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Leaf physiology does not predict leaf habit; examples from tropical dry forest

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Abstract Leaf structure and physiology are thought to be closely linked to leaf longevity and leaf habit. Here we compare the seasonal variation in leaf hydraulic conductance (k_{leaf}) and water potential of two evergreen tree species with contrasting leaf life spans, and two species with similar leaf longevity but contrasting leaf habit, one being deciduous and the other evergreen. One of the evergreen species, *Simarouba glauca*, produced relatively short-lived leaves that maintained high hydraulic conductance year round by periodic flushing. The other evergreen species, *Quercus oleoides*, produced longer-lived leaves with lower k_{leaf} and as a result minimum leaf water potential was much lower than in *S. glauca* (−2.8 MPa vs −1.6 MPa). Associated with exposure to lower water potentials, *Q. oleoides* leaves were harder, had a higher modulus of elasticity, and were less vulnerable to cavitation than *S. glauca* leaves. Both species operate at water potentials capable of inducing 20 (*S. glauca*) to 50% (*Q. oleoides*) loss of k_{leaf} during the dry season although no evidence of cumulative losses in k_{leaf} were observed in either species suggesting regular repair of embolisms. Leaf longevity in the deciduous species *Rhedera trinervis* is similar to that of *S. glauca*, although maximum k_{leaf} was lower. Furthermore, a decline in leaf water potential at the onset of the dry season led to cumulative losses in k_{leaf} in *R. trinervis* that culminated in leaf shedding.

Keywords Embolism · Leaf hydraulic conductance · Leaf water potential · Phenology · Tropical dry forest

Introduction

Seasonally dry tropical forest trees exhibit a striking range of phenological behaviors (Holbrook et al. 1995;

Reich 1995; Eamus and Prior 2001). Within these highly seasonal forests, one can find species that are leafless for as much as 6 months of the year standing next to ones that retain a full crown of leaves despite the near absence of rainfall for many months (Daubenmire 1972; Opler et al. 1980). Early studies of these forests focused on the distinction between evergreen and deciduous species, with an emphasis on elucidating the physiological and morphological traits associated with these two broad categories (e.g., Reich and Borchert 1984; Sobrado 1986). More recent work has emphasized variation within the deciduous category, a classification which ranges from species that drop all of their leaves at the onset of the dry season, often preceding any significant soil drying, to those that lose leaves slowly throughout the dry season, becoming leafless only after achieving quite negative leaf water potentials. Detailed studies of deciduous species have helped workers to understand how traits such as rooting depth and wood density are associated with patterns of leaf shedding (Nilsen et al. 1990; Olivares and Medina 1992; Borchert 1994a; Sobrado 1997). In contrast, evergreen species have received less attention, despite the fact that this phenological group also exhibits substantial diversity in leaf lifespan and foliar characteristics. This study examines seasonal variation in leaf hydraulic conductance (k_{leaf} ; $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) and water potential of two evergreen tree species with contrasting leaf life spans, and two species with similar leaf longevity but contrasting leaf habit. Our goal is to understand factors associated with leaf longevity and leaf shedding in tropical dry forest trees.

Evergreen species can be distinguished by variation in temporal patterns of leaf production and shedding as well as the longevity of their leaves. Because the evergreen condition describes the maintenance of the canopy as a whole, rather than the longevity of specific cohorts of leaves, it is possible to have evergreen species with leaf life spans that are shorter than co-occurring deciduous species (Cavender-Bares 2000). The two evergreen species contrasted here differ markedly in leaf longevity. *Simarouba glauca* (Simaroubaceae) has leaves that last approximately 35 weeks, similar to the leaf lifespan of many of the

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deciduous species at this site. In contrast, leaves of *Quercus oleoides* (Fagaceae) persist for >60 weeks. Both species produce and shed leaves throughout the year, although leaf production in *S. glauca* tends to be more continual than in *Q. oleoides* where leaf production by any one individual tends to be somewhat episodic.

In seasonally dry forests, leaf shedding in deciduous species coincides with increases in atmospheric demand (vapour pressure deficit) and declining soil moisture availability. Because of the intrinsic sensitivity of xylem to low water potentials, a decrease in the transport capacity of the xylem due to cavitation has been hypothesized to play an important role in leaf shedding in these species (e.g., Borchert 1994b). An earlier study at this site was able to document a decline in the water transport capacity of leaf-bearing branches in some, but not all, deciduous species prior to leaf fall (Brodribb et al. 2002). However, subsequent work suggested that declines in k_{leaf} were closely associated with physiological changes prior to leaf abscission (Brodribb and Holbrook 2003a). It has recently been demonstrated that much (between 30 and 80%) of the hydraulic pressure drop measured in transpiring plants occurs in the leaves (Nardini 2001; Brodribb et al. 2002). This means that the hydraulic conductance of leaves will have a disproportionately large effect on the leaf water potential, and that a decrease in k_{leaf} during rapid transpiration will be translated into a decline in leaf water potential and ultimately stomatal closure (Fredeen and Sage 1999; Brodribb and Holbrook 2003b).

The role of xylem cavitation in the phenology of evergreen species is less clear due to the fact that leaf shedding occurs throughout the year—both during period of abundant soil water resources and high humidity, as well as during the dry season. However, diurnal changes in k_{leaf} during sunny days within the rainy season are reported to occur in one of the species examined here (*S. glauca*; Brodribb and Holbrook 2004), indicating that cavitation is not limited to periods of low water availability. Here we report seasonal changes in k_{leaf} as a function of leaf age in *S. glauca* and *Q. oleoides*, as well as document seasonal patterns in k_{leaf} for the youngest fully expanded leaves. We provide comparative data for *Rhederia trinervis* (Verbenaceae) a common deciduous species at this site, which has a leaf life span approximately equal to that of *S. glauca*.

Materials and methods

Study site

This investigation was conducted in the Santa Rosa National Park, an area of 10,800 ha located on the Northern Pacific coast of Costa Rica (10°52'N, 85°34'W, 285 m above sea level). Mean annual rainfall in the park is 1,528 mm; however, >95% of this falls between the months of May and December, resulting in a pronounced dry season (Janzen 1983; Enquist and Leffler 2001). The dry season is accompanied by strong trade winds, low relative humidity and high irradiance, all of which contribute to

generate a high evaporative demand. Diurnal and seasonal temperature ranges are relatively small, with a mean annual temperature of 28°C. Measurements were made during the period June 2001 to mid May 2002, thus covering a complete cycle from bud break to leaf shedding. Vegetation in the study area comprises a heterogeneous mosaic consisting of various stages of regeneration from former pastures as well as some small areas of primary forest. Evergreen and deciduous species can be found at all successional stages; however, the % cover by evergreen species is greatest in the mature forest, and deciduous species tend to be more dominant in earlier successional stages (Janzen 1983).

Plant material

Three species were examined, two common evergreen tree species; *Quercus oleoides* (Fagaceae) and *Simarouba glauca* (Simaroubiaceae) as well as the dominant deciduous tree; *Rhederia trinervis* (Verbenaceae). The two evergreen trees were selected for their striking differences in leaf character and leaf longevity; *Q. oleoides* produces simple, highly sclerophyllous leaves, while leaves of *S. glauca* are compound and the leaflets relatively soft. *S. glauca* leaves exhibit shorter lifespan than *Q. oleoides* and as a result *S. glauca* tends to flush new leaves at least twice a year whilst *Q. oleoides* generally flushes once only. The deciduous species *R. trinervis* has simple mesophytic leaves that expand after the first rains and are maintained until the end of the wet season, resulting in leaf longevity similar to *S. glauca*. Leaf shedding in *R. trinervis* is not synchronous, with considerable variation between individuals within sites. This species is dominant on early successional sites and does not penetrate late-succession forest. Trees sampled in this study were growing together in vegetation ranging in age from 12 to 40 years since the last major fire event.

Leaf hydraulic conductance

k_{leaf} was measured using an adaptation of the method described by Kolb et al. (1996) for leaves (Nardini et al. 2001). Leaves were cut underwater from sample trees between 1030 hours and 1130 hours and left to soak in water in the light for approximately 1 h to ensure that hydraulic and osmotic gradients in the leaf were in equilibrium with the transfusing liquid (water). Leaves were then attached by the petiole to a plastic tube that led to a reservoir on a computer-interfaced balance. Hydraulic gradients were generated by placing the leaf inside a glass Ehrlenmeyer flask that was evacuated to two vacuum pressures (40 and 80 kPa). Leaves were placed underwater inside the flask to ensure that no evaporative water loss occurred during the measurements. Fluxes from the balance through the leaf were measured at 80, 40, and 0 kPa vacuum pressures and the slope of the linear regression through these data was taken as the mean conductance. To avoid problems with

stomatal closure (Sack et al. 2002) leaves were maintained in the light prior to and during measurement. Leaf area was subsequently determined using a digital camera and image analysis software (Scion Image, NIH) and k_{leaf} expressed in $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$. For each species, one leaf from five adjacent trees was collected for each period, and k_{leaf} expressed as the mean of these five samples.

Leaf pressure volume relations

Five sun-exposed leaves from each species (one leaf from five adjacent trees) were collected 3 months after expansion in July and August (mid wet season) and used for measuring the pressure–volume relations of each species. Leaves were bench dried whilst water potential and leaf mass were measured periodically during dehydration. For each leaf, elastic modulus of turgid leaves was calculated from the initial slope of the relationship between turgor pressure and relative water content (Tyree and Hammel 1972). Leaves were photographed for leaf area determination and dried at 70°C for 5 days in order to calculate dry mass per leaf area.

Effect of leaf age on leaf hydraulics

For determining the effect of leaf age on k_{leaf} 30 buds from five trees of each species were marked. In all species leaves emerge in groups of approximately five such that 30 buds yielded around 150 leaves of known age for each species. A single leaf per tree ($n = 5$ per species) was removed underwater every 5–10 weeks after expansion and returned to the laboratory for determination of k_{leaf} . Leaves were collected at between 0600 hours and 0700 hours to reduce the possibility of midday depression of k_{leaf} by cavitation (Brodribb and Holbrook 2004).

Annual variation in k_{leaf} and leaf water potential

The pattern of variation in leaf water potential and k_{leaf} was measured in a second set of five trees located close to the first. Trees were surveyed once every 5–10 weeks during which time mature leaves were selected for measurement. Although leaf age was not recorded for this set of measurements, the youngest mature leaves were always selected such that readings were taken from the most

photosynthetically active leaf cohort. Two sunlit leaves were collected from each tree ($n = 10$ per species) at pre-dawn and between 1100 hours and 1200 hours for determination of maximum and minimum diurnal leaf water potential. Leaves were placed in tightly sealed plastic bags and returned to the laboratory within 1 h of collection for pressure bomb measurement of leaf water potential. After leaves had been removed for leaf water potential, five leaves (one leaf per tree) were cut underwater for k_{leaf} determination. Leaf water potential data were plotted with data for the vulnerability of each species to leaf xylem cavitation. These leaf vulnerability data come from neighboring trees in the same year at Santa Rosa National Park and are published in Brodribb and Holbrook (2003b).

Results

Leaf characteristics

Leaf mass per area was similar in all species (Table 1); however, there were large differences recorded between the maximum elastic modulus of the three species. *S. glauca* leaves had significantly lower elastic moduli than either other the other two species (ANOVA, $P < 0.05$; Table 1).

Leaf age and k_{leaf}

k_{leaf} increased in all species following the completion of leaf expansion. In the evergreen species, k_{leaf} plateaued within weeks of leaf expansion, while in the deciduous *R. trinervis*, k_{leaf} continued to increase for several months. The two evergreen species exhibited very different patterns of variation in k_{leaf} during the year. Leaves of *Q. oleoides* reached maximum conductances of $16.3 \text{ mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ after 20 weeks, and then maintained k_{leaf} between 13.4 and $16.3 \text{ mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ for as long as 35 weeks. After 45 weeks leaf conductance began to decline and most leaves of *Q. oleoides* were shed 50–60 weeks after expansion. In contrast, *S. glauca* produced highly conductive leaves, k_{leaf} peaking at $31.7 \text{ mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ 4 weeks after expansion, after which k_{leaf} declined rapidly and leaves were shed after 35–45 weeks (Fig. 1). The deciduous species *R. trinervis* exhibited a similar leaf lifespan to the evergreen *S. glauca* although leaves were not as conductive to liquid water (maximum $k_{\text{leaf}} = 17.05 \text{ mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$).

Table 1 Minimum pre-dawn leaf water potential ($n = 5$) for the evergreen species *Simarouba glauca* and *Quercus oleoides* and the associated deciduous tree, *Rhedera trinervis*. Values represent the lowest monthly mean pre-dawn water potential measured throughout the

year. Mean leaf mass per unit area and leaf bulk modulus of elasticity ($n = 5$) are also shown for fully expanded leaves in the mid wet season (months of July and August). All values are mean \pm SD

	Mean minimum pre-dawn leaf water potential (MPa)	Leaf mass per area (g cm^{-2})	Bulk modulus of elasticity (MPa)
<i>Q. oleoides</i> (Evergreen)	-0.81 ± 0.23 (May)	0.018 ± 0.0023	23.8 ± 1.6
<i>S. glauca</i> (Evergreen)	-0.93 ± 0.01 (May)	0.016 ± 0.0014	10.8 ± 1.4
<i>R. trinervis</i> (Deciduous)	-2.59 ± 0.49 (January)	0.017 ± 0.0015	19.0 ± 2.8

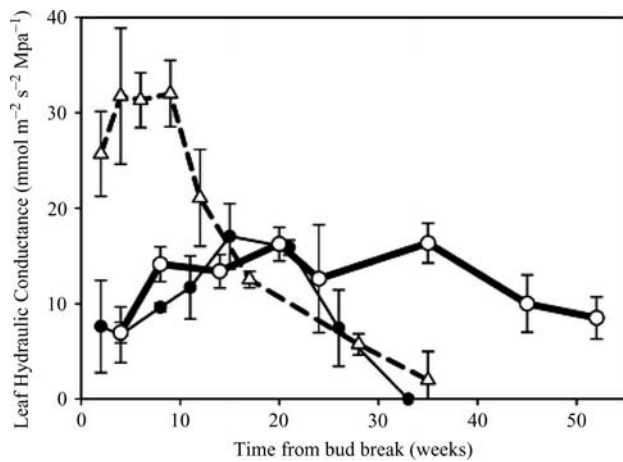


Fig. 1 Patterns of leaf hydraulic conductance from leaf expansion to leaf senescence in two evergreen species; *Simarouba glauca* (triangles), *Quercus oleoides* (open circles), and one deciduous species; *Rhedera trinervis* (filled circles). Data represent mean values from five trees \pm SD

Annual patterns of k_{leaf} and leaf water potential

Annual variation in k_{leaf} measured on the youngest mature leaves and water potential were highly variable between the three species. After the end of the rains in late November, midday leaf water potential in *Q. oleoides* leaves fell from mid wet season values of close to -1 MPa to around -3 MPa by the mid dry season. According to vulnerability curves for *Q. oleoides*, this decline in water potential is predicted to result in between 20 and 50% loss of k_{leaf} by cavitation (Fig. 2). Accordingly it was observed that over the same period k_{leaf} fell from a mean of >15 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ to mean values <10 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ (Fig. 2). The other evergreen, *S. glauca*, showed little variation in midday leaf water potential throughout the year, and even in the mid dry season (March) leaf water potential only fell to a minimum of -1.6 MPa. Based on vulnerability curves for *S. glauca* leaves, at this minimum leaf water potential the loss of hydraulic conductance by cavitation should have been $<20\%$ (Fig. 2). This was reflected in the lack of any strong seasonal trend in the k_{leaf} of *S. glauca*. Monthly mean k_{leaf} fluctuated between a minimum of 21 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ in February to a maximum of 31 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ prior to the commencement of the rains in May (Fig. 2).

Mean midday leaf water potential in the deciduous species *R. trinervis* fell from high values after leaf expansion (June) to within the region of 20–50% xylem cavitation by late September. During this same period k_{leaf} was observed to decrease steadily from 18.6 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ to 9.4 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$. Declining rainfall in late October–November saw leaf water potential fall rapidly to values likely to induce significant loss of leaf conductance by cavitation. During this period k_{leaf} was observed to fall steeply until leaves were finally shed in December–January (Fig. 2). Low pre-dawn leaf water potential during leaf shedding (Table 1) indicated soil drying in the rhizosphere of this species.

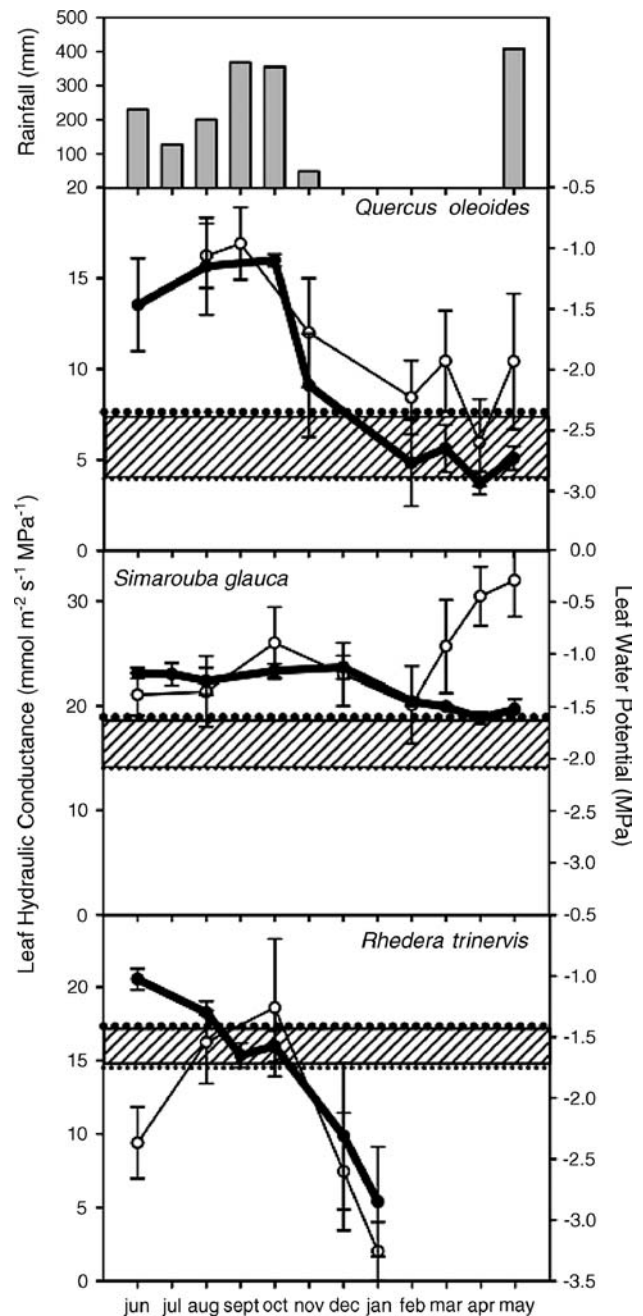


Fig. 2 Annual variation in monthly rainfall (top panel), mean leaf hydraulic conductance of the youngest mature (fully expanded) leaves (open circles, single line), and leaf water potential (filled circles, bold line) in each species ($n=5$). Throughout the year the youngest fully expanded leaves were selected for measurement. Horizontal lines show the mean water potential found to induce 20% (upper bold dotted line) and 50% (lower dotted line) loss of hydraulic conductance in leaves (data from Brodribb and Holbrook 2003b)

Discussion

The two evergreen species studied here showed very different patterns in the seasonal dynamics of k_{leaf} and leaf water potential, highlighting a lack of correspondence between leaf habit and leaf physiology. Leaves of *Q. oleoides* are

hard and relatively long lived. This structural rigidity apparently enables them to sustain low water potentials during the dry season and hence *Q. oleoides* trees are capable of extracting water from soils of low water content. Despite the apparent fortitude of this species it was observed that during the dry season of 2002 leaf water potential consistently fell into the region capable of inducing between 20 and 50% loss of k_{leaf} by cavitation (Fig. 2). The concomitant reduction in k_{leaf} measured during this period supports the case for a loss of conductance by water stress-induced cavitation (Fig. 2). Several studies have recently shown that leaves of several tree species operate close to the point of cavitation (Nardini et al. 2001; Salleo et al. 2001; Brodribb and Holbrook 2003b), and that stomatal closure during water stress is closely tied to cavitation prevention in the xylem. Evidence of midday stomatal closure in *Q. oleoides* has previously been recorded in the form of significant reductions in midday assimilation rate during the dry season (Brodribb et al. 2002) further indicating that *Q. oleoides* endures considerable water stress on account of its evergreen habit.

In contrast, the other evergreen species investigated here, *S. glauca*, exhibits leaf characteristics more reminiscent of the classic deciduous dry forest tree, including a low leaf mass per area, low modulus of elasticity and high vulnerability to cavitation. These leaf traits suggest a reduced capacity for sustaining the large negative water potentials necessary to extract water from dry soils. This was reflected in the fact that mean midday leaf water potential did not fall below -1.6 MPa (c.f. -2.8 MPa in *Q. oleoides*) during the dry season (Fig. 2). However, despite the higher water potential, leaves of *S. glauca* still remained close to the water potential capable of inducing 20% loss of k_{leaf} during the dry season. This was due to the greater vulnerability of *S. glauca* leaves to xylem cavitation compared with those of *Q. oleoides*. Detailed studies of the diurnal course of k_{leaf} in *S. glauca* have shown that regular and reversible midday depression of k_{leaf} is a regular feature of leaf hydraulics in this species (Brodribb and Holbrook 2004). Thus it appears that although leaf characteristics differ between these two evergreens, both endure significant xylem cavitation, although this cavitation may be more profound in *Q. oleoides*.

A smaller potential gradient for water transport from the soil to the leaves of *S. glauca* does not appear to result in lower stomatal conductance and photosynthesis in this species than in *Q. oleoides* (Brodribb et al. 2002). The reason for this is the very high k_{leaf} exhibited by *S. glauca* that apparently compensates for small soil to leaf potential difference. Maximum values of k_{leaf} in *S. glauca* measured here are among the highest recorded for any species, and this high dry season k_{leaf} must play an important role in enabling leaves to remain at moderate leaf water potentials during rapid transpiration. A combination of highly conductive leaf xylem with an extensive, deep root system (as evidenced by the high dry season pre-dawn leaf water potential) and high stem hydraulic conductivity (Brodribb et al. 2002) provides the means by which leaves of *S. glauca* can avoid the soil and atmospheric drought prevalent during the dry season. This (presumably costly) investment in water-conducting tissue enables *S. glauca* to

sustain photosynthetic rates higher than other associated evergreens during the dry season (Brodribb et al. 2002).

The striking difference between the deciduous *R. trinervis* and the evergreen species appears to be related to their ability to access soil moisture during the dry season (Table 1). Following the decline in rainfall at the end of October, mean midday leaf water potential in *R. trinervis* trees fell rapidly to values capable of inducing significant ($>50\%$) losses in k_{leaf} by cavitation (Fig. 2). This apparently led to the observed decline in k_{leaf} that culminated in leaf shedding. Another study has shown that photosynthesis and k_{leaf} declined in parallel during leaf senescence in *R. trinervis* (Brodribb and Holbrook 2003a). Hence we conclude that leaf senescence in this species is associated with cavitation-induced loss of k_{leaf} leading to a depression of photosynthesis. Evidence for cavitation-induced leaf shedding has also been presented for a winter-deciduous species (Salleo et al. 2002), although in this case embolism may have been related to freezing rather than water stress.

Leaf longevity was not a good index of leaf habit. *Q. oleoides* produced leaves that survived for approximately 1 year; however, leaves from the other evergreen species, *S. glauca*, only survived for 35–45 weeks, a longevity similar to that of the deciduous *R. trinervis*. Rather than being related uniquely to longevity, the characterization of these trees as evergreen or deciduous relates to the combined effects of phenology and longevity. *S. glauca* is evergreen because it expands leaves somewhat continuously during both wet and dry seasons such that the frequency of leaf production is higher than the longevity of those leaves. *Q. oleoides* expands leaves less frequently during the year, but its greater leaf longevity ensures that a crown of leaves is maintained throughout the year.

The data presented here illustrate some of the physiological diversity that exists amongst a small sample of tree species in a seasonally dry tropical forest. Curiously, we found that leaf physiology was a poor predictor of leaf habit. Most unusual was the foliage of *S. glauca*, which refutes the classic view that evergreen trees in this type of habitat bear hardy, drought-tolerant foliage. Large differences in k_{leaf} and vulnerability between species enabled *Q. oleoides* to endure large dry season water potential deficits in the leaves, while *S. glauca* was able to largely avoid water deficits induced by seasonal drought. Leaves of the deciduous species *R. trinervis* were physiologically more similar to *Q. oleoides*, but impaired water supply during the dry season due to xylem cavitation and an apparent shallow root system leads to leaf shedding.

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