Journal of Tropical Ecology (2005) **21**:297–305. Copyright © 2005 Cambridge University Press
doi:10.1017/S0266467405002324 Printed in the United Kingdom

A comparison of methods for determining soil water availability in two sites in Panama with similar rainfall but distinct tree communities

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(*Accepted 22 October 2004*)

Abstract: Plant productivity, distribution and diversity in tropical rain forests correlate with water availability. Water availability is determined by rainfall and also by the available water capacity of the soil. However, while rainfall is recognized as important, linkages between plant distribution and differences among soils in available water capacity have not been demonstrated. One reason for this may be that measurements of soil moisture, such as gravimetric water content, may be overly simplistic. To investigate this, we compared two sites in Panama, Allee and Rio Paja, which have similar rainfall but different plant communities. Soil water release curves were obtained from about −0.1 MPa to −9 MPa, permitting us to calculate available water capacity. The Rio Paja site had 17% greater available water capacity (between −0.1 MPa to −3 MPa), whereas the gravimetric water content at Rio Paja was lower by 16% in rainy season and by 41% at the end of the dry season. Hence soil gravimetric water content and soil available water capacity did not correspond. The results suggest that available water capacity may better predict plant distributions. Hence, whenever possible, available water capacity should be determined in addition to gravimetric water content.

Key Words: distribution, diversity, drought, edaphic, matric potential, Panama, productivity, soil texture

INTRODUCTION

Understanding the mechanisms that determine distribution, abundance and diversity is a major focus of investigation in the ecology of tropical rain forest plants (Givnish 1999, Grubb 1996, Hubbell 2001, Wright 2002). On a global scale, primary productivity, plant distribution and plant diversity are correlated with annual rainfall (Boyer 1982, Francis & Currie 2003, Lieth 1975, O'Brien 1993). Even within the moist and wet tropics, species' distributions and diversity gradients strongly correlate with annual rainfall, with the highest diversity found in wet forests (Bongers *et al.* 1999, Gentry 1988, Veenendaal & Swaine 1998).

Tropical forest plants are exposed to drought periods during which plants experience stress resulting from insufficient soil moisture. Therefore, in addition to total rainfall, the length and strength of the dry season strongly influences plant growth, mortality and habitat associations (Condit 1998, Engelbrecht & Kursar 2003, Nakagawa *et al.* 2000, Veenendaal *et al.* 1995, Walsh & Newbery 1999). An especially important determinant of the severity of the dry season is the amount of water stored in the soil (Brady & Weil 2000, Daws *et al.* 2002, Sollins 1998). For seedlings with shallow roots, this corresponds to the available water capacity of the upper soil layers. Because tropical soils are extremely diverse with respect to both chemical and physical properties, available water capacity should be determined for each soil type. Despite its apparent importance for the ecology of tropical rain forest plants, the role of the water-holding capacity of soils during drought has received little attention. Instead gravimetric water content, or g of water per g dry weight of soil, is reported. Gravimetric water content may not reflect water availability to plants so we compared the two methods at two sites with similar rainfall but different tree communities.

The Isthmus of Panama is an excellent area for investigating the relationship of plant distributions with precipitation and soil properties. Across an approximately 65-km-wide belt of lowland tropical forests along the

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Panama Canal there is substantial variation in rainfall and soils and a corresponding diversity of forest types. For example, Panama City, located on the Pacific side, receives about 1600 mm y^{-1} of rain; Barro Colorado Island, near the centre of the Isthmus, receives about 2600 mm y^{-1} of rain; and Ft. Sherman, on the Caribbean side, receives about 3100 mm y^{-1} of rain. Tree censuses in over 55 plots across the Isthmus of Panama showed that species turnover across the Isthmus (beta diversity) is high when compared with the beta diversity of forests in Ecuador and Peru that have an extremely high community diversity (alpha diversity; Condit *et al.* 2002, 2004; Pyke *et al.* 2001). In the Panama study, changes in community composition were predominantly correlated with rainfall, however, other factors, especially soils and the underlying geology can override the effect of rainfall. In particular, one plot located on the wetter, Caribbean side of Panama is most similar to dry-forest plots. Conversely, two plots located at Rio Paja near the centre of the Isthmus have floras similar to wet forest on the Caribbean side (Pyke *et al.* 2001).

The present study was undertaken to evaluate the relative utility of measuring available water capacity as opposed to making the much simpler measurement of gravimetric water content. We compared soils from two sites, Allee and Rio Paja that are both located near the centre of the Isthmus that differ in their floristic composition although they receive similar rainfall. Allee receives 2600 mm y^{-1} and has forest typical of the centre of the Isthmus. Rio Paja is estimated to receive 2350 mm y^{-1} (about 250 mm less than Allee; Pyke 1999) and, as was noted, has a flora typical of wet forest on the Caribbean side. We can hypothesize that the presence of wet forest species at Rio Paja is due to the fact that the Rio Paja soil has a higher capacity to supply water to plants. A test of this hypothesis requires an accurate determination of water storage by the two soils.

Water storage in soils and water transport to roots directly depend on the number and sizes of soil pores, and the soil water content at a particular soil water (matric) potential (Ψ_m) is determined by the capillary characteristics of the pores (Hamblin 1985). Pore size distribution cannot be determined from gravimetric water content although it often can be estimated from soil texture (i.e. content of clay, silt and sand particles) or organic content; soils with sand-sized particles have large pores and low available water capacity. However, many soils form micro-aggregates (Lal 1987). Even soils with high clay content can, if aggregated, have low available water capacity, although their gravimetric water content is high (El-Swaify 1980). Aggregate size distribution of these soils may not be predicted from soil texture, and pore-size distribution and available water capacity therefore cannot be calculated from soil texture in aggregated soils (Guber *et al.* 2003, Sharma & Uehara 1968). Available water capacity can, however, be determined using soil water release curves (Bruce 1972, Hamblin 1985).

We quantified the available water capacity of the soils at the two sites from soil water release curves for the upper 10 cm of soil. These curves give the decrease in Ψ_m as a function of the decrease in soil water content. Plant available water capacity was quantified as the maximum volumetric water content compared to the volumetric water content at a critical Ψ_m. In the agricultural literature the permanent wilting point, -1.5 MPa, is typically used as the critical Ψ_m. However, many woody species tolerate much lower Ψ_m (Tyree *et al.* 2003). We therefore measured available water capacity to a Ψ_m of -9 MPa.

METHODS

The study was conducted in and near Barro Colorado Island (BCI), a protected area of about 1600 ha in Central Panama (9°9′N, 79°51′W), administered by the Smithsonian Tropical Research Institute. Average annual rainfall is approximately 2600 mm, with a pronounced 4-mo dry season from about late December through the end of April (Windsor 1990). A complete ecological description of the site and its vegetation can be found in Leigh *et al.* (1996) and Croat (1978). We used two study sites, Allee and Rio Paja, both with second-growth forest about 60 y old. The Allee site is located on the east side of BCI near Allee Creek; the Rio Paja site is located about 10 km south of BCI. The soils have not been mapped and characterized in detail (see Dietrich *et al.* 1982 and Johnsson & Stallard 1989 for general descriptions) but are well aerated and not subject to flooding (Kursar *et al.* 1995). Based upon the current soil map for BCI, the Allee study site is a yellow-brown Alfisol (Yavitt 2000). The Rio Paja soil is grey-white, and no soil studies have been conducted there.

Five soil samples at each site were collected at the height of the wet season to obtain the maximum natural soil water content or field capacity. The samples were obtained along Fausto Trail markers 0 to 2 on 28 October 2001 for Allee, and from the centre and corners of plot m26 (Pyke *et al.* 2001) on 25 November 2001 for Rio Paja. After removing the litter, samples were collected from 0–10 cm using a 9-cm-diameter soil corer, taking care not to compress the sides of the hole. Volume, for calculating soil bulk density, was measured by filling the hole with water (in a thin-walled plastic bag) or with sand. Water or sand volumes were determined in a 1000-ml graduated cylinder.

In the field, fresh soil samples, having minimal disturbance, were set aside for moisture release measurements. The soil, 40–60 g wet weight, was carefully placed

in each of five chambers and these were transported to the laboratory on foam. The chambers (63 mm in diameter, by 30 mm high) were machined from brass and electroplated with nickel to minimize water adsorption. In the laboratory, rocks and roots were separated and weighed along with the remaining soil sample. Root and rock volume were 1–5% of total volume. The soils were then dried to constant weight at 105 °C, and gravimetric and volumetric water content calculated. Soil water contents at the end of one of the driest dry seasons on record (S. Paton, *pers. comm.*) were measured at the same sites in March 2003.

To obtain moisture release curves, soil weights and water potentials were measured as the soil dried (Townend *et al.* 2001). The chambers were weighed to 0.1 mg and Ψ_m was measured psychrometrically (Bristow *et al.* 1984, Riggle & Slack 1980). The chambers were connected to Peltier-type psychrometers (leaf-cutter psychrometers, Merrill Instruments, Logan, UT). The psychrometers were equilibrated in an insulated water bath at room temperature for 5 h and then Ψ_m was measured by the psychrometric mode using an automated multi-channel micro-voltmeter (Model CR7, Campbell Scientific, Logan, UT). The CR7 made water potential measurements every 15 min with 15-s thermocouple cooling currents and stable readings were usually achieved in 3 h and always within 5 h. A final set of readings used a longer, 45-s, cooling time, permitting more accurate readings when Ψ_m was less than -3 MPa. The first point of the psychrometric response curve was used in all analyses. For samples with Ψ_m higher than -1.0 MPa, we used calibrations with NaCl at -0.234, -0.462 and -0.915 MPa. For lower Ψ_m readings, we used five calibration points from -0.462 MPa to -7.134 MPa. We also checked the sensor response using a -8.7 MPa standard and only used sensors that were within ± 0.5 MPa of the value predicted by the calibration. After Ψ_m was measured, the sample was allowed to dry at room temperature for about 19 h, weighed and Ψ_m was remeasured. Initially we weighed the chamber immediately before and after Ψ_m was measured; we found changes on the order of only 0.05% of the water content and discontinued the second measurement. The measurement cycles were repeated until Ψ_m was too low to measure with our system. The samples were then dried to constant weight, and water content calculated for each measurement interval. Soil gravimetric water contents were converted to soil volumetric water content, ml water (ml soil)$^{-1}$ or θ, using the soil bulk density.

Results were fitted to equation (1):

$$\Psi_m = \Psi_s(\theta/\theta_s)^{-b}$$

where Ψ_m is the measured soil water potential in MPa, θ is the measured volumetric water content, Ψ_s is the 'saturation' soil water potential in MPa (also termed 'air-entry potential'), θ_s is the volumetric water content at the maximum natural soil water content (field capacity) and b is an empirical, dimensionless parameter (Cosby *et al.* 1984). The magnitude of b is inversely related to the average pore size (Cosby *et al.* 1984). Values for Ψ_s and b were obtained from a linear regression of log Ψ_m as a function of log (θ/θ_s). Available water capacity was calculated as the difference between soil volumetric water content at field capacity and volumetric water content at various soil water potentials.

Soil pH, organic matter, CEC (cation exchange capacity), nutrients and texture were analysed from dried soil samples at the Utah State University Analytical Labs, Logan, UT on three samples from each site. Elemental analysis was carried out by inductively coupled plasma emission spectroscopy after the soil was digested by concentrated HNO_3 followed by 30% H_2O_2 (Edgell 1988). For CEC, exchangeable cations were displaced from the soil with 1 N ammonium acetate and the solution analysed for Ca^{2+}, Mg^{2+}, K^+ and Na^+ (Thomas 1982).

RESULTS

Soil bulk density did not differ between sites (Table 1). The low bulk densities of 0.812 and 0.767 Mg m^{-3} correspond to 69–71% of the soil volume occupied by pore space (assuming a mineral density of 2.6 Mg m^{-3}). In contrast, soil texture, as well as several hydraulic and chemical soil characteristics did vary. Allee was a loam or clay-loam and Rio Paja a silt-loam (Table 2). The maximum soil water content was higher at Allee than in Rio Paja.

To obtain soil moisture release curves, the data were fitted to Eqn (1) (see Methods) as well as to a four-parameter equation (van Genuchten 1980), two-parameter logarithmic and power functions (Williams *et al.* 1983), and the four-parameter Brooks and Corey equation (Saxton *et al.* 1986). Eqn (1) gave the best fit and we present only those results.

Soil moisture release curves for the two soils also differed (Figure 1). At all values of Ψ_m, the Allee soil always had more water than the Rio Paja soil by 0.11–0.17 ml water (ml soil)$^{-1}$. In contrast, available water capacity was higher for Rio Paja than Allee. For example, from maximum water content to -1.5 MPa the soils lost 0.248 and 0.290 ml ml^{-1} for Allee and Rio Paja, respectively (Table 1). Thus, in this water potential range, the Rio Paja soil has a 17% higher available water capacity than the Allee soil.

The volumetric water content of samples collected near the end of the 2003 dry season, one of the driest recorded, were 0.279 ml ml^{-1} for Allee and 0.155 ml ml^{-1} for Rio Paja. Using the regression from the soil water release curve, this was equivalent to water potentials

Table 1. Soil structural and water-content parameters from fresh soil samples and soil moisture release curves. All volumetric data were calculated using the average bulk density for five samples. P values are for comparisons of Allee and Rio Paja by t-test (five samples per site). NS = not significant. Units for gravimetric and volumetric data are g water (g soil)$^{-1}$ and ml water (ml soil)$^{-1}$, respectively.

	Allee mean ± 1 SE	Rio Paja mean ± 1 SE	P t-test
Bulk density (Mg m^{-3})	0.812 ± 0.043	0.767 ± 0.063	0.57
Maximum gravimetric soil water content[1]	0.669 ± 0.013	0.563 ± 0.032	< 0.05
Volumetric soil water content at maximum water content[1]	0.543 ± 0.010	0.432 ± 0.024	< 0.005
− 0.3 MPa[2]	0.401 ± 0.014	0.237 ± 0.006	< 0.0001
− 0.3 MPa[3]	0.404	0.239	
− 1.5 MPa[2]	0.296 ± 0.012	0.144 ± 0.007	< 0.0001
− 1.5 MPa[3]	0.295	0.142	
− 3.0 MPa[2]	0.260 ± 0.012	0.117 ± 0.007	< 0.0001
− 3.0 MPa[3]	0.258	0.113	
− 6.0 MPa[2]	0.228 ± 0.012	0.094 ± 0.007	< 0.0001
− 6.0 MPa[3]	0.225	0.091	
− 9.0 MPa[2]	0.211 ± 0.012	0.083 ± 0.007	< 0.0001
− 9.0 MPa[3]	0.208	0.080	
Volumetric available water capacity: maximum water content to			
− 0.3 MPa[3]	0.139	0.193	
− 1.5 MPa[3]	0.248	0.290	
− 3.0 MPa[3]	0.285	0.319	
− 6.0 MPa[3]	0.318	0.341	
− 9.0 MPa[3]	0.335	0.352	
Ψ_s from regression with Eqn (1)(MPa)[2]	− 0.069 ± 0.0085	− 0.064 ± 0.017	0.80
b from regression with Eqn (1)[2]	5.39 ± 0.364	3.30 ± 0.258	< 0.005
b from texture (Cosby *et al.* 1984)	8.17	5.33	
End of dry season			
gravimetric water content	0.343 ± 0.010	0.202 + 0.006	< 0.0001
volumetric water content	0.279	0.155	
Ψ_m (MPa)[4]	− 2.02	− 1.14	
volumetric water loss [5]	0.264	0.277	

[1] Equivalent to field capacity. Calculated from the gravimetric water content of five bulk samples (about 1–1.6 kg of soil) and the average bulk density.
[2] Averages from the five individual water retention curves from each site.
[3] Calculated from Eqn (1) using $b = 5.11$ and $\Psi_s = -0.066$ MPa for Allee and $b = 3.10$ and $\Psi_s = -0.048$ MPa for Rio Paja. Each set of b and Ψ_s values was obtained from a single regression which included the data from all five chambers.
[4] Calculated from Eqn (1) using end of the dry season value for θ, the volumetric water content, and the values for b and Ψ_s that were obtained from regression with Eqn (1).
[5] Calculated as maximum volumetric water content minus the end-of-dry-season volumetric water content.

of − 2.02 MPa and − 1.14 MPa for Allee and Rio Paja, respectively. Thus, soil water potentials were higher at Rio Paja at the end of the dry season, while soils at both sites had lost about the same amount of water, 0.264 and 0.277 ml ml^{-1} at Allee and Rio Paja, respectively (Table 1).

The values Ψ_s and b were obtained from the soil water release data by regression from Eqn (1). Five regressions were made per site and the average determined (Table 1). The values for the dimensionless parameter b were 3.3 for Rio Paja and 5.4 for Allee (Table 1). Including all of the data in a single regression (Figure 1a), gave b values of 3.1 and 5.1 for Rio Paja and Allee, respectively. Since the magnitude of b is inversely related to the average pore size (Cosby *et al.* 1984), the lower b values for Rio Paja indicate larger pores than the Allee soil. In contrast, had the values for b been estimated from soil texture (Cosby *et al.* 1984), much higher values would have been obtained, 5.3 for Rio Paja and 8.2 for Allee.

Rio Paja soils were quite acid, pH 4.1, and had substantially lower P, cation exchange capacity, Fe, Mg and Al than the Allee soil (Table 2).

DISCUSSION

Despite similar rainfall regimes, forest species composition differed between our two study sites, with one site, Rio Paja, representing species typical of much wetter sites. Because the species differences may be influenced by rhizosphere water availability, accurate determination of

Table 2. Soil nutrient and texture parameters obtained from dried soil samples. CEC – cation exchange capacity. Data are averages ± SE. P values are for t-tests.

Chemical	Allee	Rio Paja	P
pH	5.7 ± 0.6	4.1 ± 0.2	0.06
Organic matter (%)	5.6 ± 1.7	7.6 ± 0.2	0.32
P (%)	0.025 ± 0.006	0.006 ± 0.0003	0.03
N[1] (%)	0.29 ± 0.06	0.26 ± 0.01	0.61
CEC (meq (100 g)$^{-1}$)	57.4 ± 4.6	12.3 ± 0.2	< 0.001
K (%)	0.13 ± 0.02	nd[2]	
Mg (%)	1.00 ± 0.14	0.02 ± .006	< 0.005
Ca (%)	0.35 ± 0.03	< 0.02[3]	
Fe (g Kg^{-1})	57.7 ± 3.0	4.5 ± 0.3	< 0.0001
Al (g Kg^{-1})	47.8 ± 4.3	15.2 ± 1	< 0.005
Soil texture			
Sand (%)	37 ± 3.4	6.7 ± 0.3	
Silt (%)	36.3 ± 1.2	71.7 ± 0.9	
Clay (%)	26.7 ± 2.7	21.7 ± 0.9	
Texture	loam to clay loam	silt loam	

[1] total Kjeldhal nitrogen.
[2] not detected. Detection limit = 0.01%.
[3] not detected in two samples 0.02% in one sample. Detection limit = 0.01%.

this parameter is important. We found that at Rio Paja the available water capacities to − 1.5 and to − 3.0 MPa, 0.290 and 0.319 ml ml^{-1}, respectively, were 12–17% higher than at Allee, 0.248 and 0.285 ml ml^{-1}, respectively (Table 1). Also, soil water potential at the end of a severe dry season was much higher at Rio Paja than at Allee (− 1.1 and − 2.0 MPa, respectively), although both sites had lost about the same amount of water. Our results therefore strongly suggest that moisture availability is indeed more favourable to plants at Rio Paja. This may allow for the establishment and survival of drought-sensitive species typical of forests with considerably higher rainfall, and may thus underlie the formation of a community with a species composition typical of much wetter forests within a matrix of the 'typical' moist semi-deciduous forest. In addition to water, soils supply plants with nutrients. Our results indicate that the Rio Paja soil has a lower pH, lower cation exchange capacity, as well as lower P and other nutrients. Because sites with higher precipitation also have lower nutrients (Sanchez 1976), chemical differences also may explain the higher proportion of wet forest species at Rio Paja. Hence our data cannot determine the relative importance of water and nutrients for species composition in the two forests.

We compared the Allee and Rio Paja soil moisture release curves to published (gravimetric) soil water release curves for tropical forest soils from 0 to − 1.5 MPa, as well as to curves for 'standard' sand, loam and clay (Figure 2a). This comparison illustrates the striking diversity in the hydraulic properties of tropical soils: the range of available water capacities, as well as the range of water contents, at any given water potential is larger for the relatively few tropical soils for which such data are available, than for the whole range from 'typical' sand to clay. Also notable is that almost all of the tropical forest soils reach much lower water potentials at higher water contents than most other soils. Reports of high water *contents* of tropical soils may therefore give the misleading impression of high water potentials, allowing

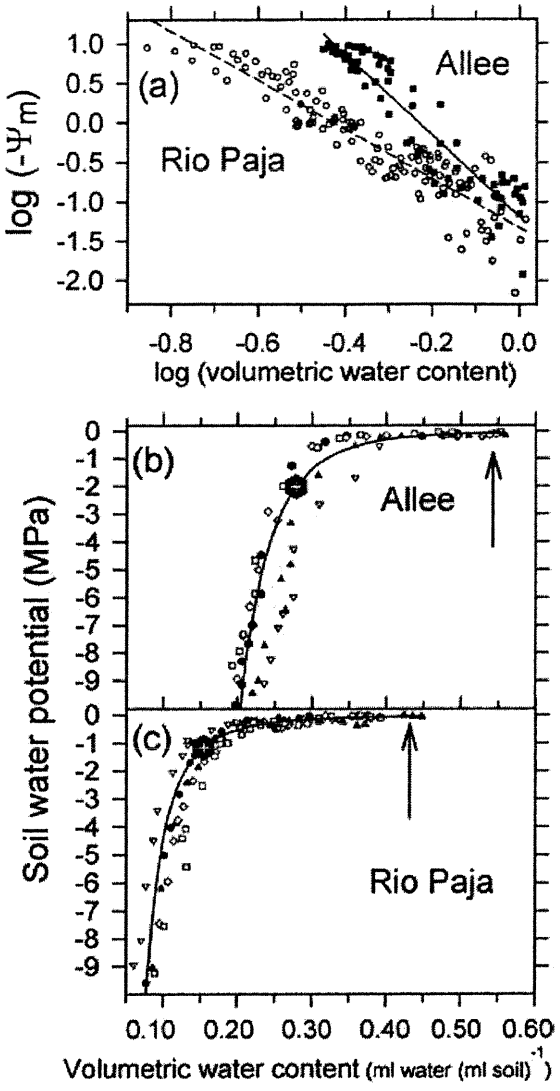

Figure 1. Soil moisture release curves (volumetric) for Allee and Rio Paja. (a) Log (− Ψ_m) as a function of log (θ). Raw data and the regression used to obtain Ψ_s and b (Table 1) are presented. (b,c) Ψ_m as a function of θ. The curves are from Eqn (1), using Ψ_s and b obtained in part (a) above. For each site, the average bulk density (n = 5 measurements per site) was used to convert gravimetric data to volumetric. Hexagons indicate the observed water content at the end of the 2003 dry season. Arrows indicate the maximum water content. Five samples were measured at each site and each sample is indicated by a different symbol. For each site five regressions were determined using Eqn (1) and the average values for b and Ψ_s (Table 1) were used to generate the solid lines.

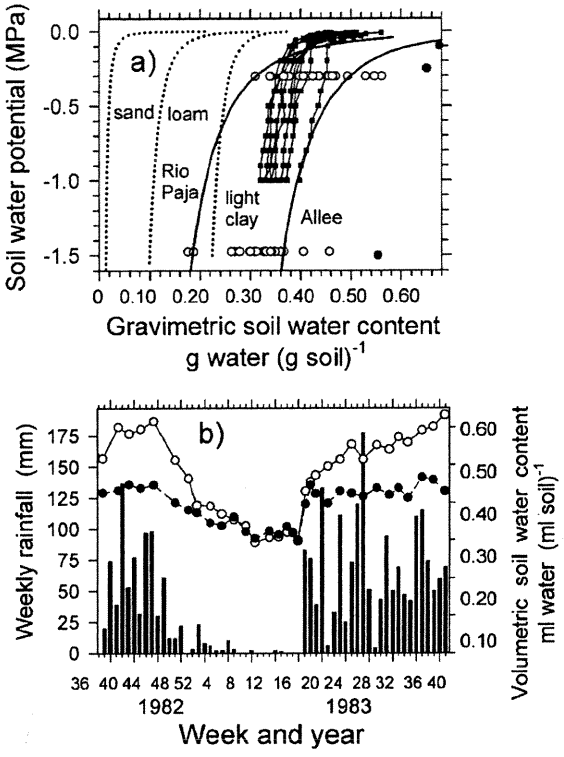

Figure 2. (a) Soil moisture release curves for tropical forest soils. Squares with thin solid lines are from the BCI plateau and slopes (Becker *et al.* 1988). Open circles are from La Selva, Costa Rica (Sollins *et al.* 1994). Filled circles are for BCI plateau and slope (estimated from Daws *et al.* 2002 assuming a bulk density of 0.80 Mg m^{-3}). Thick solid lines are for Allee and Rio Paja from this study as in Figure 1. The dashed lines were calculated for sand, loam and light clay using Eqn (1); the b and Ψ_e values were obtained from Cosby *et al.* (1984) and the bulk densities from Clapp & Hornberger (1978)(b = 2.79, Ψ_s = − 0.00068 MPa and bulk density = 1.627 Mg m^{-3} for sand; b = 5.25, Ψ_s = − 0.00348 MPa and bulk density = 1.395 Mg m^{-3} for loam; b = 11.55, Ψ_s = − 0.00459 MPa and bulk density = 1.262 Mg m^{-3} for light clay). (b) Rainfall and volumetric soil water content on Lutz Creek, BCI, during the severe 1982–83 drought. Weekly rainfall is indicated in the histogram and the volumetric soil water contents at 0–10 cm and 30–40 cm are indicated as open and closed circles, respectively. The soil water was determined gravimetrically and converted to volumetric values using the bulk density for 0–10 cm from Allee of 0.812 Mg m^{-3}. Data from Steve Paton, Smithsonian Environmental Sciences Program.

for favourable conditions for plant growth and survival. Analysis of water content data from Lutz Creek on BCI during a severe drought in 1982–1983 (Figure 2b) also suggests that relative water content may not reflect water potential. Soil water at 0–10 cm dropped to about 0.31 ml water (ml soil)$^{-1}$ after about 12 wk of drought and then remained constant for the next 6 wk of drought. Hence, any decreases in Ψ_m during the last 6 wk of the drought were not reflected by changes in soil water content. Hence, direct measures of Ψ_m best characterize soil water status.

Typical available water capacities from maximum water content to − 1.5 MPa are 0.09, 0.20 and 0.17 ml ml^{-1} for sandy loam, silt loam and clay, respectively (Brady & Weil 2000). Compared with these, the available water capacities reported for Allee and Rio Paja were high, 0.25–0.29 ml ml^{-1} (from maximum water content to − 1.5 MPa). Our values also were high compared to most values for tropical forest soils. At BCI, using reported gravimetric water contents and assuming a bulk density of 0.8 Mg m^{-3}, we calculated available water capacities of about 0.12 ml ml^{-1} (from − 0.01 to − 1.0 MPa; Becker *et al.* 1988) and about 0.15–0.20 ml ml^{-1} (between maximum water content and − 1.5 MPa; Daws *et al.* 2002). At 19 sites in a wet tropical forest at La Selva, Costa Rica, available water content in the upper horizon was considerably lower and ranged from about 0.03 to 0.15 ml ml^{-1} with an average of 0.08 ml ml^{-1} (between − 0.3 and − 1.5 MPa; Sollins *et al.* 1994). For tropical agricultural soils, the high values for available water capacities to − 1.5 MPa are about 0.17 ml ml^{-1}, but most values fall well below this (0.06–0.15 ml ml^{-1} (Buol & Eswaran 2000, Gaiser *et al.* 2000, Lal 1987, West *et al.* 1998). In contrast, a study of four soils from montane forest reported high water availability, 0.17, 0.23, 0.23 and 0.29 ml water (ml soil)$^{-1}$ from maximum water content to − 1.5 MPa (Kapos & Tanner 1985) and, in another study, values of 0.20 to 0.24 ml ml^{-1} (Dalling & Tanner 1995). The relatively high water availabilities observed in these studies and in our study may be explained by the fact that pores occupy a very high fraction of the soil, about 70% (see Results). The soil organic content correlates with available water capacity. For example, in one study every 1% increase in carbon content increased available water capacity by 2.2–3.7% (Hudson 1994). Hence, the high available water capacity at the two Panama sites may result in part from high organic carbon content (Table 2).

At high water potentials, a large decrease in water content results only in small changes of water potential. In fact between Ψ_m of near zero and − 0.3 MPa, we found large decreases in water content, about 0.14 and 0.19 ml ml^{-1} for Allee and Rio Paja, respectively. These were 41–55% of the total decrease in water content from maximum water content to − 9 MPa. The published moisture release curves for tropical forest and agricultural soils, using pressure plates with better resolution at high water potentials, show similarly large decreases in gravimetric water content between Ψ_m of near-zero and − 0.1 MPa (Figure 2a; Dalling & Tanner 1995, Kapos & Tanner 1985, Sanchez 1976, Sharma & Uehara 1968, Uehara & Gillman 1981). These data can also be presented as the change in Ψ_m when 0.1 ml ml^{-1} is lost. Between maximum water content and − 1.5 MPa, Ψ_m at Allee and Rio Paja only dropped by 0.5–0.6 MPa per 0.1 ml water lost from 1 ml of soil.

For Ψ_m lower than -1.5 MPa, moisture release curves for tropical, agricultural soils are similar to ours, showing relatively little change in soil water content between -1.5 and -10 MPa (Sanchez 1976, Sharma & Uehara 1968, Uehara & Gillman 1981). To our knowledge, data on water release of tropical forest soils at $\Psi_m < -1.5$ MPa are not available, although values below -1.5 MPa represent an ecologically important range in which drought stress and mortality occur. For example, seedlings of five tropical woody plants with severe stress (severe wilting and extensive leaf necrosis, but that recovered after watering) experienced very low leaf water potentials, -3.6 to -10 MPa (or less). For the same five species, even slight wilting did not occur until plants reached fairly negative water potentials of -1.0 to -4.8 MPa (Tyree *et al.* 2003). Because of the near-hyperbolic shape of the soil water release curves, available water was very small at the dry end of the curve (e.g. only 0.033–0.050 ml ml^{-1} from -3 to -9 MPa, a decrease of 6 MPa). While osmotic adjustment on the order of 1–2 MPa (Tobin *et al.* 1999) can improve desiccation tolerance, osmotic adjustment at water potentials less than -3 MPa provides access to little additional water (Taiz & Zeiger 2002, p. 597).

The soil structural parameters most commonly reported for tropical forest soils, gravimetric water content, texture and bulk density are not indicative of the ability to supply water. For example, Rio Paja, the site with higher available water capacity, had a much lower maximum water content, as well as lower water contents at all water potentials than did Allee (Table 1). The high gravimetric water content and low available water capacity of the Allee soil is indicative of an aggregated clay soil (El-Swaify 1980). Measurement of soil water content, as opposed to soil water release, would have led to misinterpretations of the differences in water availability between the sites. Soil texture is commonly used to estimate soil water release characteristics. In the case of aggregated soils, texture is not a suitable measure of pore size distribution and abundance (Bruce 1972, Sharma & Uehara 1968). For example, the *b* values obtained from our empirical soil water release curves (5.1 for Allee and 3.1 for Rio Paja) indicated considerably larger pore sizes than the *b* values that were predicted from soil texture (8.2 for Allee and 5.3 for Rio Paja). We interpret these data to indicate that both sites have aggregated soils and that the *b* values determined from the water release curves are more accurate. Larger pores may also imply lower soil hydraulic conductance under drought conditions than expected from soil texture. For soils with larger pores or for plants with a low root-to-leaf area ratio, water transport in the rhizosphere is the principal factor that determines hydraulic conductance along the soil-plant-atmosphere continuum (Hacke *et al.* 2000). This suggests that, for seedlings with few roots (Kitajima 1994, Tyree *et al.* 1998) that establish in aggregated, tropical soils, rhizosphere processes may be the main constraint on water transport, suggesting that more attention should be paid to soil hydraulic properties in tropical rain forests.

Differences in plant communities caused by soils often have been ascribed to soil chemical properties (e.g. pH, nutrients, aluminium; Baker *et al.* 2003, Clark *et al.* 1999, Pyke *et al.* 2001, Tuomisto *et al.* 2002) or, in some cases, to the depth of the water table (Pélissier *et al.* 2002). Although less studied, major determinants of distributions of tropical tree species are differential drought survival and differences among sites in water availability that are mediated by topography, soil depth, soil hardness or barriers, the available water capacity of the soil, as well as rainfall (Itoh *et al.* 2003, Richards 1996 p. 317, p. 411, Sollins 1998). Our data show that available water capacity varies strongly among tropical forest soils, and may contribute to variation in the plant community composition. Taking soil hydraulic characteristics into consideration may thus advance our understanding of the mechanisms that determine distribution, abundance and diversity of tropical forest plants. Measurements of soil water release curves provide a relatively simple way to quantify soil water capacity for seedlings of tropical forest trees.

ACKNOWLEDGEMENTS

This work was supported by a grant from the Andrew W. Mellon Foundations, the University of Utah and the U.S. Forest Service. We appreciate excellent technical assistance from Beatriz Baker, Kelly Anderson, Carl Salk and Matthew Gilbert and data provided by Steve Paton of the Smithsonian Environmental Sciences Program. Martin Kellman, Phyllis Coley and Rick Condit provided helpful comments on the manuscript.

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