

# Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest

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**Abstract:** We determined seasonal variation in soil matric potentials ( $\psi_{\text{soil}}$ ) along a topographical gradient and with soil depth in a Bolivian tropical dry (1160 mm  $\text{y}^{-1}$  rain) and moist forest (1580 mm  $\text{y}^{-1}$ ). In each forest we analyzed the effect of drought on predawn leaf water potentials ( $\psi_{\text{pd}}$ ) and drought response (midday leaf water potential at a standardized  $\psi_{\text{pd}}$  of  $-0.98$  MPa;  $\psi_{\text{md}}$ ) of saplings of three tree species, varying in shade-tolerance and leaf phenology.  $\psi_{\text{soil}}$  changed during the dry season and most extreme in the dry forest. Crests were drier than slopes and valleys. Dry-forest top soil was drier than deep soil in the dry season, the inverse was found in the wet season. In the moist forest the drought-deciduous species, *Sweetia fruticosa*, occupied dry sites. In the dry forest the short-lived pioneer, *Solanum riparium*, occupied wet sites and the shade-tolerant species, *Acosmium cardenasii* drier sites. Moist-forest species had similar drought response. The dry-forest pioneer showed a larger drought response than the other two species. Heterogeneity in soil water availability and interspecific differences in moisture requirements and drought response suggest great potential for niche differentiation. Species may coexist at different topographical locations, by extracting water from different soil layers and/or by doing so at different moments in time.

**Key Words:** *Acosmium cardenasii*, *Ampelocera ruizii*, Bolivia, drought, leaf water potential, soil depth, soil water availability, *Solanum riparium*, *Sweetia fruticosa*, *Trema micrantha*

## INTRODUCTION

Tropical lowland forests are found under different rainfall regimes. The majority of tropical forests have a pronounced dry season, and, even in perhumid forests, extended periods of drought can occur (Burslem *et al.* 1996, Potts 2003, Walsh & Newbery 1999). Tropical tree diversity and species distribution are to a great extent explained by the amount of annual precipitation, length of the dry period and the cumulative water deficit (Bongers *et al.* 1999, Engelbrecht *et al.* 2007, Gentry 1988, Killeen *et al.* 2007, Poorter *et al.* 2004, Swaine & Becker 1999) and within forests, topographical variation in water availability is an important factor influencing species distribution (Clark 1999, Comita & Engelbrecht 2009, Valencia *et al.* 2004, Webb & Peart 2000).

Topography controls the distribution of water and, through surface run-off or lateral flow, sediments and

solutes are redistributed over the landscape. This affects soil depth, the ground water depth and soil properties (Lavelle & Spain 2002, Sollins 1998). On crests, ridges and steep upper slopes, high sediment removal rates result in shallow soils with a high sand content. Lower slopes and flat valleys, where weathering rates may exceed sediment removal, have deeper soils with higher clay and silt contents (Itoh *et al.* 2003, Johnsson & Stallard 1989, Lescure & Boulet 1985, Pachepsky *et al.* 2001). Resulting differences in soil texture influence plant water availability as fine soils have a higher water retaining capacity than coarse soils (Jenny 1980) and thus soil water availability generally increases down-slope (Becker *et al.* 1988, Daws *et al.* 2002). Furthermore, in valleys or on lower slopes the duration of drought can be shorter than at higher elevations, effectively shortening the dry season in these habitats (Daws *et al.* 2002). This variation in soil water availability with topography can have a strong effect on patterns of seedling emergence and mortality (Daws *et al.* 2005).

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Soil water availability, especially in the dry season, is greater in deep soil layers (Engelbrecht *et al.* 2006, Hodnett *et al.* 1995, Meinzer *et al.* 1999, Stratton *et al.* 2000) and consequently young trees will experience most drought stress as they have limited access to soil water with their relatively short or shallow root systems (Gilbert 2001, Markesteijn & Poorter 2009, Poorter & Hayashida-Oliver 2000). The success of species in occupying different niches with respect to water availability will thus largely depend on their ability to tolerate water stress and compete for water during drought (Engelbrecht & Kursar 2003). Drought-tolerance is codetermined by a suite of functional traits, which include for instance high cavitation resistance (Tyree *et al.* 1994, Zimmermann 1983), strong stomatal control (Jones & Sutherland 1991, Slot & Poorter 2007, Sperry *et al.* 1993) or the maintenance of tissue turgor pressure at low leaf water potentials (Baltzer *et al.* 2008, Engelbrecht & Kursar 2003, Nunes *et al.* 1989). It has been found that their capacity to tolerate low leaf water potentials strongly determines drought survival and distribution of tropical tree species (Engelbrecht *et al.* 2007, Kursar *et al.* 2009).

While water availability is an important environmental factor for species occurrence in and among tropical forests, studies that actually quantify variation in soil water availability in tropical forests are rare (Becker *et al.* 1988, Hodnett *et al.* 1995, Kursar *et al.* 2005, Lescure & Boulet 1985). In this study we addressed this variation in a tropical dry deciduous forest and a tropical moist semi-deciduous forest by examining seasonal changes in soil matric potentials along a topographical gradient and with soil depth. We also investigated the implications of drought on the water status of saplings of tree species by monitoring the relative changes in predawn and midday leaf water potentials throughout the dry season. We hypothesized that (1) the dry season will be longer and more severe in the dry forest than in the moist forest and soil water availability will increase down slope. (2) Soil water availability will increase with soil depth. (3) The water status of tree saplings will track seasonal changes in soil water availability and dry-forest species will tolerate lower leaf water potentials than moist-forest species.

## METHODS

### Study sites

Fieldwork was carried out in a lowland moist and a dry tropical forest in the department of Santa Cruz, Bolivia. Both forests are located at an altitude between 300 and 500 m on the Precambrian Brazilian shield (Cochrane 1973) in the transition between the Amazonian wet forests in the north and the thorn-shrub formations of the Gran Chaco in the south (Jardim *et al.* 2003, Killeen *et al.* 1998). Both forests are long-term research sites of

the Instituto Boliviano de Investigación Forestal (IBIF) and differ considerably in terms of structure, diversity and species composition (Peña-Claros *et al.* unpubl. data).

The moist site (La Chonta; 15°47'S, 62°55'W; 30 km east of Ascension de Guarayos) is classified as a tropical lowland semi-evergreen moist forest and has a mean annual precipitation of 1580 mm with a dry season (<100 mm mo<sup>-1</sup> rainfall) between April and October (meteorological data from 2000–2007 at La Chonta). Monthly potential evapotranspiration exceeds rainfall only in July. The mean annual temperature is 25.3 °C. Soils are fertile inceptisols with a high cation exchange capacity and especially rich in P and Ca (Peña-Claros *et al.* unpubl. data). The forest has a mean stem density of 367 trees ha<sup>-1</sup>, a basal area of 19.3 m<sup>2</sup> ha<sup>-1</sup>, and a species richness of 59 ha<sup>-1</sup> (trees ≥10 cm dbh, Peña-Claros *et al.* 2008). The average canopy height is about 27 m and c. 30% of the canopy species shed their leaves in the dry season. Most common species are *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr. (Moraceae), *Ampelocera ruizii* Klotzsch (Ulmaceae) and *Hirtella triandra* Sw. (Chrysobalanaceae).

The dry site (Inpa; 16°07'S, 61°43'W), classified as a tropical lowland dry deciduous forest, has a mean annual precipitation of 1160 mm and a dry season (<100 mm mo<sup>-1</sup> rainfall) from April to October with a period of 3 mo (June–September) when the potential evapotranspiration exceeds rainfall (meteorological data from 1943–2005 from AASANA for Concepción at 40 km). Mean annual temperature is 24.3 °C. The study area has generally poor soils, classified as oxisols. The forest has a mean stem density of 420 trees ha<sup>-1</sup>, a basal area of 18.3 m<sup>2</sup> ha<sup>-1</sup>, and a species richness of 34 ha<sup>-1</sup> (trees ≥10 cm dbh; Peña-Claros *et al.* unpubl. data). Average canopy height is 20 m and virtually all canopy trees shed their leaves in the dry season. The most dominant species are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Casearia gossypiosperma* Briquet (Flacourtiaceae) and *Caesalpinia pluviosa* DC. (Fabaceae). (For further site description see Peña-Claros *et al.* 2008, Villegas *et al.* 2009.)

### Soil water availability

In both forests soil water availability was assessed along a topographical gradient. Applying a stratified random design, ten valley bottom-, slope- and crest-locations were randomly selected in the landscape. Different sampling points were located at least 50 m from each other. Sampling was conducted in the last week of every month, starting in April 2007, at the end of the wet season, and continuing throughout the dry season until the beginning of the next wet season in November 2007. Within each forest site all soil samples were taken on the same day and sampling on rainy days was avoided. For logistic reasons

there were two days between sampling in the moist and dry forest.

Leaf litter and coarse debris were carefully removed from the soil surface before sampling. Soil samples were taken with a Dutch auger, pooling the first 20 cm of top soil. For logistic reasons only at four of the ten locations per topographical position, soil samples were taken at six different depths, if possible, ranging from 20 to 120 cm. Again every 20 cm of soil was pooled. Sampling at deeper soil layers was often only possible at the valley positions, as the majority of the slope and crest positions had very shallow soils, often not more than 40 cm deep. Samples were sealed into plastic bags and transported to the field station.

Soil water availability was expressed as the soil matric potential ( $\psi_{\text{soil}}$ ). The matric potential of the soil becomes more negative with increasing drought and incorporates both the soil moisture content and the adhesive and cohesive forces in the soil matrix that capture the water between the soil particles (Jenny 1980). Soil matric potentials were determined with the filter paper method (Deka *et al.* 1995, Fawcett & Collis-George 1967). Collected soil samples were loosened, after which half of the sample was placed in a small plastic container, covered by three Whatman no. 42 filter papers (Whatman International Ltd., Kent, UK) and topped with the second half of the sample. Containers were completely filled, firmly pressed, to avoid air pockets, hermetically sealed with duck tape, tagged and stored for at least 7 d. After this incubation period the three filter papers were carefully removed from the soil sample. The middle paper was superficially cleaned of remaining soil particles and immediately weighed with a microbalance (with a 0.001-g precision) to determine its mass. With the dry mass of the filter papers known, the soil matric potential was estimated from the filter paper moisture content (FMC) following the protocol described by Deka *et al.* (1995), in which;

$$\begin{aligned} \text{Log}_{10}(-\psi_p) &= 5.14 - 6.70 \times \text{FMC}, \\ &\text{if } \psi_p < -51.6 \text{ kPa} \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Log}_{10}(-\psi_p) &= 2.38 - 1.31 \times \text{FMC}, \\ &\text{if } \psi_p > -51.6 \text{ kPa} \end{aligned} \quad (2)$$

### Plant water status

To study the effects of continued drought on the water status of juvenile trees we measured the predawn ( $\psi_{\text{pd}}$ ) and midday leaf water potentials ( $\psi_{\text{md}}$ ) of three different species at monthly intervals in both a dry and a moist tropical forest. Tree species were selected at the extremes of the shade- and drought-tolerance continuum: we included a common shade-tolerant species and a common

**Table 1.** Relationship between species-specific midday leaf water potentials and soil matric potentials ( $\psi_{\text{soil}}$ ), and midday and predawn leaf water potentials ( $\psi_{\text{pd}}$ ). Under guild ST = shade tolerant, DD = drought deciduous and SLP = short-lived pioneer. The table shows the linear relations between the midday leaf water potentials, soil matric potentials and predawn leaf water potentials of the five moist- and dry-forest tree species (log-log scale);  $n = 28$  (4 trees  $\times$  7 mo), except for *Sweetia fruticosa* ( $n = 24$ ), as it shed its leaves in August.  $r^2$  and the significance level are given ( $\alpha = 0.05$ );  $^{\text{ns}}$   $P > 0.05$ ,  $^*$   $P < 0.05$ ;  $^{**}$   $P < 0.01$ ;  $^{***}$   $P < 0.001$ . The last column gives the midday leaf water potential ( $\psi_{\text{md}}$ ) of the species at a standardized predawn leaf water potential of  $-0.98$  MPa. Numbers with different letters vary significantly, as determined with pairwise comparisons of the estimated marginal means of  $\psi_{\text{md}}$ .

Species	Guild	$\psi_{\text{soil}}$	$\psi_{\text{pd}}$	$\psi_{\text{md}}$ (MPa)
Moist forest				
<i>Ampelocera ruizii</i>	ST	0.21*	0.41***	-1.83 <b>a</b>
<i>Sweetia fruticosa</i>	DD	0.45***	0.65***	-1.97 <b>a</b>
<i>Trema micrantha</i>	SLP	0.16*	0.28**	-1.67 <b>a</b>
Dry forest				
<i>Acosmium cardenasii</i>	ST	0.13 <sup>ns</sup>	0.78***	-2.92 <b>b</b>
<i>Sweetia fruticosa</i>	DD	0.01 <sup>ns</sup>	0.56***	-3.12 <b>bc</b>
<i>Solanum riparium</i>	SLP	0.16*	0.69***	-3.33 <b>c</b>

short-lived pioneer with an evergreen leaf habit at the sapling stage, and a drought-deciduous species in each forest (Table 1). One species was in common between forests. Leaf water potentials were measured using the pressure bomb technique (Tyree & Hammel 1972). Leaf water potential measurements were taken in the same period as those of the soil water potential. Ten saplings per species (1–1.5 m tall) with fully illuminated crowns were selected along logging roads at similar elevation to standardize the growth environment of the saplings and avoid phenotypic variation in our measurements. Leaf water potentials were measured predawn (c. 5h30) and at midday (c. 14h00) on mature, exposed and fully expanded leaves, showing no signs of pathogen or herbivore damage. Next to each sapling soil samples (0–20 cm) were collected with an auger at midday to assess the soil matric potentials. Soil sampling and estimation of soil matric potentials were performed as described above.

### Data analysis

To improve normality and homoscedasticity of the data, the soil and leaf water potentials were  $\log_{10}$ -transformed ( $y = -\log_{10}(-\psi + 1)$ ). To evaluate how seasonal and topographical variation in soil matric potential varied between forests, we conducted a repeated-measures ANOVA. Soil matric potential was included as the dependent variable, and forest (moist, dry) and topographical position (valley, slope, crest) as independent factors. The values for each month were included as the repeated measure over time ( $n = 7$ ; April–October). The amount of variation explained by the forest, species and time was calculated as the sum of squares of the effect divided by the total sum of squares

**Table 2.** Seasonal and topographical variation in soil water availability of two tropical forests. The table shows the results of an ANOVA with time as a repeated measure, forest and topographical position as independent factors and soil matric potential as the dependent variable. F and P-values of within- and between-subject effects are given, as is  $\eta^2$ , a measure of the total amount of variation explained by the effects.

Effects	Statistics	
	F	$\eta^2$ (%)
<b>Within-Subjects</b>		
Time	61***	45
Time $\times$ Forest	14***	10
Time $\times$ Topography	3**	4.4
Time $\times$ Forest $\times$ Topography	1 <sup>ns</sup>	1.1
<b>Between-Subjects</b>		
Forest	274***	12
Topography	32***	2.8
Forest $\times$ Topography	1 <sup>ns</sup>	0.0

of the model ( $\eta^2 \times 100\%$ ).  $\eta^2$  is equivalent to  $R^2$ . The generally shallow soils at slope and crest positions resulted in missing values from deep soil layers. To avoid an unbalanced design and loss of degrees of freedom only the values for the first 20 cm of top soil were included in this analysis.

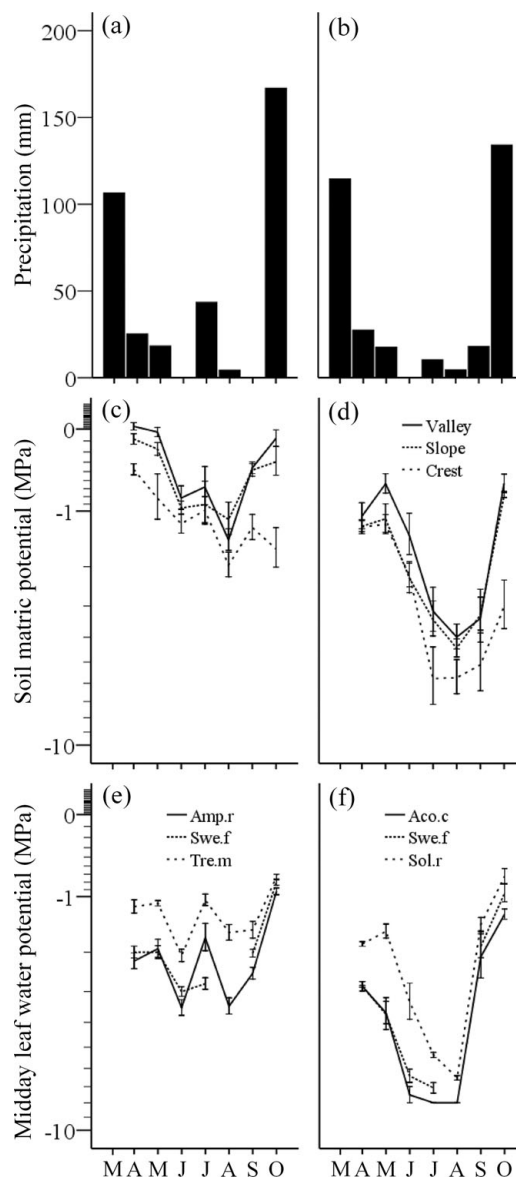
To evaluate how soil water potentials varied with soil depth and how these patterns shift with ongoing drought, a repeated-measures ANOVA was conducted. The model included the observed soil matric potential as the dependent variable, and forest (moist, dry) as the independent factor. This particular model included two repeated measures. As before, 'month' was included as the measure over time, and additionally 'depth' was included as a repeated measure along the soil profile. The analysis was run on the soil matric potential values collected at valley positions only, as the shallow soils at slope and especially crest positions generally prevented sampling deeper than 40–60 cm.

To evaluate how different tree species respond to a given plant water availability a repeated-measures ANCOVA was carried out. Midday leaf water potential was included as the dependent variable with species as independent factor and predawn leaf water potential as a covariable. All statistical analyses were carried out with SPSS 15.0 (SPSS Inc. Chicago, Illinois, USA).

## RESULTS

### Between-forest variation in seasonal and topographical soil water availability

The  $\psi_{\text{soil}}$  showed a clear seasonal pattern of variation, which varied with forest type and topography (Table 2, Figure 1). Time explained 45% of the total variation, the interaction forest  $\times$  time explained 10%, and



**Figure 1.** Seasonal variation in precipitation, soil matric potentials and midday leaf water potentials. The graph shows the precipitation in the moist (a) and dry forest (b). The bars represent the sum of the precipitation of March 2007 and the months covered by this study (April–October 2007) (data from the nearby towns of Ascención de Guarayos (a) and Concepción (b)). The central graphs give the seasonal and topographical variation in soil matric potentials (logarithmic scale) in the moist (c) and dry forest (d) respectively, with different topographical positions represented by the different lines. Valleys are represented by the continuous black lines, slopes by the small dotted lines and crests by the large dotted lines. The lower graphs give the seasonal variation in the mean midday leaf water potential (logarithmic scale) of three moist forest (e) and three dry forest species (f). Amp.r = *Ampelocera Ruizii*; Swe.f = *Sweetia fruticosa*; Tre.m = *Trema micrantha*; Aco.c = *Acosmium cardenasii*; and Sol.r = *Solanum riparium*. Midday leaf water potentials could not be measured for Swe.f in August as the species sheds its leaves in the dry season. Whiskers give the standard error for every month.

topography  $\times$  time 4% of the variation. The three-way interaction was not significant (Table 2).

The first  $\psi_{\text{soil}}$  measurements were taken in April, at the onset of the dry season, when monthly precipitation had first dropped below 100 mm (Figure 1). In April  $\psi_{\text{soil}}$  values were still relatively high in both moist ( $-0.2$  MPa) and dry forest ( $-1.1$  MPa), probably due to residual soil moisture from March, when precipitation was still relatively high ( $> 100$  mm). From April onwards  $\psi_{\text{soil}}$  values declined until reaching their lowest values in August (on average  $-1.4$  MPa in the moist forest vs.  $-4.4$  MPa in the dry forest), at the height of the dry season. In the dry forest  $\psi_{\text{soil}}$  was persistently low in July, August and September. In contrast, in the moist forest  $\psi_{\text{soil}}$  was relatively high in July, probably in response to erratic rainfall in that month (Figure 1). In the moist forest, increased  $\psi_{\text{soil}}$  in September suggested an earlier end of the dry season.

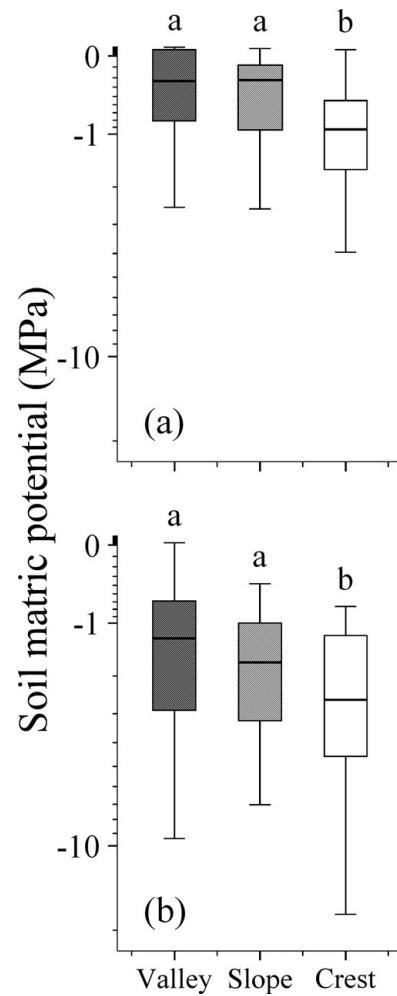
On average,  $\psi_{\text{soil}}$  was lower in the dry forest ( $-2.1$  MPa) than in the moist forest ( $-0.7$  MPa) and varied among valleys ( $-0.9$  MPa), slopes ( $-1.1$  MPa) and crests ( $-1.8$  MPa). In both moist and dry forest, crest positions were significantly drier ( $-1.0$  and  $-2.7$  MPa) than valleys ( $-0.4$  and  $-1.6$  MPa) and slopes ( $-0.5$  and  $-2.0$  MPa) (Figure 2). The variation explained by topography was relatively low, but separate repeated-measures ANOVAs for each forest revealed that the effect of topography was more pronounced in the dry forest ( $F = 17.8$ ,  $df = 2$ ,  $P < 0.001$ ) than in the moist forest ( $F = 15.0$ ,  $df = 2$ ,  $P < 0.001$ ) and accounted for 4.4% versus 1.5% of the within-forest variation.

### Seasonal variation in soil matric potentials with soil depth

At valley positions, soil depth did not significantly affect  $\psi_{\text{soil}}$  over the season, nor did the interaction depth  $\times$  forest (Table 3). Soil depth and time strongly interacted and so

**Table 3.** Seasonal changes in soil water availability with soil depth in two tropical forests. The table shows the results of an ANOVA with time and soil depth as repeated measures, forest as independent factor and soil matric potential as the dependent variable. F and P-values of within- and between-subject effects are given, as is  $\eta^2$ , a measure of the total amount of variation explained by the effects.

Effects	Statistics	
	F	$\eta^2$ (%)
Within-Subjects		
Time	16***	57
Time $\times$ Forest	1.8 <sup>ns</sup>	6.3
Depth	1.2 <sup>ns</sup>	0.3
Depth $\times$ Forest	2.5 <sup>ns</sup>	0.6
Depth $\times$ Time	6.7***	5.3
Depth $\times$ Time $\times$ Forest	4.5***	3.6
Between-Subjects		
Forest	41***	12

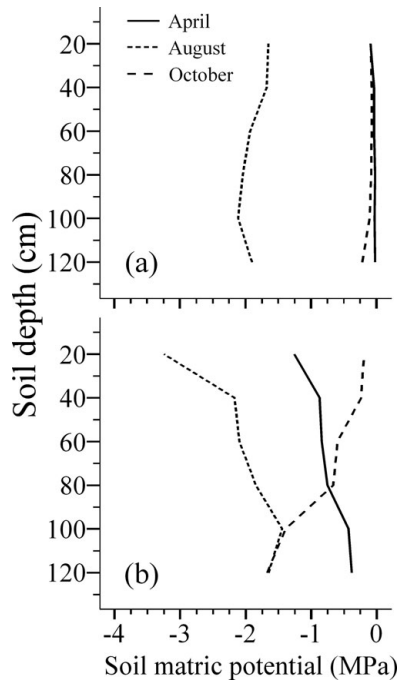


**Figure 2.** Differences in soil matric potentials within forests along a topographical gradient. The graph describes soil matric potentials (logarithmic scale) in the moist (a) and dry forest (b) at different topographical positions; valleys, slopes and crests. The median (black horizontal bar), interquartile range (upper and lower limits of the boxes; 75 and 25 percentile), and the total variation in soil matric potentials are given. Within forests, topographical positions with different letters vary significantly ( $\alpha = 0.05$ ) (Tukey test); \*\*\*  $P < 0.001$ .

did depth, time and forest (Table 3). These results suggest that the pattern of soil matric potential with depth tends to shift from month to month and in different ways in the moist and dry forests (Figure 3).

At the onset of the dry season, in April (Figure 3), soils were still relatively wet and in the dry forest the upper soil layers were drier than the deeper layers (Figure 3b). With progressing drought, the entire soil profile dried out, which resulted in largely similar patterns with depth throughout the dry season, until August (Figure 3). The difference in soil matric potentials between the upper and deeper soil layers slightly increased over time, however, indicating that top soils dried out faster. In October, after the onset of the wet season, the vertical pattern suddenly shifted. Deeper soil layers ended up being





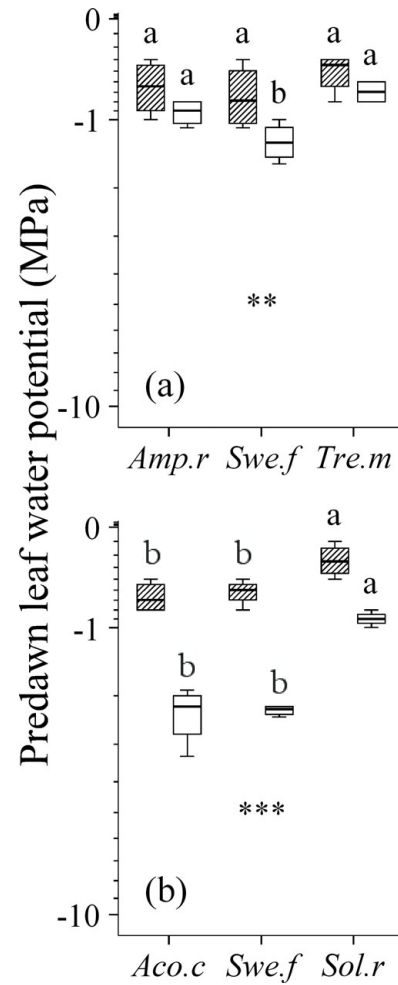
**Figure 3.** Changes in soil matric potential with soil depth in the moist (a) and dry forest (b) spanning the dry season (April, early dry season; August, mid-dry season; and October, first month of the wet season).

much drier than upper soil layers, as it took a considerable amount of time for rain water to percolate down the soil profile.

#### The effect of drought on the water status of juvenile trees

The repeated-measures ANOVA clearly demonstrates a change in  $\psi_{pd}$  through the dry season in both forests and also a significant interaction between time and species (Table 4). This interaction was significant in the moist forest, but not in the dry forest ( $P > 0.05$ ). Seasonal patterns in  $\psi_{pd}$  track the seasonal changes in  $\psi_{soil}$ .

$\psi_{pd}$  differed among species in both the moist (repeated-measures ANOVA:  $F = 10.7$ ,  $df = 2$ ,  $P < 0.01$ ) and the



**Figure 4.** Differences in plant water availability among species within a tropical moist and dry forest. The graph describes predawn leaf water potentials (logarithmic scale) in the moist (a) and dry forest (b) of five different species at the onset of the dry season (April; hatched boxes) and halfway through the dry season (July; white boxes). Amp.r = *Ampelocera ruizii*; Swe.f = *Sweetia fruticosa*; Tre.m = *Trema micrantha*; Aco.c = *Acosmium cardenasii*; and Sol.r = *Solanum riparium*. The median (black horizontal bar), interquartile range (upper and lower limits of the boxes; 75 and 25 percentile), and the total variation in predawn leaf water potentials are given. Within forests and within months, species with different letters vary significantly (ANOVA with post hoc Tukey test); \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

**Table 4.** Seasonal changes in predawn leaf water potentials among moist- and dry-forest tree species. The table shows the results of an ANOVA with time as a repeated measure, species as independent factor and predawn leaf water potential as the dependent variables. F and P-values of within- and between-subject effects are given, as is  $\eta^2$ , a measure of the total amount of variation explained by the effects.

Effects	Statistics	
	F	$\eta^2$ (%)
Within-Subjects		
Time	47***	50
Time $\times$ Species	6***	31
Between-Subjects		
Species	17***	3.5

dry forest (repeated-measures ANOVA:  $F = 36.6$ ,  $df = 2$ ,  $P < 0.001$ ). At the beginning of the dry season all moist-forest species were found on similarly wet soils (Figure 4a), but during the dry season differences among species became more pronounced. Finally the short-lived pioneer species *Trema micrantha*, and the shade-tolerant species *Ampelocera ruizii* were on average found at wetter sites (lower  $\psi_{pd}$ ) than the drought-deciduous species *Sweetia fruticosa* (Figure 4a). In the dry forest this distinction among species was more pronounced (Figure 4b). The short-lived pioneer *Solanum riparium* was continuously found on the wettest soils, while the shade-tolerant species

**Table 5.** One-way ANCOVA showing the effect of species ( $n = 6$ ) on midday leaf water potentials. Predawn leaf water potential ( $\psi_{pd}$ ) was included as covariate. Degrees of freedom, mean squares, F-values, significance levels (\*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ ) and the amount of explained variation ( $\eta^2$ ) of the effects are given.

Effect	df	MS	F	$\eta^2$ (%)
Corrected Model	11	0.45	36.8***	51
Intercept	1	0.80	64.9***	8.1
Species	5	0.01	1.18 <sup>ns</sup>	0.7
$\psi_{pd}$	1	1.85	150***	19
Species $\times$ $\psi_{pd}$	5	0.06	4.98***	3.1

*Acosmium cardenasii* and the deciduous species *Sweetia fruticosa* were found on the driest sites.

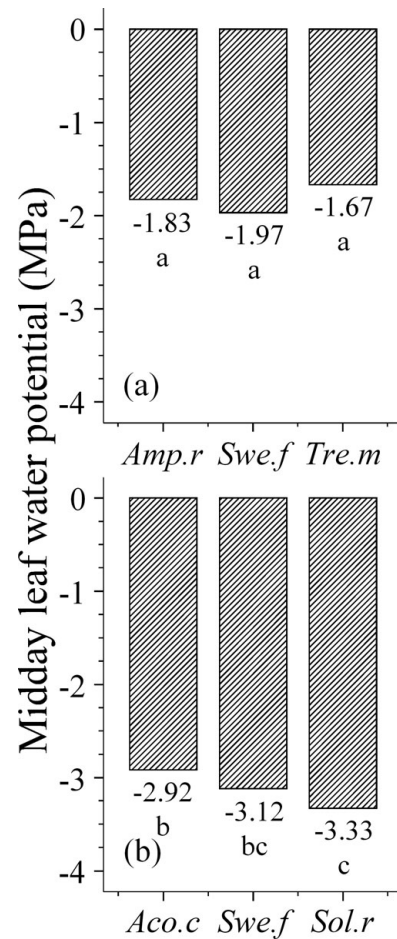
By comparing the  $\psi_{md}$  among species at a common  $\psi_{pd}$ , the drought response of saplings could be assessed. The ANCOVA showed that there was a strong and significant effect of  $\psi_{pd}$  on  $\psi_{md}$ , explaining 19% of the total variation. The interaction effect of  $\psi_{pd}$  with species explained an additional 3% of the variation (Table 5). This indicated that the slopes of the relationship between predawn and midday leaf water potentials were different among species. At the standardized  $\psi_{pd}$  of  $-0.98$  MPa, species differed substantially in  $\psi_{md}$  (Figure 5). Interestingly, *Solanum riparium*, the dry-forest pioneer, that was found in relatively wet micro-habitats in the dry forest, showed the greatest drought response ( $-3.33$  MPa). Among moist-forest species no differences in  $\psi_{md}$  were found, but moist-forest species did have higher  $\psi_{md}$  than the dry-forest species (Figure 5).

## DISCUSSION

### Seasonal and topographical soil water availability

In both moist and dry forest,  $\psi_{soil}$  varied across the dry season and tracked the monthly precipitation. Topography affected  $\psi_{soil}$  similarly at both sites, but the extent to which drought was expressed differed between forests.

In line with our hypothesis, the dry season lasted longer in the dry forest than in the moist forest and during the dry season  $\psi_{soil}$  was consequently lower in the dry forest, indicating that drought was more severe. These marked differences in  $\psi_{soil}$  occurred despite relatively small differences in precipitation between the two forests, which suggests that soil properties have a considerable influence on soil water availability. Preliminary results show that the dry-forest soils had higher clay contents ( $\sim 24\%$ ) than the moist-forest soils ( $\sim 13\%$ ) (Peña-Claros *et al.* unpubl. data), and clay soils have a greater water-retaining capacity, which implies that the matrix potential is lower as well (Jenny 1980, Saxton *et al.* 1986).



**Figure 5.** Among-species differences in midday leaf water potentials (at a standardized predawn leaf water potential of  $-0.98$  MPa). The graph describes midday leaf water potentials (logarithmic scale) of three moist- (a) and dry-forest tree species (b). Among species, different letters indicate significant differences ( $P < 0.001$ ) as resulted from an F-test ( $\alpha = 0.05$ ), based on independent linear pairwise comparisons of standardized species means (with a Bonferroni adjustment for multiple comparisons).

Other abiotic factors may explain some of the  $\psi_{soil}$  differences between forests. In the dry forest almost all dominant canopy trees shed their leaves during the dry season, and while transpiration will be much reduced, the evaporative demand and atmospheric water deficit will be higher in the dry forest. Such high evaporative demand may explain why in August the top soils in the dry forest have such low matric potentials, while deeper soil layers retain more water (Figure 3b). Conversely, in the moist forest the relatively closed canopy can act as a buffer to excessive evaporation and substantially alter the subcanopy microclimate. However, evergreen canopy trees in the moist forest will maintain transpiration during the dry season and will continue extracting water from deeper soil layers. This may explain why in our moist forest changes in soil matric potential with soil depth

are relatively small in August. Continued dry-season transpiration and soil water extraction by evergreen canopy trees may further explain why in moist forests soils in gaps are wetter than those under the closed forest canopy (Veenendaal *et al.* 1996).

Within-forest topography had a clear effect on soil water availability. In line with our hypothesis soil water availability increased down slope with the result that in both forests valleys and slopes were relatively wet compared with crests. This corroborates with the findings of several other studies (Becker *et al.* 1988, Daws *et al.* 2002, Gibbons & Newbery 2003, Ishizuka *et al.* 1998, Lescure & Boulet 1985, Yanagisawa & Fujita 1999), underlining the importance of topography in redistributing soil water over the landscape.

### Seasonal changes in plant water status

Before evaluating the effect that seasonal drought had on the water status of juvenile trees we first assessed how to best express or define water availability to the plant. Plant water availability was measured in two ways; (1) as the soil matric potential (0–20 cm) next to the sapling using the filter paper method (Deka *et al.* 1995), and (2) as the predawn leaf water potential, which reflects the mean soil water potential next to the roots. The midday leaf water potential was measured as an expression of the maximum drought response of the tree at a given soil water potential. Linear regression analyses examined the dependence of the midday leaf water potential on the soil matric potential and the predawn leaf water potential, respectively, and showed that for all species predawn leaf water potentials better explained midday leaf water potentials than soil matric potentials did, especially for dry-forest species. These results indicated that predawn leaf water potentials more closely described the actual plant water availability than the soil matric potential of the topsoil next to the plant.

In line with our hypothesis, temporal variation in  $\psi_{pd}$  closely tracked  $\psi_{soil}$ , and the precipitation. The  $\psi_{pd}$  is a good estimator of the actual water availability to a plant as it expresses the water potential of the soil immediately next to the root at any given moment in time.  $\Psi_{md}$  on the other hand expresses the minimum water potential a plant has to tolerate due to the leaf-level water deficit at a given moment in time (Pockman & Sperry 2000). Although we sampled saplings growing under similar light conditions we found some differences in  $\psi_{pd}$  among species.  $\psi_{pd}$  was similar among moist-forest species, but the dry-forest pioneer *Solanum riparium* had a higher  $\psi_{pd}$  than the other species, both in the wet and the dry season. This indicates that *S. riparium* grew on relatively wet soils in comparison with the other species (Figure 4). Pioneer species are light-demanders that generally realize high growth rates as to

quickly reach a dominant position in the forest canopy after disturbance or gap creation (Whitmore 1989). Pioneer species follow an acquisitive resource strategy and realize high photosynthetic rates with a high stomatal conductivity in order to maximize carbon gain and growth (Ellis *et al.* 2000, Poorter & Bongers 2006). However this comes at the cost of an increased transpirational water loss from the leaf. Especially in dry forests, where evaporative demand is greater than in moist forests and the dry season forms a bottleneck for survival of juvenile trees (Engelbrecht *et al.* 2006), pioneer species will be filtered out of the landscape and persist in relatively wet habitats. In a recent study we addressed such hydraulic habitat partitioning among 40 different dry-forest tree species and our findings suggested that, similar to *S. riparium*, other pioneer species also had greater moisture requirements, and were thus less drought-tolerant, than shade-tolerant species (Markesteijn 2010).

By comparing the  $\psi_{md}$  at a standardized  $\psi_{pd}$  of  $-0.98$  MPa, we were able to evaluate species responses to drought under equal moisture conditions. In line with our hypothesis dry-forest species tolerated lower midday leaf water potentials than moist-forest species. While *S. riparium* grows in relatively wet soils compared with the other two dry-forest species, it also had the lowest standardized  $\psi_{md}$  and thus the greatest drought response. The fact that *S. riparium* showed the greatest drought response even though it occupied relatively wet habitats underlines the drought-intolerant nature of the species. Even with better access to soil water than the other dry-forest species, the leaf-level water deficits, catalysed by high transpiration and low stomatal control, result in a disproportionate decrease of  $\psi_{md}$ . The relatively large potential gradient that is formed between soil and leaf will probably facilitate an increased hydraulic conductivity and promote continued physiological activity in the dry season. We did not actually combine leaf water-status measurements with photosynthesis measurements, and thus it is hard to say whether at the height of the dry season *S. riparium* was still fully active. We observed that saplings of this species showed signs of wilting and a loss of turgor at midday in August, when drought was strongest, which suggests that the species was functioning suboptimally.

The drought-deciduous species *S. fruticosa* had relatively low  $\psi_{pd}$ , in the dry forest and in the moist-forest dry season only. This species can thus grow on relatively dry soils compared with evergreen pioneers such as *T. micrantha* and *S. riparium*. The deciduous leaf habit of *S. fruticosa* allows this by avoiding extreme water stress in the dry season. While leaf shedding differs among species, soil water availability is generally assumed to be the factor controlling it (Olivares & Medina 1992, Reich & Borchert 1984). Nonetheless, *S. fruticosa* was leafless in both forests at the same time rather than at the same soil water potential. For *S. fruticosa* the timing of leaf



shedding is apparently genetically determined or induced by other environmental factors than soil water, such as air humidity and temperature (Wright 1991), leaving little room for phenotypic plasticity.

That *S. fruticosa* was able to grow on relatively dry soil in the moist forest may indicate that it occupies a clear ecological niche in this system. As niche differentiation between the evergreen species *A. ruizii* and *T. micrantha* seems to be governed by light partitioning under wet conditions, *S. fruticosa* can coexist with these species by being the better competitor in drier micro-habitats, where its survival probability is greater. Deciduousness is a major factor enhancing drought survival of tropical tree seedlings from both forests (Poorter & Markesteijn 2008).

Studies tend to find clear patterns of species-habitat associations along topographical gradients in tropical forests (Clark 1999, Comita & Engelbrecht 2009, Valencia *et al.* 2004, Webb & Peart 2000) and, for example, Mediterranean chaparral scrublands (Ackerly *et al.* 2002, Meentemeyer *et al.* 2001). Still in many studies the topographical gradient is only assumed to represent a gradient in soil water availability, without actually quantifying to what extent water availability actually differs among locations. Species-habitat associations in the two forests we addressed here will still have to be investigated, but based on our present results we can at least point out that there is a great potential for habitat differentiation, especially in the dry forest, and that different species may be physiologically or morphologically adapted to compete for water at different positions along the topographical gradient or to acquire water from different soil layers.

Biomass allocation to the roots and species-specific differences in rooting depth will be important for the water status of species, especially in the dry forest, where we found such a steep vertical gradient in soil water availability. Preliminary observations in the field suggested that saplings of *S. riparium* form rather extensive root systems with a lot of lateral branching and seem to exploit a greater volume of soil than the other species. We found this to be typical for seedlings of pioneer species in general (Markesteijn & Poorter 2009). In contrast, seedlings of many shade- and drought-tolerant species were found to forage for water in deeper soil layers (Markesteijn & Poorter 2009). Still, at first sight saplings of *A. cardenasii* and *S. fruticosa* did not clearly show deep rooting (Poorter pers. obs.). In line with our hypothesis and with the findings of several other studies we show that soil water availability in the dry season is greatest in deep soil layers (Hodnett *et al.* 1995, Jackson *et al.* 1995, Meinzer *et al.* 1999, Moreira *et al.* 2000, Stratton *et al.* 2000). None of these studies report this trend to be subject to clear temporal variation, as we do here. Analyses of the stable hydrogen isotope composition of soil and xylem

water showed that coexisting species differ substantially in the depth from which water is extracted (Jackson *et al.* 1995, Meinzer *et al.* 1999, Stratton *et al.* 2000). Temporal variation in soil water with soil depth suggests that deep-rooting species would have an advantage in acquiring water from deeper soil layers in the dry season, while shallow-rooting species may be the first to exploit relatively wet upper soil layers at the start of the wet season (Cao 2000). Shallow rooting may also facilitate in exploiting incident rainfall as was the case in the moist forest in July, when midday leaf water potentials increase back to normal wet-season values.

## Conclusions

In this study we demonstrated that tropical forests and especially dry systems show a great deal of temporal and spatial variation in soil water availability. Temporal variation mainly depends on the annual cycle of precipitation, although many other factors may be of influence. Spatial heterogeneity can be seen as two-dimensional. First of all there is a horizontal component in which soil water availability differs between forests and within forest along a topographical gradient. Secondly spatial variation is manipulated by the vertical redistribution of the water with soil depth. When combining the three dimensions topography, soil depth and time, a very complex mosaic of water availability emerges that shows a great potential for niche partitioning at various levels. In both moist and dry forests, saplings of different tree species were shown to vary in moisture requirement and to respond differently to drought with a progressing dry season. If morphological and physiological adaptations permit species to successfully compete for water at different topographical locations, or to tap their water from different soil layers and/or do so at different moments in time, a great variety of species may be allowed to coexist. Heterogeneity of soil water availability should thus be considered as one of the key processes explaining the high biodiversity of tropical forest in general and seasonally dry forests in particular.

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