

# Plant water relations of selected species in wet and dry tropical lowland forests in Costa Rica

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**Abstract:** The water relations of early and late-successional plant species of pre-montane wet forest and lowland dry forest in Costa Rica were compared during the dry season. Early-successional species had higher stomatal conductances ( $g$ ) than late-successional species at both sites. The same pattern did not hold for plant water potentials ( $\Psi$ ). A wide array of daily patterns of  $\Psi$  and  $g$  was found among species of the same successional status. Midday stomatal closure was found in more than half of the wet forest species and nearly all of the dry forest species examined. Despite the absence of substantial rainfall for several months, all species in the dry forest with expanding leaves at the time of sampling had predawn  $\Psi$  values that were above  $-1.0$  MPa, indicating available sources of soil water.

Early-successional tree species in temperate forests generally have higher stomatal conductances, weaker stomatal control, and are more tolerant of water deficits than late-successional species (Bazzaz, 1979). Bazzaz and Pickett (1980) predicted that the same pattern will also hold for tropical forests because of the similarity between early-successional environments in tropical and temperate forests. These habitats in both regions characteristically have higher irradiances, temperatures, and vapor pressure deficits than the undisturbed forest environment. High stomatal conductances in early-successional habitats permit high rates of carbon assimilation and may decrease leaf temperatures. Likewise, tolerance of water deficits and reduced stomatal control should allow photosynthesis to continue under conditions of high evaporative demand. However, there are few comparisons of the water relations of tropical species with which to test the Bazzaz and Pickett (1980) prediction; the few extant data tend to support it. Whitehead *et al.* (1981) and Grace *et al.* (1982) found that the conductances of two fast growing plantation trees, *Gmelina arborea* Roxb. and *Tectona grandis* L.f. (teak), were very high ( $3 \text{ cm} \cdot \text{s}^{-1}$ ) and sensitive to vapor pressure deficit. Fetcher (1979) compared the water relations of five

tropical tree species at Barro Colorado Island, Panama, and found fairly high conductances and midday stomatal closure linked to vapor pressure deficit in *Cordia alliodora*, a species that colonizes treefall gaps. Oberbauer and Strain (1984) found that early-successional species from Costa Rica had higher conductances than late-successional species when grown under controlled environments.

The objectives of this study were to compare the water relations of early and late-successional species within two lowland tropical forests during the dry season, and to assess the severity of drought stress and the resulting plant responses during the dry season in both forests.

## MATERIAL AND METHODS

The two forests studied, the dry lowland forest of Guanacaste and the pre-montane wet forest of the Sarapiquí region, represent extremes in lowland tropical forest types. The study was conducted at the Palo Verde and La Selva biological stations of the Organization for Tropical Studies. The Palo Verde Station is situated within the COMELCO Ranch, Guanacaste, 40 km south of the Pan American Highway ( $10^{\circ}21'N$ ,  $85^{\circ}22'W$ ). In Guanacaste, the an-

TABLE 1

Mean maximum-stomatal conductance ( $g, cm \cdot s^{-1}$ ) of species at Palo Verde and La Selva  
( $n = 6$ ). SE = standard error

Palo Verde	$g_{max}$	La Selva	$g_{max}$
Gap or Pioneer			
<i>Cordia alliodora</i> **	k 0.39	<i>Cordia alliodora</i>	0.51
<i>Guazuma ulmifolia</i> *	= 0.19	<i>Heliocarpus appendiculatus</i> *	0.28
<i>Pachyptera hymenaea</i> **	= 0.17	<i>Luehea seemanii</i> **	0.42
		<i>Solanum rugosum</i>	0.41
	$\bar{x}$ = 0.25	<i>Cassia fruticosa</i> *	0.41
	SE = 0.07	<i>Hamelia patens</i> **	0.36
			$\bar{x}$ = 0.41
			SE = 0.03
Late Successional			
<i>Capparis indica</i> **	0.22	<i>Pentaclethra macroloba</i>	0.15
<i>Andira inermis</i> *	0.12	<i>Andira inermis</i> *	0.19
<i>Brosimum alicastrum</i> **	0.07	<i>Brosimum alicastrum</i>	0.23
<i>Jacquinia pungens</i> **	0.16		
<i>Petastoma patelliferum</i> **	0.12		$\bar{x}$ = 0.19
<i>Luehea candida</i> **	0.17		SE = 0.02
<i>Randia spinosa</i> *	0.15		
	$\bar{x}$ = 0.14		
	SE = 0.02		

\* Species with maximum  $g$  in the morning

\*\* Species that showed some recovery from midday declines.

annual rainfall of 1,200-1,400 mm is distributed almost entirely in May to November, with frequent hot dry winds during the dry season. Most tree species are dry-season deciduous (Frankie *et al.*, 1974), but some species produce leaves at the peak of the drought (Daubenmire, 1972). The La Selva Station is located in the northern province of Heredia near the confluence of the Rio Puerto Viejo and Río Sarapiquí (10°26'N 84°02'W). The annual rainfall at La Selva (4,000 mm) is distributed fairly evenly throughout the year although a distinct dry season usually occurs from January through May; the predominant trees are evergreen (Frankie *et al.*, 1974). Despite the striking differences between the two sites, approximately 20 tree species, mostly pioneers, inhabit both (G. Hartshorn, personal communication). Three of these species, *Andira inermis*, *Brosimum alicastrum*, and *Cordia alliodora* were measured at both sites.

Xylem pressure potentials ( $\psi$ ) were determined with a pressure chamber. Stomata conductances ( $g$ ) were measured with a diffusion porometer calibrated according to Kanemasu *et al.* (1969). Measurements were made from

15-26 March at Palo Verde and from 28 March to 9 April 1979 at La Selva. One or more daily courses of stomatal conductance and xylem pressure potential were followed for each of the species listed in Table 1. Predawn xylem potentials were measured for additional species not included in the diurnal course studies. Measurements at La Selva were made on saplings in all cases except *Andira inermis*, which is a sub-canopy species. Samples were taken from three or more plants of each species during the diurnal courses for all but two species; in the cases of *Andira inermis* and *Spondias mombin*, only a single individual was measured. Measurements at Palo Verde were made on a single mature individual of each species.

Measurements of irradiance, vapor pressure deficit, and air temperature were made concurrently with plant measurements. Irradiance measurements were made with a light meter calibrated with a quantum sensor (Li-Cor model Li-185, Lincoln, Nebraska). These measurements were intended to characterize the overall light regime and were not intended to measure light levels received by individual leaves. Vapor pressure deficit was

calculated from relative humidity and air temperature measured with a sling psychrometer.

## RESULTS AND DISCUSSION

**Leaf conductance and stomatal closure:** Gap and pioneer species in the wet forest at La Selva had significantly higher ( $p < 0.05$ ) mean maximum stomatal conductances ( $\bar{x} = 0.39 \text{ cm}^2 \text{ s}^{-1}$ , Table 1) than late-successional species ( $\bar{x} = 0.19 \text{ cm}^2 \text{ s}^{-1}$ ) as tested by the Mann-Whitney U-test. This finding is in agreement with Bazzaz's (1979) generalization that early-successional species have higher conductance to water vapor than late-successional species. Because of the different habitats in which early and late-successional species are found, it is possible that the higher conductances found in this study for the early-successional species were a result of physical factors, particularly higher irradiances. However, Oberbauer and Strain (1984) found that early-successional species from La Selva had higher conductances than late-successional species when grown and measured under similar environmental conditions in artificial environments. The same tendency was found in the seasonal dry forest at Palo Verde, but differences were not significant. The open nature of the forest at Palo Verde complicates the comparison because the successional ranks of the species sampled are not as distinct or as well known as at La Selva.

Mean maximum stomatal conductances at both sites were not high, but they were within the range found for other tropical species (Medina *et al.*, 1978; Fetcher, 1979; Oberbauer and Strain, 1984) and for temperate forest trees (Korner *et al.*, 1979). However, they were much lower than those found by Grace *et al.* (1982) for *Gmelina arborea* and *Tectona grandis*. Conductances were significantly higher at La Selva than at Palo Verde, where the evaporative demand was considerably higher. Vapor pressure deficits at Palo Verde ranged from 0.38-5.1 kPa with the daily maximum exceeding 4.0 kPa, whereas at La Selva they ranged from 0 to 2.0 kPa. Air temperatures were also higher at Palo Verde (23.6-39.4 °C versus 22.7-33.1 °C at La Selva).

Plants of most species tested at both sites showed reductions in conductance at midday on clear days. At La Selva, 60% of the species

sampled, including one of the three shade-tolerant species, had maximum conductances between 0800 and 0930 hr solar time (Table 1). Half of those species with morning maxima showed some increase in conductance later in the afternoon following the midday decline. Nearly all of the species sampled at Palo Verde had morning maxima with midday declines from which most showed some recovery later in the day (Table 1). As at La Selva, both early and late-successional species at Palo Verde showed midday stomatal closure. Apparently stomatal closure in response to high evaporative demands is not uncommon in at least saplings of tropical trees.

The three species sampled at both sites, *Brosimum alicastrum* (shade-tolerant evergreen), *Andira inermis* (shade-tolerant evergreen), and *Cordia alliodora* (shade-intolerant deciduous) had lower stomatal conductances at Palo Verde than at La Selva (Fig. 1). Midday stomatal closure occurred in all three species at Palo Verde, but at La Selva *Cordia alliodora* had maximum conductance at midday.

**Plant water potentials:** Predawn water potentials of all species tested at La Selva were near -0.1 MPa indicating an absence of plant water stress due to low soil moisture (Table 2). These measurements included the final days of a two week period without rain. Water potentials frequently did not decline from predawn levels until after 0800 hr, by which time dew-fall on the leaves had evaporated.

The lowest mean minimum (midday) water potentials found were -1.59 MPa for *Cordia alliodora*, -1.57 MPa for *Luehea seemannii*, and -1.55 MPa for *Pentaclethra macroloba*. There was no apparent pattern of segregation of  $\psi$  in terms of successional status.

Predawn  $\psi$  values at Palo Verde differed greatly among species, ranging from -0.24 MPa for *Andira inermis* rooted at the edge of a swamp to -3.05 MPa for *Calycophyllum demissum* (Table 2). Most minimum  $\psi$  values were between -2.0 and -3.0 MPa, and values below -3.5 MPa occurred in *Cordia alliodora*, *Capparis indica*, and *Randia spinosa*. The largest daily ranges of P from predawn to midday were found in *Randia spinosa* (2.75 MPa) and *Jacquinia pungens* (2.62 MPa). Minimum  $\psi$  values were attained between 1200 and 1400 hr.

Of the species in common to the two sites, *Cordia alliodora* had considerably lower  $\psi$  at

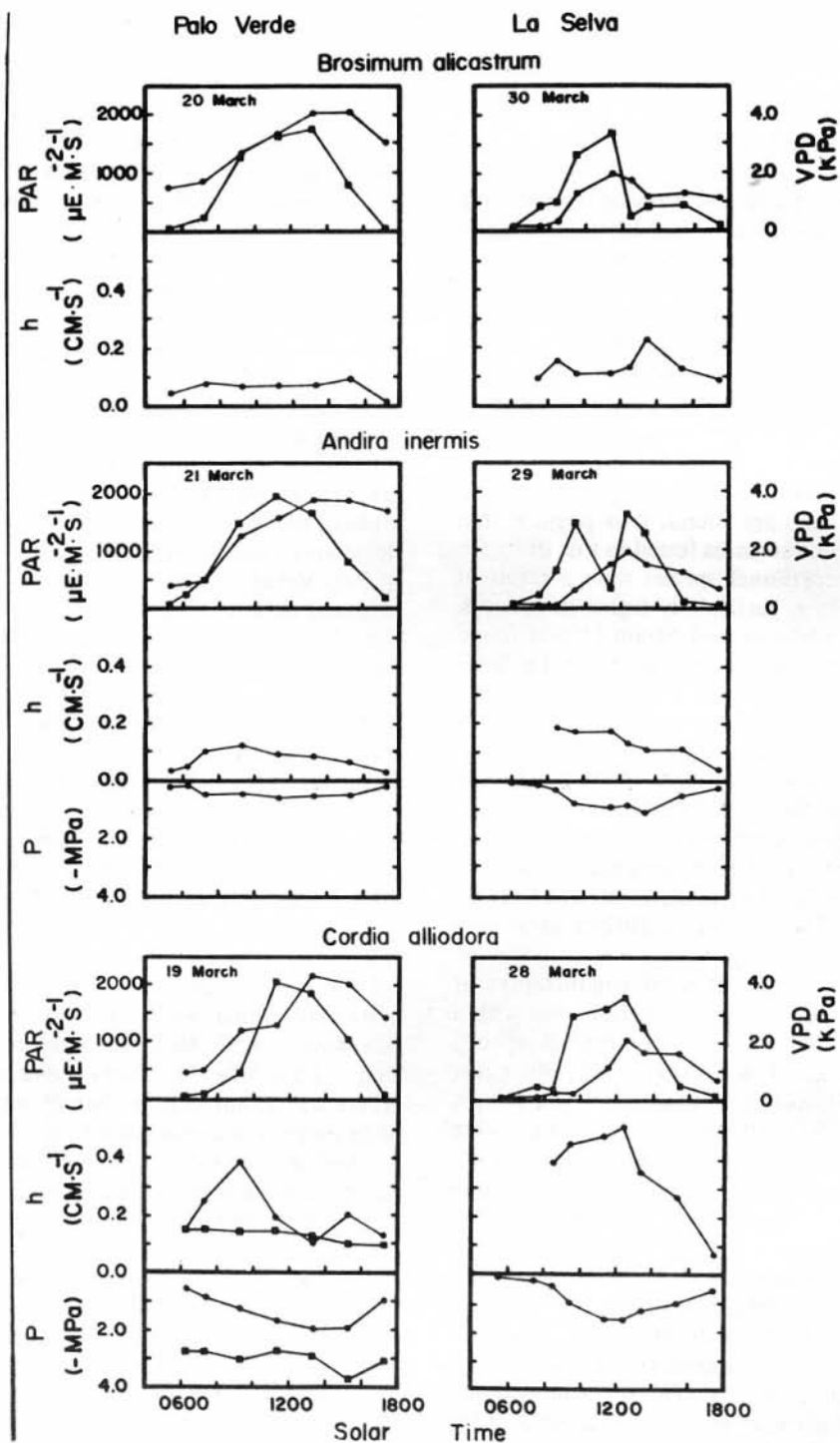


Fig. 1. Daily changes in vapor pressure deficit (VPD, ●), photosynthetic photon flux density (PPFD, ▲), mean stomatal conductance (g, n = 6), and mean xylem pressure potential ( $\psi$ , n = 3) for *Brosimum alicastrum* (water potential not measured), *Andira inermis*, and growing (●) and senescing (▲) *Cordia alliodora* at Palo Verde and La Selva.

TABLE 2

Summary table of mean predawn and minimum water potentials (MPa) and growth status at La Selva and Palo Verde (n = 3). Symbols are: (+) predawn, showing new growth, (-) predawn, showing no new growth, and (x) minimum water potential.

LA SELVA	0	-1.0	-2.0	-3.0	-4.0	Range
<i>Heliocarpus appendiculatus</i> Turcz.	+_____x					0.95
<i>Hamelia patens</i> Jacq.	+_____x					1.17
<i>Cassia fruticosa</i> Mill.	+_____x					1.23
<i>Solanum rugosum</i> Dunal.	+_____x					1.39
<i>Pentaclethra macroloba</i> Willd. Ktze.	+_____x					1.42
<i>Cordia alliodora</i> (R & P) Cham.	+_____x					1.44
<i>Luehea seemannii</i> Triana & Planch.	+_____x					1.46
<i>Spondias mombin</i> L.	.....x					0.60
<i>Andira inermis</i> (Swartz) H. B. K.	.....x					1.04
	$\bar{x} = -0.12$	$\bar{x} = -1.29$			$\bar{x} = 1.19$	
<b>PALO VERDE</b>						
<i>Spondias purpurea</i> L.	+					...
<i>Bursera simaruba</i> (L.) Sarg.	+x					0.01
<i>Luehea candida</i> (DC.) Mart.	+_____x					0.89
<i>Petastoma patelliferum</i>	+_____x					0.99
<i>Cordia alliodora</i> (R & P) Cham.	+_____x					1.39
<i>Pithecelobium saman</i> (Jacq.) Benth.	+_____x					1.50
<i>Lysiloma seemannii</i> Britt. & Rose	+					...
<i>Acacia spadicigera</i> Schlecht & Cham.	+_____x					1.89
<i>Pachyptera hymenaea</i> (DC.) A. Gentry	+_____x					2.01
<i>Randia spinosa</i> (Jacq.) Karst.	+_____x					2.75
<i>Andira inermis</i> (Swartz) H.B.K.	.....x					0.35
<i>Cordia alliodora</i> (R & P) Cham.	.....x					1.00
<i>Guazuma ulmifolia</i> Lam.	.....x					1.39
<i>Capparis indica</i> (L.) Fawc. & Rendle	.....x					2.13
<i>Jacquinia pungens</i> Gay	.....x					2.62
<i>Pithecellobium dulce</i> (Roxb.) Benth.	-					...
<i>Guaiacum sanctum</i> L.	-					...
<i>Calycophyllum candidissimum</i> (Vahl) DC.	-					...
	$\bar{x} = -0.79$		$x = -2.30$		$\bar{x} = 1.46$	

Palo Verde whereas *Andira inermis* had slightly higher  $\psi$  at Palo Verde, probably because of lower stomatal conductances.

The lowest mean predawn  $\psi$  found in a species with active leaf expansion at Palo Verde was  $-0.98$  MPa for *Acacia spadicigera* (Table 2). Some species with expanding leaves had high  $\psi$  values at predawn. For example, trees of *Bursera simaruba* and *Spondias purpurea* with expanding leaves had predawn  $\psi$  values above  $-0.4$  MPa even though there had been no rain-fall in several months (Table 2).

Borchert (1980) and Reich and Borchert (1982) have suggested that the leaf drop and subsequent leaf flush of tropical trees during the dry season result from disequilibria of the water balance within the trees. According to their hypothesis, leaf drop occurs in response to

leaf water stress before all available soil water is depleted. Thus, leafless trees continue to take up water while transpiring very little until plant water potentials are adequate for new leaf expansion. Such a mechanism may explain leaf expansion before the start of the rainy season in species such as *Bursera simaruba* and *Spondias purpurea*, both of which had fairly high water potentials. However, the presence of competitors for moisture, particularly evergreens, may mean that sufficient water will not be available for leaf expansion of some species until after the start of the rainy season.

Large differences in the diurnal responses of  $\psi$  and g were present among the species sampled at both sites. For example at La Selva, *Spondias mombin* and *Heliocarpus appendiculatus*, both shade-intolerant species, had com-

relatively high water potentials. On the other hand, *Cordia alliodora*, also a shade-intolerant species, had the lowest  $\psi$  and the highest conductances. A shade-tolerant species, *Pentalathra macroloba*, had relatively low water potentials and low, constant conductances. A similar situation was found at Palo Verde. Stomatal conductances of *Capparis indica* remained near maximum levels until noon despite  $\psi$  values as low as  $-3.5$  MPa and a diurnal change in  $\psi$  of 2.13 MPa. In contrast, *Randia spinosa* had similar water potentials to those of *Capparis indica*, but conductances declined very early in the day and remained low. A nearby *Luehea candida* had newly expanding leaves, high water potentials, and conductances near maximum levels throughout the day.

### CONCLUSIONS

1. Leaf conductances of early-successional tropical species are higher than those of late-successional tropical species, as predicted by Bazzaz and Pickett (1980).
2. Stomatal closure is common in, but not limited to, early-successional species in the wet forest even in the absence of soil water stress. In the dry forest, stomatal closure at midday occurs in nearly all species that retain or produce leaves during the dry season.
3. There were large differences in the patterns of  $\psi$  and  $g$  among species of the same successional status under the same conditions. A total water-use approach is required to determine the significance of these different patterns of  $\psi$  and  $g$ .

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### RESUMEN

Durante la época seca en Costa Rica (febrero-abril), se midió relaciones hídricas en varias etapas sucesionales de bosques húmedo y seco. En ambos, la conducción estomática es mayor en el bosque secundario que en las etapas posteriores. El potencial hídrico ( $\psi$ ) es variable en

cada estadio. En casi todas las especies del bosque seco, y en más de la mitad de las del bosque húmedo, los estomas se cierran cerca del medio día. En todas las especies con hojas nuevas en el bosque seco, el potencial hídrico superó el  $-1.0$  MPa antes de la madrugada, a pesar de varios meses de poca lluvia. Ello indica la existencia de agua en el suelo.

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