

## Responses of Tropical Understory Plants to a Severe Drought: Tolerance and Avoidance of Water Stress<sup>1</sup>

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### ABSTRACT

Shade-tolerant understory shrubs and subcanopy trees constitute most of the woody species in Neotropical moist forest, but studies demonstrating physiological differences among these species are few. Shade-tolerant species that coexist in the forest understory exhibit differences in leaf life span that have been associated with variation in physiological traits. We hypothesized that water relations of understory species with widely divergent leaf life spans differ in response to drought. Although severe drought is infrequent in Neotropical moist forest, we studied the water relations of shade-tolerant understory species with short or long leaf life spans during the severe 1991–1992 dry season on Barro Colorado Island, Panama. The predawn leaf water potential declined to  $-2.8$  and  $-3.6$  MPa during the dry season in *Hybanthus prunifolius* and *Psychotria horizontalis*, respectively, two species with short leaf life spans, but remained above  $-1.3$  MPa in two species with long leaf life spans, *Swartzia simplex* and *Ouratea lucens*. The midday leaf water potential dropped as low as  $-3.4$  and  $-4.5$  MPa for *H. prunifolius* and *P. horizontalis*, respectively. The osmotic potential of *H. prunifolius* and *P. horizontalis* and another species with short leaf life span, *Alseis blackiana*, decreased early in the dry season, a period during which all three had substantially negative predawn water potential. In contrast, the osmotic potential of *S. simplex*, *O. lucens*, and *Licania platypus*, a third species with long leaf life span, declined late in the dry season, even though we observed little change in predawn water potential for *S. simplex* and *O. lucens*. We conclude that the variable and potentially severe dry season in Neotropical moist forest can be sufficiently intense to severely limit soil moisture availability for understory plants. *H. prunifolius* and *P. horizontalis* tolerated dehydration, whereas *S. simplex* and *O. lucens* postponed dehydration.

*Key words:* drought; leaf life span; leaf water potential; Panama; pressure–volume curves; tropical moist forest; water relations.

IN NEOTROPICAL MOIST FORESTS, PLANTS EXPERIENCE MODERATE WATER STRESS REGULARLY and severe water deficits every few years, even though soil moisture is abundant throughout most of the year (Robichaux *et al.* 1984). Soil moisture can decrease dramatically during the annual dry season in the tropical moist forest (Becker *et al.* 1988). Understory plants have been observed to experience substantial water stress and even wilt during the dry season (Robichaux *et al.* 1984, Wright 1991).

Even though shade-tolerant shrubs and subcanopy trees constitute most of the woody species in tropical moist forest (Hubbell & Foster 1992), few

studies have examined the physiological differences among these species. Tropical shade-tolerant species differ considerably in physiology, including drought acclimation (Wright *et al.* 1992), light induction of photosynthesis (Kursar & Coley 1993), and a number of other physiological traits (Mulkey *et al.* 1993).

The leaf life span of tropical shade-tolerant species also varies considerably, ranging from nine months to five years (Coley 1981). A long leaf life span has been suggested to improve carbon balance and nutrient-use efficiency, thereby providing an advantage in environments poor in nutrients, light, and water (Chapin 1980, Chabot & Hicks 1982). The variation in leaf life span among tropical tree species has been correlated with leaf physiology and morphology (Reich *et al.* 1991). Additionally, leaf life span has been related to leaf, plant, and stand traits across ecosystems and biomes (Reich *et al.*

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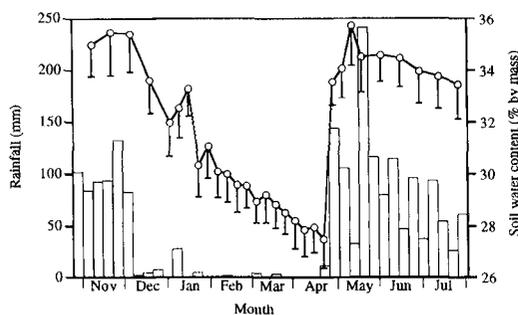


FIGURE 1. Rainfall and soil moisture in a tropical moist forest on Barro Colorado Island for the 1991–1992 study period. The bars represent rainfall and the open circles represent gravimetric soil water content at 30 to 40 cm. Error bars represent SE (data from Smithsonian Environmental Studies Program).

1992). These studies suggest that the leaf life span of a species is only one of a suite of interdependent physiological traits that consistently co-occur. Variation in leaf life span among shade-tolerant species may reflect their physiology and constrain their responses to changes in resource availability in contrasting ways.

We evaluated the response of shade-tolerant understory plants to a severe dry season in a tropical moist forest on Barro Colorado Island (BCI) in Panama. We hypothesized that shade-tolerant species with divergent leaf life spans differ in their response to drought. To test our hypothesis, we compared species with short leaf life spans (1–2 yr) to those having long leaf life spans (3–6 yr). Since we predicted that species with similar leaf life spans would be physiologically convergent, unrelated species were compared to avoid possible phylogenetic constraints on physiology. We evaluated the devel-

opment of water stress through the dry season by monitoring seasonal changes in predawn and mid-day leaf water potential ( $\Psi_L$ ). Acclimation to drought was assessed by measuring changes in leaf water relations through the dry season using the pressure–volume technique.

## MATERIALS AND METHODS

**SITE AND SPECIES.**—The plants monitored in this study occur in the understory of the tropical moist forest on Barro Colorado Island, Republic of Panama (9°9'N, 79°51'W). The island receives an average annual precipitation of 2600 mm and experiences a pronounced dry season from mid-December to April or May (Fig. 1; Windsor 1990). Soil water potentials decline steadily during the dry season, increasing only after heavy rains (Wright 1991), and have been measured as low as  $-2.0$  to  $-2.3$  MPa at a depth of 20 cm in the understory (Becker *et al.* 1988).

The following six shade-tolerant species were chosen for this study because of the large variation in the longevity of their leaves (species after Croat 1978): the shrub *Hybanthus prunifolius* (Schult.) Schultze (Violaceae), the shrub *Psychotria horizontalis* Sw. (Rubiaceae), the tree *Alseis blackiana* Hemsl. (Rubiaceae), the treelet *Swartzia simplex* (Sw.) Spreng. (Caesalpinioideae), the treelet *Oouratea lucens* (H.B.K.) Engler in Mart. (Ochnaceae), and the tree *Licania platypus* (Hemsl.) Fritsch (Chrysobalanaceae). Although leaf life spans vary continuously and do not fall into two clear categories, we grouped species with similar leaf life spans into categories of short or long leaf life span for this study (Table 1).

TABLE 1. Leaf life span category, leaf life span, specific leaf area (SLA), and leaf dry mass:turgid mass ratio for six shade-tolerant plant species. Values of SLA and leaf dry mass:turgid mass ratio are means  $\pm$  SE of five leaves collected during the early dry season.

Species	Leaf life span category	Leaf life span (yr)	SLA (cm <sup>2</sup> /g)	Leaf dry mass:turgid mass ratio (mass/mass)
<i>Hybanthus prunifolius</i>	short	0.8 <sup>a</sup>	308 $\pm$ 13	0.227 $\pm$ 0.004
<i>Psychotria horizontalis</i>	short	<2.0 <sup>b</sup>	231 $\pm$ 8	0.234 $\pm$ 0.008
<i>Alseis blackiana</i>	short	0.8 <sup>c</sup>	350 $\pm$ 16	0.251 $\pm$ 0.003
<i>Swartzia simplex</i>	long	4.0 <sup>d</sup>	157 $\pm$ 13	0.388 $\pm$ 0.013
<i>Oouratea lucens</i>	long	4.7 <sup>d</sup>	123 $\pm$ 5	0.412 $\pm$ 0.020
<i>Licania platypus</i>	long	~3.0 <sup>d</sup>	147 $\pm$ 8	0.359 $\pm$ 0.012

<sup>a</sup> Aide (1989).

<sup>b</sup> C. Sagers (pers. comm.).

<sup>c</sup> Coley (1988).

<sup>d</sup> Kursar and Coley (pers. comm.).

**LEAF WATER RELATIONS.**—Predawn and midday  $\Psi_L$  were determined for four of the six study species during the 1991–1992 study period. All of the plants sampled were 1- to 3-m tall and located in the understory of a level 2-ha area. Individuals with different leaf life spans were sometimes located within a meter of each other. Leaf age was standardized within species by selecting mature leaves at the same distance from the branch tip and having similar epiphyll cover (Coley *et al.* 1993). Sampled leaves were estimated to have completed 40–80 percent of their lifetime. A leaf from each of five replicate plants was sampled at predawn and midday on four measurement dates: 22 November 1991, and 24 February, 16 April, and 3 July 1992. The leaves were placed in a plastic bag immediately after excision. The  $\Psi_L$  was determined in the field with a pressure chamber (PMS Inc., Corvallis, Oregon) and completed within 5 min of excision.

Additionally, predawn and midday  $\Psi_L$  were measured for five individuals of *P. horizontalis* and *O. lucens* on three measurement dates (3 February, 5 March, and 8 April 1993) through the 1992–1993 dry season at two ridge sites. Aluminum foil was placed over the leaf and enclosed in a plastic bag the preceding night to prevent declines in  $\Psi_L$  due to nocturnal stomatal conductance.

**PRESSURE–VOLUME CURVES.**—The water relations of bulk leaf tissue were analyzed with the pressure-chamber technique (Tyree & Jarvis 1982). Leaves of all study species were collected during four census periods: late wet season (November–December), early dry season (February–March), late dry season (April), and early wet season (June–July) in the 1991–1992 study. During each census period, we attempted to complete pressure–volume (P-V) curves for five leaves from different individuals of each species. We applied the same criteria for choosing plants and leaves as those used in sampling for water potential measurements, except that individual plants were different for each census.

Leaves were collected over a 3-h period (1 h apart) beginning at 0530 h. Immediately after excising the leaf, the petiole was recut underwater and sealed inside a plastic bag with the petiole immersed in distilled water for a 3-h rehydration period. During the first census, the petiole was not recut underwater and the collection time of the leaves was not staggered; thus the time of rehydration varied from 3 to 6 h. During the early-dry-season census (second census), two adjacent leaves were collected from each plant. The additional leaf was sealed in a bag immediately after excision and

measurements were begun within 15 min. This procedure allowed a comparison of water relations for rehydrated versus non-rehydrated leaves.

A P-V curve was generated by measuring leaf mass and balance pressure at periodic intervals; the leaf was allowed to dry on the laboratory bench between measurements (Hinckley *et al.* 1980). The mass of the leaf was determined immediately before and after the balance–pressure measurement. The average of these two values was used to calculate relative water content [(fresh mass–dry mass)/(saturated mass–dry mass)]. These measurements were continued until a relative water content of *ca* 0.5 had been reached. The number of points taken after turgor loss was kept to fewer than seven to minimize loss of leaf structural integrity due to repeated pressurization. After measurements had been completed, the leaves were dried at 60°C for 2 to 3 d to determine dry mass.

The saturated mass of each leaf was estimated by extrapolating a plot of fresh mass against balance pressure to zero after excluding plateau points (Kubiske & Abrams 1990, 1991a, b). The estimated saturated mass of non-rehydrated samples was not considered reliable unless the highest balance pressure was >0.4 MPa. For each leaf, we plotted the reciprocal of the balance pressure against the relative water deficit (1–relative water content). The osmotic potential at full turgor ( $\Psi_{\pi}^{100}$ ) was obtained from the y-intercept of a least squares linear regression fit to the linear portion of this plot. The osmotic potential at zero turgor ( $\Psi_{\pi}^z$ ) was derived from the y-coordinate of the turgor loss point. The leaf dry mass:turgid mass ratio was calculated as the dry mass of a leaf divided by its estimated saturated mass. During the early dry season, we collected an additional five leaves of each species and measured the area of each using a leaf area meter (LI-3000 and LI-3050A, LI-COR, Lincoln, Nebraska), determined its dry mass, and used these to calculate specific leaf area (SLA; leaf area/leaf mass).

**STATISTICAL ANALYSIS.**—The analysis of predawn and midday  $\Psi_L$  measured at different sites during the 1992–1993 dry season was treated as a mixed model ANOVA using the JMP statistical package (Version 2.05, SAS Institute, Cary, North Carolina). Site, species, date, and all interactions were treated as fixed effects and repeatedly measured individual plants were treated as random effects. Site, species, and their interaction were tested against individuals nested within site and species. Since measures were repeated on individual plants, we

tested date effects and all interactions with date against the individual plant by date error term.

The analysis of the effect of rehydration on  $\Psi_{\pi}^z$  was treated as a mixed model ANOVA. Leaf life span and rehydration treatment were considered fixed effects. Species was nested within leaf life span, and species and interactions with species were considered random effects. The effect of an individual plant was nested within species, and this plant effect and its interactions were considered random effects. Hypothesis tests were constructed accordingly to account for paired sampling of leaves from individual plants.

The analysis of the water relations parameter  $\Psi_{\pi}^{100}$  was treated as a mixed model nested ANOVA. Date and leaf life span were treated as fixed effects, and species and interactions with species were treated as random effects (Sokal & Rohlf 1981). Hypothesis tests were as shown in Table 3. The fit model contains random effects and unequal cell sizes; thus the denominator in some hypothesis tests was synthesized by making a linear combination of the mean squares of more than one effect (JMP, SAS Institute). The denominator used in the actual hypothesis test may therefore deviate slightly from the approximate one given in Table 3. The denominator degrees of freedom given in the text also deviate slightly from the actual values. In all analyses, we examined the residuals for normality and homoscedasticity and found no need for transformation.

## RESULTS

The understory plant community experienced severe water stress during the 1991–1992 dry season. The dry season was not unusually long, but was one of the driest, and the following wet season was one of the wettest in the last 30 years (Paton 1993). The only substantial amount of rainfall during the dry season occurred in early January (Fig. 1). Soil moisture was partially recharged, but overall gravimetric soil water content declined steadily throughout the dry season (Fig. 1).

**WATER POTENTIAL.**—The predawn and midday  $\Psi_L$  did not differ among species in the late wet season on 22 November (Fig. 2). The similarity among species in midday  $\Psi_L$  was probably the result of constant rain during the  $\Psi_L$  determination. In the early dry season on 24 February, and especially in the late dry season on 16 April, *S. simplex* and *O. lucens* had substantially higher predawn  $\Psi_L$  than *H. prunifolius* and *P. horizontalis*. By the late dry

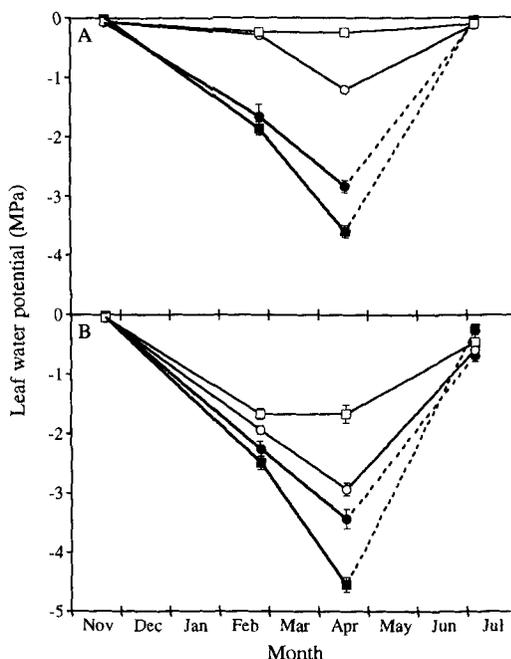


FIGURE 2. Predawn (A) and midday (B) leaf water potential for *O. lucens* (open squares), *S. simplex* (open circles), *H. prunifolius* (closed circles), and *P. horizontalis* (closed squares) for dates in the late wet season, early dry season, late dry season, and early wet season (1991–1992). Open and closed symbols represent species with long and short leaf life spans, respectively. The dashed lines represent leaf turnover. Points are means ( $\pm$ SE) of five observations.

season census, *H. prunifolius* and *P. horizontalis* had a predawn  $\Psi_L$  of  $-2.8$  and  $-3.6$  MPa, respectively, below their turgor loss points. Both predawn and midday  $\Psi_L$  increased in all species during the rainy season and did not differ among species on 3 July. The February predawn  $\Psi_L$  of the two species not included in the seasonal measurements, *A. blackiana* and *L. platyphus*, were  $-1.8$  and  $-0.3$  MPa, respectively, for five haphazardly chosen individuals.

The predawn  $\Psi_L$  for *P. horizontalis* and *O. lucens* at two ridge sites during the relatively mild 1992–1993 dry season showed a pattern similar to the 1991–1992 data, but the magnitude of the changes was smaller (Fig. 3). The seasonal change in  $\Psi_L$  differed between the two species ( $F_{2,28} = 64.30$ ,  $P < 0.0001$ ), with the  $\Psi_L$  of *P. horizontalis* decreasing substantially as the dry season progressed while the  $\Psi_L$  of *O. lucens* remained relatively constant (Fig. 3). The effect of site also differed for the two species ( $F_{2,28} = 10.71$ ,  $P < 0.001$ ). *O. lucens* showed little difference in  $\Psi_L$  be-

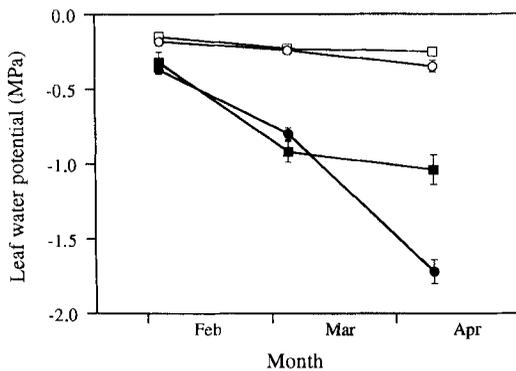


FIGURE 3. Predawn leaf water potential for *O. lucens* (open symbols), a species with a long leaf life span, and *P. horizontalis* (closed symbols), a species with a short leaf life span, for dates in the early, mid, and late dry season (1992–1993). The circle and square symbols represent different sampling sites. Points are means ( $\pm$ SE) of five observations.

tween sites on any date, but *P. horizontalis* had substantially different  $\Psi_L$  ( $-1.0$  and  $-1.7$  MPa) between sites in the late dry season on 8 April (Fig. 3).

**OSMOTIC POTENTIAL.**—Although plant material used for generating P-V curves is rehydrated routinely to allow observations to begin near full turgor, some researchers have found that rehydration can alter parameters derived from P-V curves, thereby masking seasonal change (Kubiske & Abrams 1991a) or response to water deficits (Eamus & Narayan 1990). We evaluated the effect of rehydrating the excised leaves for 3 h on  $\Psi_{\pi}^z$  during the first census period of the dry season. Limited pressure–volume data for non-rehydrated leaves did not allow comparisons of additional parameters. The comparison of  $\Psi_{\pi}^z$  for rehydrated and non-rehydrated leaves was significant across species ( $F_{1,5} = 6.93$ ,  $P < 0.05$ ). Increases in  $\Psi_{\pi}^z$  after

TABLE 3. Analysis of variance for osmotic potential at full turgor ( $\Psi_{\pi}^{100}$ ).

Source of error	Hypothesis test	df	MS	F
A. Date	A/E	3	1.11	26.85**
B. Leaf lifetime	B/C	1	0.34	0.54
C. Species	C/E	3	0.70	17.01**
D. Leaf life span				
× Date	D/E	3	0.24	5.82*
E. Species × Date	E/F	9	0.04	1.41
F. Error		88	0.03	

\*  $P < 0.05$ ; \*\*  $P < 0.001$ .

rehydration ranged from 0.02 to 0.51 MPa (Table 2). The effect of rehydration did not vary among species ( $F_{4,4} = 2.06$ ,  $P > 0.25$ ) or vary between the species with short and long leaf life spans ( $F_{1,3} = 1.10$ ,  $P > 0.35$ ). Although rehydration increased  $\Psi_{\pi}^z$  in leaves, there was no significant difference among species or between leaf life span categories. Such a rehydration-induced increase in  $\Psi_{\pi}^z$  has been observed in other species (Saliendra & Meinzer 1991), and may result from loss of symplastic solutes. Regardless of the origin, we conclude that the rehydration-induced artifacts for our study species were consistent in direction and magnitude and did not distort our analysis.

We were unable to complete P-V curves for all species during the late-dry-season census period (April). *P. horizontalis* leaves partially lost structural integrity, so P-V curves were not possible. Also, the wet season rains began before all April P-V curves had been completed for *H. prunifolius*, *A. blackiana*, and *L. platypus*. The additional P-V curves were completed for all four species, but the  $\Psi_{\pi}^{100}$  values appeared to increase for some species within days of the first substantial precipitation. The  $\Psi_{\pi}^{100}$  values increased for *H. prunifolius* from  $-1.8$  MPa ( $N = 1$ ) before the rain to  $-1.7$  MPa ( $N = 2$ ) and  $-1.5$  MPa ( $N = 2$ ) 5 and 7 d after the

TABLE 2. Osmotic potential at zero turgor ( $\Psi_{\pi}^z$ ) of non-rehydrated and rehydrated leaves excised in pairs from individuals of six shade-tolerant plant species. Values are means  $\pm$  SE of samples collected during the early dry season.

Species	N	$\Psi_{\pi}^z$ (MPa)	
		Non-rehydrated	Rehydrated
<i>Hybanthus prunifolius</i>	7	$-1.87 \pm 0.18$	$-1.74 \pm 0.09$
<i>Psychotria horizontalis</i>	5	$-2.04 \pm 0.08$	$-1.86 \pm 0.04$
<i>Alseis blackiana</i>	5	$-2.55 \pm 0.16$	$-2.04 \pm 0.07$
<i>Swarzizia simplex</i>	5	$-2.12 \pm 0.15$	$-1.88 \pm 0.13$
<i>Ouratea lucens</i>	5	$-1.87 \pm 0.05$	$-1.84 \pm 0.07$
<i>Licania platypus</i>	5	$-1.43 \pm 0.21$	$-1.41 \pm 0.13$

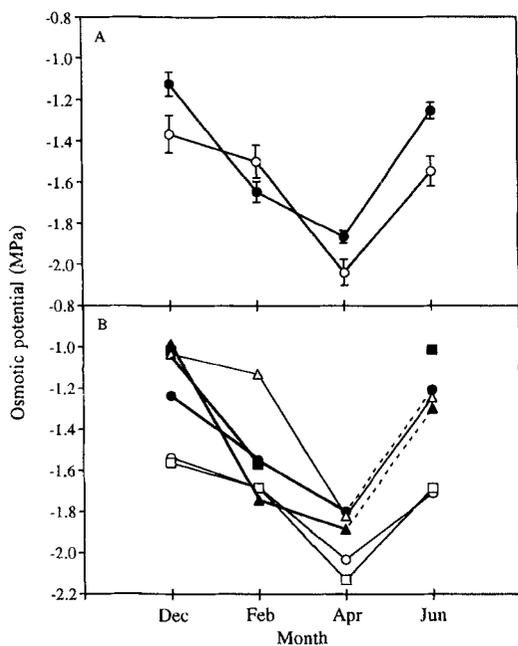


FIGURE 4. (A) Osmotic potential at full turgor for species with long leaf life spans (open circles) and short leaf life spans (closed circles). Points are means ( $\pm$ SE) of three species with long leaf life spans and two with short leaf life spans. (B) Osmotic potential at full turgor for species as in Figure 2 plus *L. platypus* (open triangles) and *A. blackiana* (closed triangles). Open and closed symbols represent species with long and short leaf life spans, respectively. The dashed lines represent leaf turnover. Data points are means of four to six observations except for April, in which  $N = 3$  for *A. blackiana*,  $N = 1$  for *H. prunifolius*, and data for *P. horizontalis* were excluded (see Results). Error bars were not included to improve clarity.

rain, respectively. *L. platypus* went from  $-1.8$  MPa ( $N = 2$ ) before the rain to  $-1.4$  MPa ( $N = 2$ ) 5 d after the rain. The  $\Psi_{\pi}^{100}$  values for *A. blackiana* did not change with rainfall. The  $\Psi_{\pi}^{100}$  values of leaves collected after the first rain were not used in the analysis of seasonal changes in  $\Psi_{\pi}^{100}$ . Although the  $\Psi_{\pi}^{100}$  of samples collected after the rain appeared to increase for some species, these data were consistent with the highly negative values obtained for the species during the late dry season.

The  $\Psi_{\pi}^{100}$  and  $\Psi_{\pi}^z$  followed the same pattern among species and throughout the season; thus only an analysis of  $\Psi_{\pi}^{100}$  is presented. The  $\Psi_{\pi}^{100}$  of the species analyzed decreased significantly during the dry season (Date, Table 3; Fig. 4). The seasonal changes in  $\Psi_{\pi}^{100}$  were significantly different for species grouped by leaf life span (Leaf life span  $\times$  Date, Table 3). The  $\Psi_{\pi}^{100}$  of *H. prunifolius* and *A. blackiana* decreased in the early dry season,

but the  $\Psi_{\pi}^{100}$  of *S. simplex*, *O. lucens*, and *L. platypus* decreased only slightly in the early dry season and then much more in the late dry season (Fig. 4A). The  $\Psi_{\pi}^{100}$  of *P. horizontalis*, excluded from the statistical analysis, decreased in the early dry season, as did those of *H. prunifolius* and *A. blackiana* (Fig. 4B). The seasonal changes in  $\Psi_{\pi}^{100}$  were similar among *S. simplex*, *O. lucens*, and *L. platypus*, even though the  $\Psi_{\pi}^{100}$  was substantially higher in *L. platypus* than the other two species.

## DISCUSSION

The seasonal patterns of predawn  $\Psi_L$  during the 1991–1992 study period suggest that *S. simplex* and *O. lucens*, species with long leaf life spans, experienced water stress later in the dry season than species with short leaf life spans, *H. prunifolius* and *P. horizontalis* (Fig. 2). Differences in predawn  $\Psi_L$  among co-occurring species during drought have been related to rooting depth (Hinckley *et al.* 1981, 1983; Davis & Mooney 1986). Similarly, in a tropical dry forest, the decrease in predawn  $\Psi_L$  of deeper rooted evergreens during the dry season lagged several months behind that of the more shallowly rooted deciduous species (Sobrado & Cuenca 1979, Sobrado 1986). On BCI, greater rooting depth among understory species has been related to maintenance of a higher water potential during the dry season (Rundel & Becker 1987, Wright 1992). *P. horizontalis* and *H. prunifolius* have shallow rooting depths (0.3 and 0.6 m, respectively; Becker & Castillo 1990) and extract moisture from surface soil layers that can develop soil water potentials of  $-2.3$  MPa in the understory during even mild dry seasons on BCI (Becker *et al.* 1988). Our results suggest that *S. simplex* and *O. lucens* have a greater rooting depth, enabling them to maintain a high  $\Psi_L$  as the soil dries out.

During the 1992–1993 dry season, *O. lucens* maintained a high predawn  $\Psi_L$ , while the predawn  $\Psi_L$  of *P. horizontalis* declined steadily (Fig. 3). Although this dry season was less severe, differences in predawn  $\Psi_L$  between *P. horizontalis* and *O. lucens* were apparent at the beginning of March and were substantial by April, late in the dry season. The two populations of *O. lucens* we compared did not show differences in predawn  $\Psi_L$ . In contrast, the two populations of *P. horizontalis* had different predawn  $\Psi_L$  by the end of the dry season (Fig. 3). There may be considerable spatial heterogeneity in the water stress experienced by shallowly rooted species such as *P. horizontalis*.

The seasonal changes in  $\Psi_{\pi}^{100}$  were correlated

with the two categories of leaf life span. The  $\Psi_{\pi}^{100}$  of *H. prunifolius*, *P. horizontalis*, and *A. blackiana* decreased in the early dry season concomitantly with decreases in predawn  $\Psi_L$  (Figs. 2 and 4). The  $\Psi_{\pi}^{100}$  of *S. simplex*, *O. lucens*, and *L. platypus* decreased in the late dry season at a point when the midday  $\Psi_L$  indicated that at least one of these species, *S. simplex*, had experienced substantial midday water stress (Figs. 2 and 4). Substantial decreases in  $\Psi_{\pi}^{100}$  for *O. lucens* between the early and late dry season without major changes in predawn and midday  $\Psi_L$  may be a response to drying roots in the upper soil layers (Davies & Zhang 1991).

The range of changes we observed in  $\Psi_L$  and  $\Psi_{\pi}^{100}$  and the differentiation of these between species with short and long leaf life spans may not be discernable during less severe dry seasons. For example, *P. horizontalis* had a predawn  $\Psi_L$  of  $-3.6$  MPa in April 1992, but did not have a predawn  $\Psi_L$  below  $-1.0$  MPa when measured in February and April 1989 (Wright *et al.* 1992).

Without irrigating plants, it is not possible to differentiate between osmotic adjustment in response to limited soil water availability, atmospheric changes, or one of internal origin (*e.g.*, ontogeny or seasonal endogenous rhythms). Nevertheless, the observed dry season decreases in  $\Psi_{\pi}^{100}$  are likely, in part, a response to water limitations. Irrigation on BCI of five species of understory shrubs in the genus *Psychotria* throughout a mild dry season did not diminish the seasonal decrease in  $\Psi_{\pi}$  relative to control plants (Wright *et al.* 1992). In a study conducted during an earlier dry season, however, one of these species, *Psychotria limonensis*, did have lower  $\Psi_{\pi}$  in nonirrigated plants relative to irrigated plants (Mulkey *et al.* 1991). Decrease in  $\Psi_{\pi}$  due to water limitation also can be inferred for *P. horizontalis*. Individuals growing in sites with lower water availability, as indicated by lower predawn  $\Psi_L$ , had lower  $\Psi_{\pi}^{100}$ , suggesting an osmotic response to greater levels of water stress (Becker *et al.* 1988). Finally, effects of leaf aging alone cannot explain the late-dry-season decrease in  $\Psi_{\pi}^{100}$  of *S. simplex*, *O. lucens*, and *L. platypus*. In these species,  $\Psi_{\pi}^{100}$  rose in the early wet season to pre-dry-season levels in leaves that had been retained through the dry season (Fig. 4). It appears that decreases in  $\Psi_{\pi}$  in response to drought are superimposed onto internal or atmosphere-related changes, and are discernible in understory plants only during severe dry seasons.

The 1991-1992 dry season was severe. In the early dry season, *H. prunifolius* and *P. horizontalis* both had substantially negative predawn  $\Psi_L$  and

lost turgor during midday. In the late dry season, they had a predawn  $\Psi_L$  below their turgor loss point. Only one of the two species that experienced less water stress, *S. simplex*, lost turgor at midday late in the dry season. Thus, although all species returned to pre-dry-season water status when the wet season began in April, *H. prunifolius* and *P. horizontalis* dehydrated during this severe dry season, whereas *S. simplex* and *O. lucens* postponed dehydration.

Drought occurs on BCI with a frequency that suggests understory plants will experience multiple periods of severe water limitation during their lifetimes. Dry seasons with lower than normal rainfall on BCI have been related to El Niño Southern Oscillation (ENSO) events (Windsor 1990). ENSO is an aperiodic, unstable interaction between the Pacific Ocean and the atmosphere that causes widespread climatic perturbations on an interannual 2- to 5-year cycle (Enfield 1992). ENSO has existed over at least the last 5000 years (Enfield 1992), suggesting that the fauna and flora of affected regions may be adapted to patterns of climate produced by ENSO (Nicholls 1992). Water stress associated with severe drought may have major impacts on the local abundance and regional distribution of shrubs and trees in the tropical moist forest (Condit *et al.* 1995). The populations of *H. prunifolius*, *P. horizontalis*, *A. blackiana*, *S. simplex*, and *O. lucens* in a 50-ha upland forest site increased between 1982 and 1985 (Hubbell & Foster 1990), a time period including the most severe drought recorded for BCI (Leigh *et al.* 1990). This suggests that these species have high survivorship through periods of drought, although increased light availability and reduced competition may play important roles in the survival of drought by understory species (Aide & Zimmerman 1990). Although the understory species studied responded differently to drought, they appear to have high survivorship during severe dry seasons.

We hypothesized that shade-tolerant understory species may differ considerably in physiology, even though these species are often lumped into a single group or guild. Our results demonstrate considerable differentiation in drought response among shade-tolerant species with divergent leaf life spans. Specifically, some species avoided water stress while other species tolerated water stress. Although our study species fell into only two groups, an analysis at the community level would likely demonstrate a continuum of responses to drought in shade-tolerant species. Substantial differences among shade-tolerant understory species are a gen-

eral phenomenon, observed in the rates of photosynthetic induction, epiphyll colonization of leaves, survivorship in low light, maximum growth rate, susceptibility to pathogens, and other traits (Augspurger 1984, Hubbell & Foster 1992, Wright *et al.* 1992, Coley *et al.* 1993, Kursar & Coley 1993, Mulkey *et al.* 1993, Kitajima 1994). Overall, these results suggest considerable physiological differentiation among shade-tolerant understory plants in the Neotropical moist forest.

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