *Life zone ecology*. Tropical science center, San José
- Jonasson S (1989) Implications of leaf longevity, leaf nutrient re-absorption and translocation for the resource economy of five evergreen plant species. *Oikos* 56:121–131
- Killingbeck K (1996) Nutrients in senesced leaves: key to the search for potential resorption and resorption proficiency. *Ecology* 77:1716–1727
- Kitajima K, Mulkey SS, Wright SJ (1997) Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. *Am J Bot* 84:702–708
- Lawton JRS, Akpan EEJ (1968) Periodicity in *Plumeria*. *Nature* 218:384–386
- Lim PO, Kim HJ, Nam HG (2007) Leaf senescence. *Annu Rev Plant Biol* 58:115–136
- Martin CE, Loeschens VS, Borchert R (1994) Photosynthesis and leaf longevity in trees of a tropical deciduous forest in Costa Rica. *Photosynthetica* 30:341–351
- Meinzer FC, Goldstein G, Franco AC, Bustamante M, Iglar E, Jackson P, Caldas L, Rundel PW (1999) Atmospheric and hydraulic limitations on transpiration in Brazilian cerrado woody species. *Funct Ecol* 13:273–282
- Nielsen E, Muller W (1981) Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. *Ecol Monogr* 51:323–341
- Olivares E, Medina E (1992) Water and nutrient relations of woody perennials from tropical dry forests. *J Veg Sci* 3:383–392
- Pacheco A (2001) Efecto de la edad de la hoja sobre el inicio de la caída del follaje en dos especies del bosque tropical seco con fenología contrastante, *Bombacopsis quinata* (bombacaceae) y *Astronium graveolens* (anacardiaceae). Tesis. Escuela de Biología. Univ. de Costa Rica. 57 p
- Reich PB (1984) Loss of stomatal function in ageing hybrid poplar leaves. *Annu Bot* 53:691–698
- Reich PB (1995) Phenology of tropical forests: patterns, causes, and consequences. *Can J Bot* 73:164–174
- Reich PB, Borchert R (1988) Changes with leaf age in stomatal function and water status of several tropical tree species. *Biotropica* 20:60–69
- Sobrado MA (1994) Leaf age effects on photosynthetic rate, transpiration rate and nitrogen content in a tropical dry forest. *Physiol Plant* 90:210–215
- van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical trees: adaptive significance and consequences for primary consumers. *Ann Rev Ecol Syst* 24:353–377
- Wright SJ, Cornejo FH (1990) Seasonal drought and leaf fall in a tropical forest. *Ecology* 71:1165–1175
- Yeang H-Y (2007) Synchronous flowering of the rubber tree (*Hevea brasiliensis*) induced by high solar radiation intensity. *New Phytol* 175:283–289