Plant and Soil **238:** 79–90, 2002.

Topographic position affects the water regime in a semideciduous tropical forest in Panamá

Matthew I. Daws[1,4], Christopher E. Mullins[1], David F.R.P. Burslem[1], Steven R. Paton[2] & James W. Dalling[3]

[1]*Department of Plant and Soil Science, University of Aberdeen, St Machar Drive, Aberdeen, AB24 3UU, UK.* [2]*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá.* [3]*Department of Plant Biology, University of Illinois, 149 Morril Hall, 505 S Goodwin Avenue, Urbana, Illinois 61801, USA.* [4]*Corresponding author**

Received 22 February 2001. Accepted in revised form 17 September 2001

Key words: matric potential, niche specialisation, water balance, water regime

Abstract

The effects of topographic position on water regime in a semideciduous tropical forest on Barro Colorado Island in Panamá were assessed by measuring soil matric potential using the filter paper technique and by using measured soil water release characteristics to convert a long-term (20 years) gravimetric water content data-set to matric potential. These were also compared against predictions from a simple water balance model. Soil matric potentials on slope sites were significantly higher than on plateau sites throughout the measurement interval and slopes experienced a shorter duration of drought during the annual dry-season. Measured values of matric potential agreed with those predicted from converting the gravimetric measurements using water release characteristics. Annual duration of drought predicted by the simple water balance model agreed with values determined from the converted long term water content data-set and was able to predict the annual duration of drought on plateau sites. On slope sites, the water balance systematically and significantly overestimated the duration of drought obtained from the water content data-set, suggesting that slope sites were supplied with water from upslope. Predictions of annual drought duration from sites with higher annual rainfall than Barro Colorado Island (BCI), suggest that while plateau sites on BCI experience a water regime consistent with annual rainfall, slopes experience a water regime more similar to that of forests with much higher rainfall. We conclude that such large variations in water regime over small spatial scales may play a role in maintaining high species richness through providing opportunities for niche specialisation and by buffering slopes against possible climate change.

Introduction

The mechanisms maintaining the high species richness of tropical forests are subject to debate. Predictions from resource-based competition theory suggest that stable co-existence between species depends on each being a superior competitor within its own niche (Williamson, 1957). However, all plants require the same resources and acquire them in a limited number of ways, so species are not usually tightly grouped within sharply defined niches (Grubb, 1977; Mahdi et al., 1989; Tilman, 1984). Although it might be expected that a few species would out-compete all others, this does not usually occur. A number of theoretical solutions have been proposed to explain the maintenance of high species richness. Several of these invoke some degree of niche differentiation within a heterogeneous environment as necessary for species co-existence (Ashton, 1969; Denslow, 1980; Tilman, 1982).

Many of the hypotheses involving niche differentiation focus on the light environment and its variability between sites, particularly with reference to gap dynamics (Denslow, 1980; Ricklefs, 1977). The light

---

* FAX No: +1224-27-2763. E-mail: m.daws@abdn.ac.uk

environment of intact forests and canopy gaps has been quantified at a number of sites (Chazdon and Fetcher, 1984; Chazdon, 1988). Studies with both temperate and tropical tree seedlings have demonstrated a range of seedling responses to irradiance (Augspurger, 1984; Brokaw and Scheiner, 1989; Canham et al., 1999; Kobe, 1999) and this partitioning of available resources is hypothesised to contribute to species coexistence. However, with the exception of light conditions, the spatial and temporal variation in available resources within tropical forests has been poorly studied (Bazzaz, 1984).

Within both temperate and tropical forests, numerous studies have observed an effect of topography on the distribution of plants (for example Basnet, 1992; Harms, 1997; Hubbell and Foster, 1986). Despite the existence of distinct vegetation patterns that relate to topography, few studies have measured variation in the availability of resources that might cause these patterns. Hydrological models based on water movement in uniform soil slabs predict that, after drainage, the water content of soil on a slope is greatest at the base and becomes progressively less towards the top. Soil moisture deficits are thus smallest at the slope base where further rainfall will rewet the soil most quickly. This will then be maintained by through-flow from upslope (Hewlett and Hibbert, 1963; Knapp, 1978). While these models imply that slopes will be wetter than plateau sites, this has not been consistently demonstrated; published studies have indicated that slopes may be wetter, drier or no different to plateau sites (Becker et al., 1988; Helvey, 1971; Werling and Tajchman, 1983, 1984; Young and Young, 1983).

In regional scale studies, differences in the soil water regime between wet evergreen and moist semi-deciduous tropical forest in Ghana (Veenendaal et al., 1996) have been related to variation in plant species composition (Hall and Swaine, 1976). Furthermore, the relationship between plant biodiversity and rainfall in the tropics is well known (Wright, 1992). However, with the exception of Becker et al., (1988) no studies in intact tropical forests have measured soil water availability at the scale of local topographic differences that might be important in producing the distributions of plant species that are commonly observed.

Becker et al. (1988) measured soil water potential within the semi-deciduous forest of Barro Colorado Island (BCI), Panamá, on the gentle slopes and the neighbouring high plateau of a 50 ha forest dynamics plot (Hubbell and Foster, 1983). They found that higher soil water potentials were maintained on slope sites compared to the plateau during the dry season and that this was related to observed differences in leaf water potential. This study drew attention to the issue of topographically induced differences in soil water availability, but used soil psychrometers with an accuracy of only ± 50 kPa (Mullins, 2000) and failed to provide any statistical backing for its conclusions. Thus, the work of Becker et al. (1988) points to the likely existence of topographic differences and to their effect on vegetation, but requires further support.

The objectives of this study were therefore to test for topographically induced patterns of water availability, in the semi-deciduous tropical forest of BCI. In order to extend the information obtained from a short database of detailed measurements of soil matric potential back over a number of years, we have also tried two different approaches. Firstly, we have used an existing long-term data set of measurements of soil water content and converted these to matric potentials using measured soil water release characteristics. Secondly, we have compared these results against predictions based on a simple soil water balance model that uses rainfall and an estimate of evapo-transpiration. Finally, we have tried to compare the relative importance for plants of differences in soil water regime caused by topographic differences with those caused by regional differences in rainfall for plants in Panamá.

Methods

Study site

The study was conducted in the semi-deciduous forest on Barro Colorado Island (BCI), Republic of Panamá (9 °10′ N, 79 °51′ W), which is described in detail elsewhere (Leigh et al., 1982). Rainfall on BCI averages 2600 mm/yr, with a pronounced dry season between January and April (Dietrich et al., 1982). The Lutz catchment, which is located in the east of the island (Figure 1), close to the laboratory clearing, was used for this study. The entire catchment is forested and its soils have been classified as alfisols (Yavitt and Wieder, 1988) and are usually less than 500 mm deep (Dietrich et al., 1982). The island was declared a reserve in 1923 and its vegetation has been little disturbed since the late nineteenth century, when the French attempted to build a canal (Leigh, 1999).

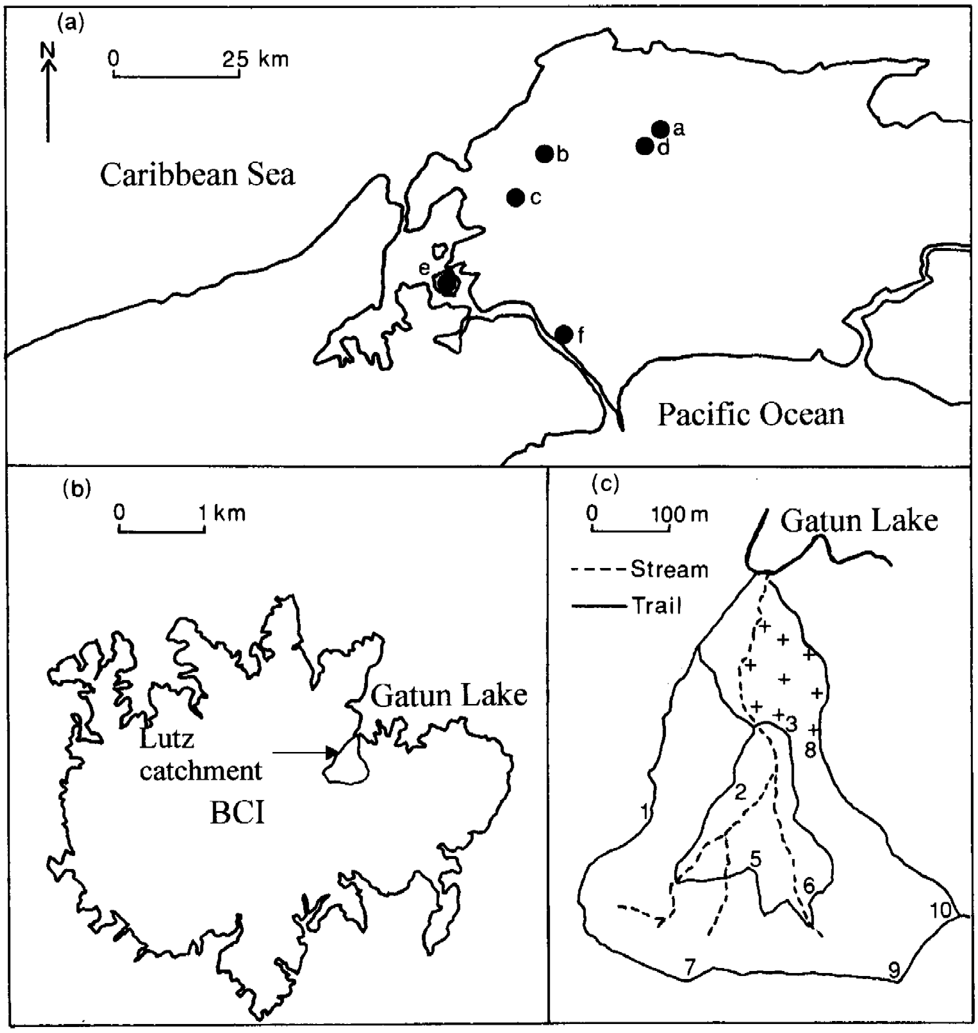

Figure 1. (a) Map of Panamá showing the location of the Panamá Canal Authority rain gauge sites and Barro Colorado Island (a, San Miguel; b, Aguaclara; c, Ciento; d, Candeleria; e, Barro Colorado Island; f, Empire Hill). (b) Location of the Lutz catchment on BCI and (c) location of the three transects for measurement of soil matric potential using the filter paper technique (sites indicated by +) and the nine gravimetric water content sampling sites (sites 1,2,3,5,6,7,8,9 and 10), within the Lutz catchment.

Soil matric potential measurements

Soil matric potential was measured using the filter paper technique (Deka et al., 1995) along three transects within the Lutz catchment (Figure 1). Three topographic positions along these transects were classified as slope bottom, middle of slope and plateau. Slope bottom sites were adjacent to streams (at less than 5 m distance), plateau sites were areas with convex topography and no up-slope contributing area, and mid-slopes were approximately half way up slopes. Soil samples were taken at a depth of 0–1 cm and 19–21 cm approximately every 10 days from 1 March to 3 July 1999 from within 1 m^2 plots at each position. Soil samples were placed in direct contact with filter papers (Whatman No 42, diameter 55 mm) in 50 mm tall (150 cm^3) plastic jars. Jars were then immediately closed and placed in a thermally insulated box, which was then stored at room temperature (to avoid thermal distillation) and allowed to equilibrate for seven days. After equilibration the gravimetric water content of the filter papers was determined. All weights were measured to an accuracy of 0.1 mg. Soil matric potential was calculated from gravimetric water content using the calibration curve in Deka et al. (1995).

Gravimetric water content determination

Soil gravimetric water content has been determined at one or two week intervals since 1981. Using an ‘Oakfield punch’, 2.5 cm diameter soil cores were collected from depths of 0–10 cm and 30–40 cm at each of 10 locations (Figure 1) within the Lutz catchment (Windsor, 1990). Samples were sealed in pre-weighed metals canisters, transported to the laboratories on BCI, weighed, dried to constant mass and reweighed to determine gravimetric soil water content. Data from nine of these ten locations (site 4 was too stony) were then used as a basis for calculating matric potential using water release curves. For comparison with the matric potential measurements that were taken at plateau, mid- and bottom-slope sites the nine sites were divided into two categories; slope (sites 2, 3, 5, 6 and 7) and plateau (sites 1, 8, 9 and 10). Sites with concave topography and an up-slope contributing area were designated as slopes, sites with no up-slope contributing area and convex topography as plateau. The five slope sites were generally located at a position on the slopes that was intermediate between the bottom- and mid-slopes sites used for filter paper measurements. Additionally all five sites were approximately 100 m from the top of the slopes.

Water release curves

Undisturbed soil cores (4 cm × 5.64 cm diameter) were collected from soil depths of 3–7 and 33–37 cm by pushing metal rings with sharpened edges into the soil. The cores were dug out with a trowel, trimmed, fitted with caps at both ends and sealed with tape. Three cores and approximately 100 g of loose soil were sampled from each depth at each of the nine gravimetric water content sampling sites. The cores were saturated and then a tension table was used to determine water retention at matric potentials of -1, -5 and -16 kPa (Townend et al., 2000). Water retention at -100 and -1500 kPa (the permanent wilting point) was determined using a pressure plate apparatus (Townend et al., 2000).

Water balance calculations

Soil water deficit (W_d) is the amount of rainfall required to return a soil profile to field capacity (Marshall et al., 1996) and provides a simple estimate of the limitation imposed on plant water uptake as a result of drought. It is calculated by assuming the soil profile is at field capacity following heavy rains and then repeatedly applying the following formula:

$$W_\mathrm{d}(t_{n+1}) = W_\mathrm{d}(t_n) - P(t_{n+1}) + E \qquad (1)$$

$W_\mathrm{d}(\mathrm{t}_n)$ and $W_\mathrm{d}(t_{n+1})$ refer to the water deficit on day n and $n + 1$, respectively, P is precipitation and E potential evapo-transpiration. When the deficit takes a positive value we have assumed that drainage would have occurred and reset it to zero. This model represents a very basic approach that does not allow for any possible by-passing that could result in drainage from a profile that was under deficit and assumes that profiles are freely draining. When the available water within a profile is fully exhausted, it is impossible for plants to extract further water. Thus a maximum limit was set to W_d in Equation (1) and W_d values greater than this were reset to this limiting profile available water capacity (Z_awc). Precipitation on BCI was measured with a rain gauge situated within the laboratory clearing. Potential evapo-transpiration at the Lutz catchment was estimated using an ETgage Model A (ETgage Company, Loveland, USA), situated at the top of a canopy tower. Potential evapo-transpiration data were only available for the 5 year period, 1994–1999. Therefore, to enable longer-term calculations of soil water deficit, mean monthly potential evapo-transpiration over the 5-year period was used for time intervals outside the data range. Drought was defined as the period of time during which W_d was equal to Z_awc. Z_awc was estimated by plotting soil water deficit (calculated during periods when the profile was drying from near field capacity) versus measured values of gravimetric water content at 30–40 cm. It was assumed that, when the soil had reached the water content at the permanent wilting point (determined from the laboratory water release characteristics), that the whole profile had no remaining water. Consequently W_d at this point was taken to be equal to Z_awc. Modelling profile drying in this way is subject to a number of possible limitations. In particular, actual evapo-transpiration will decline as the forest is stressed, whereas we have assumed that it continues at the potential rate until the whole profile reaches wilting point. Additionally, the ETgage can only be expected to give a crude estimate of potential evapo-transpiration that may have systematic error.

Duration of drought at other locations

BCI lies at the midpoint of a rainfall gradient between the tropical deciduous dry forests of the Pacific shore, with an annual rainfall of 1800 mm, and the evergreen wet tropical forests of the Caribbean coast, with an annual rainfall of over 3000 mm (Windsor, 1990). Rainfall data from several sites across the isthmus of Panamá (Figure 1) was supplied by the Panamá Canal Authority and used to compare the estimated duration of drought at sites with differing annual rainfall using the water balance method previously described. In the water balance calculation, it was both assumed that Z_{awc} and evapo-transpiration at all of the geographically separated sites, were the same as at BCI. Whilst these assumptions are not necessarily true and can only be rough approximations, they were considered adequate for a comparison between magnitude, and hence importance, of local variations in water regime due to topography and differences in water regime occurring over a large area due to differences in rainfall.

Statistical methods

Soil matric potentials measured by the filter paper technique were log-transformed prior to Repeated Measures Analysis of Variance (ANOVA) conducted using SPSS version 9.0. This was used to test for the effects of season, soil depth and topographic position on soil matric potential.

The curve fitting function in Sigmaplot 5 was used to fit second order polynomials to the water release curves. As these curves were used to predict soil matric potential (x) from gravimetric water content (y) the data was regressed y on x for curve fitting. The equations of these curves were then used to convert the long-term gravimetric water content data set to matric potential. The resulting plots of soil matric potential against time were used to calculate the annual severity of drought (defined as the duration when there was a soil matric potential below wilting point, −1500 kPa) at each of the nine sites. Water release curves can be conveniently modelled as a straight line relationship between log (volumetric water content) and log (matric suction) for a wide range of matric suctions (Felton and Nieber, 1991). To compare water release characteristics of soils from different sites, straight lines were fitted to the log-log plots and tested for differences using linear regression.

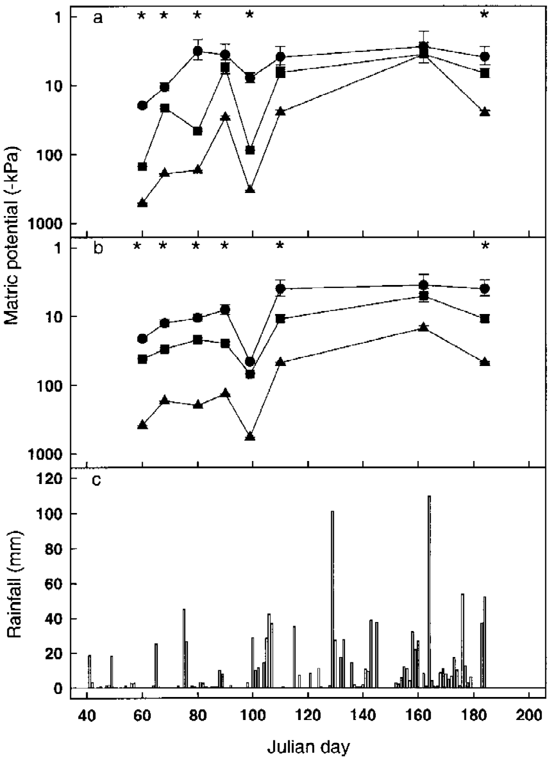

Figure 2. (a). The effect of season, topography (slope bottom, circles; mid slope, squares; and plateau, triangles) and soil depth on soil matric potential measured using the filter paper technique between 1 March (day 60) and 3 July (day 184) 1999 at a depth of 0–1 cm and (b) at a depth of 19–21 cm, $n = 3$. Error bars are ± 1 standard error and when not shown are smaller than the symbol. Time periods marked by an asterisk indicate a significant difference in soil matric potential between all three topographic positions. (c). Daily rainfall between 1 March and 3 July 1999.

Repeated Measures ANOVA on log transformed data was also used to make a comparison between soil matric potential measured using the filter paper technique and that calculated from the gravimetric water content data set. The filter paper data revealed that slope position had a pronounced effect on matric potential. However, since the wetness of a slope is likely to be affected by the size of the area contributing drainage and because it was not clear that the slope sites used for matric potential measurements and gravimetric water content determination had the same upslope contributing area, only plateau sites were compared directly. Since measurements of soil matric potential and gravimetric water content were not made on the same days, matric potentials from the long-term data set were interpolated to enable a direct comparison to be made.

The slopes of regression lines were compared to null lines with a slope of one or zero using a t-test. Tests for equality of slopes of two regression lines were carried out using the F-test.

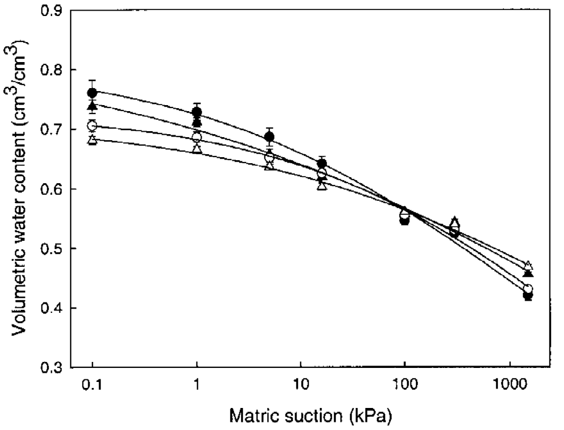

Figure 3. Average soil water release characteristics for slope (circles) and plateau (triangles) sites at 0–10 (closed symbols) and 30–40 cm (open symbols). Error bars are ± 1 standard error and when not shown are smaller than the symbol.

Results

Soil matric potential measurements

Filter paper measurements of soil matric potential commenced during the dry-season, by which time soil matric potential had already fallen to approximately -500 kPa at a depth of 20 cm on the plateau sites (Figure 2). During the remainder of the dry-season, matric potential fluctuated according to occasional rainfall events. During the dry to wet-season transition in mid April–early May (approximately days 100–125), matric potential increased to field capacity with the increasing probability and amounts of daily rainfall. Throughout the period of measurement, there was a highly significant effect of topographic position on soil matric potential (Repeated Measures ANOVA, F = 26.2, $P < 0.01$) and plateau sites were almost always drier than slope sites. The matric potential at the bottom of slopes was only once less than -25 kPa, whilst the matric potential on plateau sites fell as low as -550 kPa.

Gravimetric water content (GWC) data set

For all nine sites and both soil depths, soil water release characteristics could be described using second order polynomials (in all cases $r^2 > 0.89$, $P < 0.05$). Straight lines fitted to log-log data ($r^2 > 0.90$, $P < 0.05$) to test for differences in slope and intercept revealed no significant differences either between sites or soil depths ($P > 0.05$; Fig. 3).

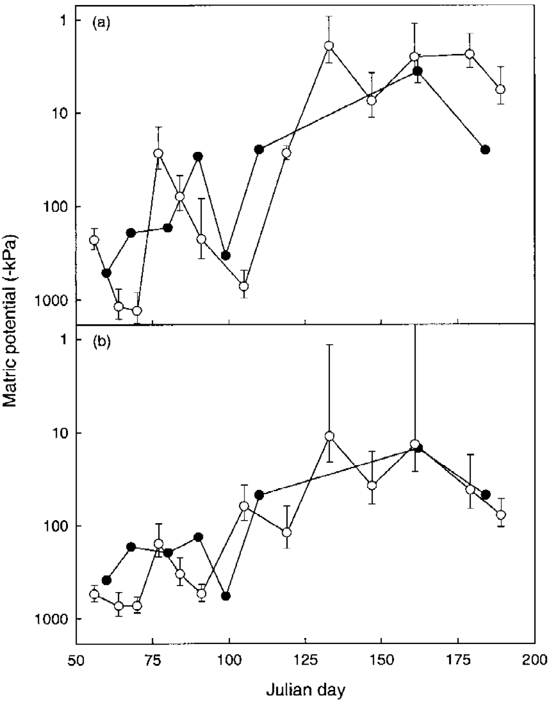

Figure 4. Comparison between soil matric potential between 1 March (day 60) and 3 July 1999 (day 184) measured with the filter paper technique (closed circles) and calculated from the gravimetric water content (GWC) data set (open circles). (a) Filter paper measurements at 0–1 cm, GWC 0–10 cm, (b) filter paper 19–21 cm, GWC 30–40 cm.

Comparisons of soil matric potential on plateau sites measured using filter papers and calculated from the water release curves (Figure 4) for the period 1 March–3 July 1999, revealed no significant difference between results from the two methods (Repeated Measures ANOVA, $F = 1.140$, $P = 0.303$).

Soil matric potential plots (calculated from the GWC data) showed that there was a high variability in the duration of drought between different years (Figure 5). In some years (1984, 1996, 1999), there was little or no drought. In comparison, there were over 100 days of drought in each of 1983, 1985, 1997 and 1998. Comparing the annual totals of days of drought on slope versus plateau sites (Figure 6) revealed that although the two are correlated (0–10 cm; $r^2 = 0.49$, $P = 0.002$: 30–40 cm; $r^2 = 0.43$, $P = 0.003$), slopes were consistently wetter than plateau sites. For both soil depths, the slopes of the regression lines were significantly less ($P < 0.01$) than one and greater ($P < 0.01$) than zero. This difference was even maintained in the driest years: at a depth of 0–10 cm, when slopes had approximately 25 days of drought plateau sites

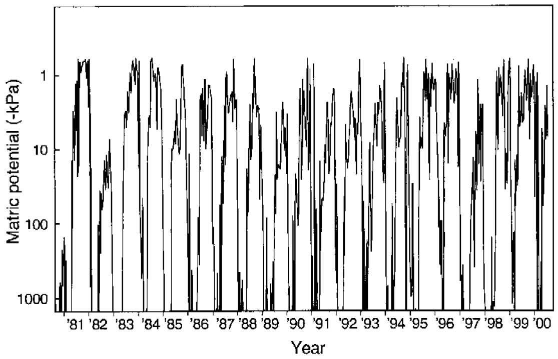

Figure 5. Soil matric potential at site 1 (plateau), calculated from soil water content data for the period 1982–2000, at a soil depth of 0–10 cm. The bottom of the graph represents the permanent wilting point, a potential of −1500 kPa.

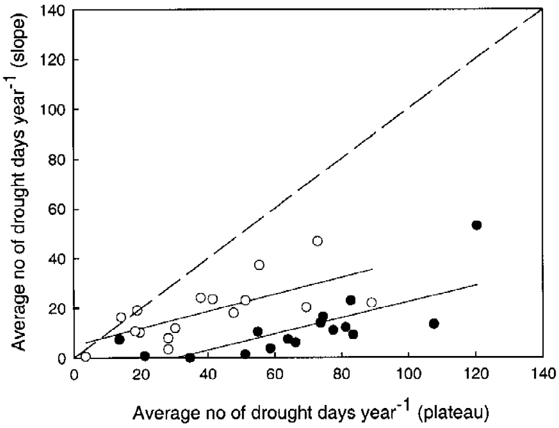

Figure 6. Comparison of the annual severity of drought on plateau and slope sites on BCI determined from converted gravimetric water content measurements. Closed circles: 0–10 cm; open circles: 30–40 cm. Dashed line shows 1:1 prediction.

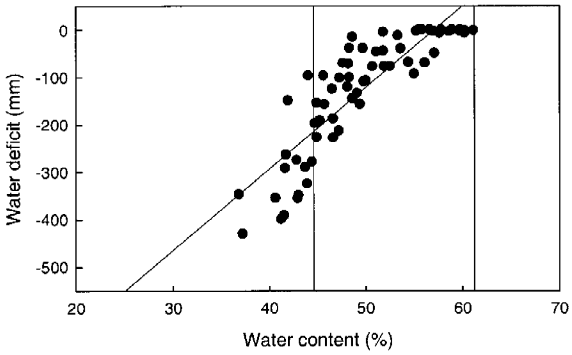

Figure 7. Regression of soil water deficit against soil gravimetric water content for site 1 (plateau). The vertical lines at gravimetric water contents of 44.6 and 61.2% correspond to wilting point and field capacity, respectively. Data is from 1981–2000 and represents deficits when the profile was drying from field capacity.

were experiencing an average of 120 days of drought. The difference between slope and plateau sites was evident at both soil depths and there was no significant difference between the slopes of the regression lines for the two soil depths.

Water balance

At a depth of 30–40 cm, there was a significant linear relationship between soil water deficit (calculated from rainfall and potential evapo-transpiration during periods when the profile was drying from field capacity) and soil gravimetric water content for all nine gravimetric water content sampling sites. Figure 7 ($r^2 = 0.75$, $P < 0.001$) is a typical example of the graphs obtained for the four plateau sites. Since calculation of soil water deficit is not applicable to soils that are receiving water from upslope, graphs for the slope sites were not used. On the plots for plateau sites, the intercept between the regression line and a water content corresponding to wilting point (−1500 kPa) was calculated. The mean value and standard error for the four plateau sites were 231.2 ± 28.4 mm. This value was taken as the profile available water capacity (Z_{awc}) that was used in the water balance calculation.

The water balance calculations for each day over the period 1981–2000 revealed a similar trend to the GWC data set, in relation to the annual severity of drought. Figure 8a shows the correspondence between the number of drought days estimated from the water balance (number of days with a soil water deficit greater than 231 mm) and the average number of drought days per year (number of days with a soil matric potential less than −1500 kPa) for the four plateau sites. The slopes of the regression lines for the two soil depths do not differ significantly from each other or from a slope of one ($P > 0.05$). In comparison, the slopes of the regression lines for the two soil depths, using data from the five slope sites (Figure 8b), are both significantly less than one ($P < 0.05$).

A sensitivity analysis was conducted to determine how the value used for Z_{awc} affected the duration of drought predicted from the water balance. For the Z_{awc} value of 231 mm that we used there was a good relationship between the predicted and measured number of drought days, although there was a systematic tendency to over predict the actual number of drought days (Figure 9). With a greater Z_{awc} of 600 mm, the water balance fails to predict prolonged drought when it was observed. With a low Z_{awc} value of 50 mm,

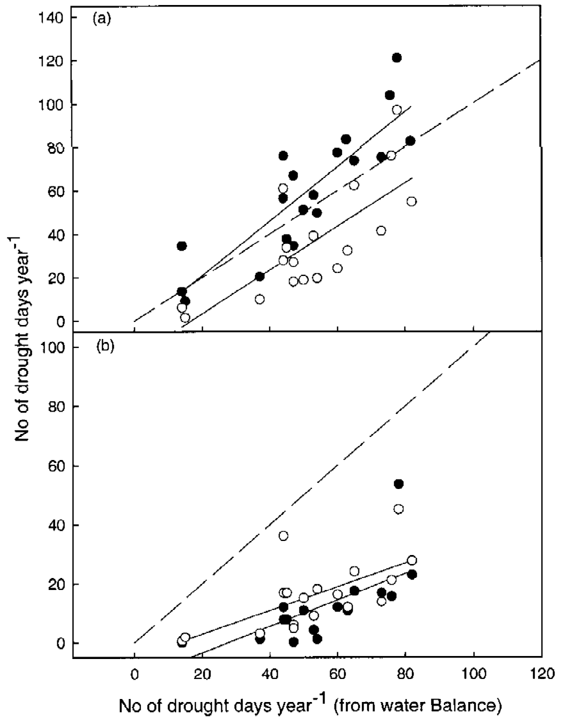

Figure 8. Regression of mean annual duration of drought (obtained from the gravimetric water content data) on (a) plateau sites and (b) on slope sites, against duration of drought predicted from the water balance equation. Closed circles: 0–10 cm; open circles: 30–40 cm. Dashed line shows 1:1 prediction.

the water balance greatly overestimated the duration of drought.

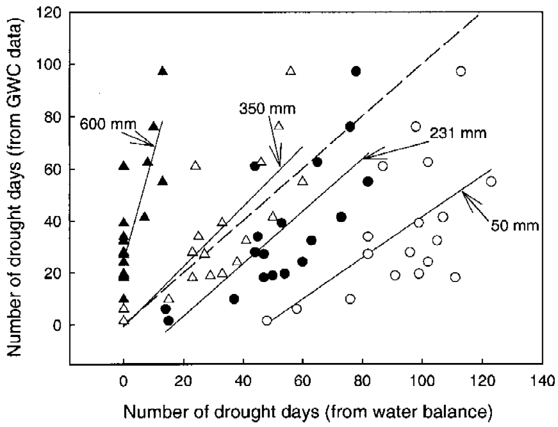

Figure 9. The effect of altering Z_{awc}, on the accuracy of drought prediction at a depth of 30–40 cm on plateau sites using the water balance equation. Z_{awc} of 600 mm (closed triangles), 350 mm (open triangles), 231 mm (closed circles), 50 mm (open circles). Dashed line shows 1:1 prediction.

Table 1. The mean number of days per year (for the period 1982–1999) for which the water deficit (W_d) exceeds Z_{awc} (231 mm) at sites, in Panamá, with different annual rainfall. The actual duration of drought on BCI slopes determined from the gravimetric water content data is provided for comparison.

Site	Co-ordinates	Annual rainfall (mm)	Days $W_d > 231$ mm	Standard error
San Miguel	9° 25′ N 79° 30′ W	3727	1.4	1.0
Aguaclara	9° 22′ N 79° 42′ W	3604	15.5	5.6
Ciento	9° 18′ N 79° 45′ W	2960	27.7	6.7
Candeleria	9° 23′ N 79° 31′ W	2940	16.6	4.2
BCI	9° 10′ N 79° 51′ W	2592	52.6	4.5
Empire Hill	9° 03′ N 79° 40′ W	1989	73.3	14.3
BCI slopes	9° 10′ N 79° 51′ W	2592	16.2	2.7

Duration of drought at Panamá Canal Authority sites

The period for which soils, at a range of sites in Panamá, experienced a soil water deficit of 231 mm or greater was calculated by applying the water balance equation for the period 1980–1998 to daily rainfall data from five sites. The mean number of days per year for which soil water deficit exceeded 231 mm is shown for the various sites in Table. 1. Along a gradient of increasing annual rainfall from 1989 to 3727 mm, the mean number of days with a water deficit greater than 231 mm decreased from 73.3 to 1.4. For comparison, the mean annual duration of drought on BCI slopes (calculated from the soil gravimetric water content data) is included. This figure (16.2 days) is much closer to the values for Aguaclara and Candelaria which had 3604 and 2940 mm, respectively, of rainfall per year than it is to the value for plateau sites on BCI (52.6 days).

Discussion

Soil matric potential

Our findings using the filter paper technique agree broadly with those of Becker et al. (1988) who demonstrated that slopes in the 50 ha plot on BCI remained at higher water potentials than adjacent plateau sites during the dry season of 1985. The magnitude of the differences in water availability we observed between slopes and plateau sites is also similar to those observed by Becker et al. (1988). In 1985, dry season soil water potential, at a depth of 20 cm, on slopes of the 50 ha plot reached −1500 kPa, with plateau sites −2000 kPa (Becker et al., 1988). Similarly, we observed a large (500 kPa) difference between matric potential on slopes and plateau at a depth of 20 cm, however potentials at slope bottoms were rarely less than −25 kPa. Total dry season rainfall was greater in 1999 than 1985 (472 mm between January and April inclusive *versus* 94 mm). Furthermore, Figure 6 suggests that the difference in water availability between topographic positions would be magnified more in a drier year, at least with respect to the duration of drought, indicating that slopes in the Lutz catchment may be significantly wetter during the dry season than the slopes in the 50 ha plot studied by Becker et al. (1988).

The amount of water that can supplement rainfall on slopes is highly dependent on the size of the catchment area above any point (Beven and Kirkby, 1979). This is apparent from our filter paper measurements of matric potential which reveal a gradient of water availability down slopes in the Lutz catchment; slope bottom sites remain significantly wetter during the dry season than both plateau and mid-slope sites. This may also explain why slopes in the Lutz catchment remain wetter in the dry season than those in the 50 ha plot. The sites chosen by Becker et al. (1988) for water potential measurements were no more than 50 m from the top of slopes. However, our slope bottom sites were approximately 100 m from the top of the slopes and will, therefore, have potentially been receiving water from a greater upslope area.

The longer-term study of soil matric potential using the gravimetric water content data set confirmed that there was a consistent difference between slope and plateau sites (Figure 6). There are many possible limitations in attempting to determine matric potential from gravimetric water content. For example, those resulting from hysteresis (the water release characteristics being dependent on the previous wetting or drying history of the soil) (Marshall et al., 1996) or differences in soil properties between the positions sampled for gravimetric water content and the release characteristics. It is, therefore, reassuring that there was good agreement (Figure 4) between the two estimates at the level of accuracy required for site and seasonal comparisons and no significant differences in soil water release characteristics between the nine gravimetric water content sampling sites.

The duration of drought was highly variable between years, with the driest years generally coinciding with the El Niño events in 1983, 1988, 1992 and 1998. These results confirm that El Niño events resulted in severe dry seasons on BCI (Windsor, 1990) and that the high inter-annual variability of drought on BCI, also observed in other tropical forests (Veenendaal et al., 1996) may provide a bottleneck for the successful regeneration of species, especially at the seedling stage (Condit et al., 1995).

Soil water balance

The soil water balance model assumes that the profile was freely draining. Whilst this was not true for slope sites, where overland flow was observed after heavy rainfall we have no evidence of poor drainage on the plateau sites. Figure 9 shows that, reasonable estimates of the duration of drought were obtained in the range $231 < Z_{\mathrm{awc}} < 350$ mm. Consequently, the model was not very sensitive to quite large changes in the chosen value of Z_{awc}. Using a single value for Z_{awc} to model profile water balances can only be a rough approximation, because the rate of transpiration and hence profile water extraction will actually decrease as soil moisture deficit increases, rather than remaining constant until it drops to zero, as assumed in our simple model. This means that extreme moisture stress will actually take considerably longer to develop than predicted by the model, or alternatively that a considerably greater value of Z_{awc} is needed to make the model fit observations that actually existed in the field. The limited profile information for BCI supports this proposition. Our value for Z_{awc} of 231 mm corresponds to a soil depth of approximately 1.2–1.4 m which is almost certainly a considerable overestimate of actual rooting depth. The typical soil depth to bedrock quoted by Dietrich et al. (1982) is 500 mm and it is reasonable to assume that there was only limited water extracted from the weathered basalt bedrock below this. Furthermore, Odum (1970) found that in this catchment, roots were distributed throughout the entire soil profile, with only limited root penetration into the weathered bedrock below.

Figure 8 also shows our prediction of drought duration for slope sites using the water balance equation. This equation supplies a simple model for predicting the annual severity of drought in the Lutz catchment, in any given year, using only daily rainfall and potential evapo-transpiration. The model reveals that slopes are significantly wetter than predicted from the equation, which suggests that they are receiving water from upslope, in accordance with predictions from hydrological models (Hewlett and Hibbert, 1963; Knapp, 1978).

Implications of soil water regime for plant growth and survival

Along a gradient of increasing rainfall, the annual severity of drought decreases (Table 1). As might be expected, this coincides with a change from dry deciduous to evergreen wet forest (Windsor, 1990). The predicted duration of drought on BCI plateau sites is similar to other sites with approximately the same annual rainfall, but much greater than for significantly wetter sites. The much lower value for average annual drought duration on slopes on BCI is closer to values for sites with an annual rainfall up to 1000 mm greater than BCI. This result highlights the large effects that topographic position can have on water regime and suggests that the water regime on slopes of the Lutz catchment is more similar to that of wet evergreen forest than that of the semi-deciduous forest on BCI.

The upslope area contributing drainage will affect the water regime at any point (Beven and Kirkby, 1979; Figure 2). Thus, it is not possible to generalise the effect of topography on water availability, and hence plant growth and survival, since the amount of water movement will be dependent upon the characteristics of that particular slope. As a result, there will be a gradient of water availability on any given slope (see Figure 2), with the water regime on slopes or locations on slopes which only have a small upslope area being similar to that on plateau sites.

There is ecological evidence that topographically induced variation in water regime may contribute to habitat specialisation in tropical forest plants. For example, *Piper* spp. are most abundant and represented by the largest number of species in tropical wet forest (Opler et al., 1980). Interestingly, the majority of understorey *Piper* spp. on BCI are slope specialists (Harms, 1997). In addition, studies in temperate systems, have revealed partitioning of the moisture environment by a range of species, which presumably leads to coexistence (Picket and Bazzaz, 1978; Silvertown et al., 1999). Thus, it is possible that the environmental heterogeneity resulting from topography may help maintain high species richness in this forest by providing a range of distinct hydrologically defined niches. This is supported by the common occurrence of slope specialists in the tropics (Ashton, 1969; Hubbell and Foster, 1986; Harms, 1997) and points to a role for habitat heterogeneity in fostering species coexistence.

Condit et al. (1996a) investigated population change within plant functional groups in the 50 ha plot on BCI. They found that between 1982 and 1995 the population of understorey slope specialists declined by 46.9%, compared to a value of 1.5% for generalist understorey species. They hypothesised that an increasing annual severity of drought over recent years has caused greater relative mortality among slope specialists because they are moisture demanding. They suggest that given recent increases in drought duration, due to putative climate change, these moisture demanding specieswill become extinct on BCI (Condit et al., 1996b). However, our findings suggest that slopes, such as those of the Lutz catchment, may continue to provide a suitable habitat for growth of these moisture demanding species. It is possible that the wetter water regime of these slopes, which have a greater upslope area contributing drainage than those in the 50 ha plot, could provide a buffer against environmental perturbations. Furthermore, coupled with the possible impacts of climate change, slopes such as these in the Lutz catchment, may become increasingly important refugia for wet forest species within drier forest types, as illustrated by the distribution of *Piper* spp. on BCI.

If topographic position can have such an important effect on local differences in water regime, it is clearly important to make further studies of these relationships in other tropical forests. It is difficult to generalise this finding, and its possible implications for plant growth and survival, to other tropical forests or catchments since both the drainage area above any point and the relationship between rainfall intensity and soil physical properties, such as infiltration capacity and moisture conductivity, will affect how much water is available to move into and through the soil. Nonetheless, the magnitude of the differences in water regime we observed over fairly small spatial scales suggests it is important to investigate both the effect of these factors on soil hydrology as well as the effect of these topographically induced moisture gradients on the establishment and survival of different plant functional groups.

Acknowledgements

We thank Brian Murray and Ignacio Barberis for technical assistance. Rainfall data was kindly provided by the Meteorology and Hydrology Branch of the Panama

Canal Authority. Financial support was provided by the Natural Environment Research Council (studentship to MID).

References

Ashton P S 1969 Speciation among tropical forest trees: some deductions in light of recent evidence. Biol. J. Linn. Soc. 1, 155–196.

Augspurger C K 1984 Light requirements of neotropical tree seedlings: A comparative study of growth and survival. J. Ecol. 72, 777–795.

Basnet K 1992 Effect of topography on the pattern of trees in Tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. Biotropica 24, 31–42.

Bazzaz F A 1984 Dynamics of wet tropical forests and their species strategies. *In* Physiological Ecology of Plants of the Wet Tropics. Eds E Medina, H A Mooney and C Vasquez–Yanes. pp 233–244. Dr W. Junk Publishers, The Hague.

Becker P, Rabenold P E, Idol J R and Smith A P 1988 Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. J. Trop. Ecol. 4, 173–184.

Beven K J and Kirkby M J 1979 A physically based, variable contributing area model of basin hydrology. Hydrol. Sci. Bull. 24, 43–69.

Brokaw N V L and Scheiner S M 1989 Species composition in gaps and structure of a tropical forest. Ecology 70, 538–541.

Canham C D, Kobe R K, Latty E F and Chazdon R L 1999 Interspecific and intraspecific variation in tree seedling survival: Effects of allocation to roots versus carbohydrate reserves. Oecologia 121, 1–11.

Chazdon R L 1988 Sunflecks and their importance to forest understorey plants. Adv. Ecol. Res. 18: 1–63.

Chazdon R L and Fetcher N 1984 Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. J. Ecol. 72, 553–564.

Condit R, Hubbell S P and Foster R B 1995 Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. Ecol. Monogr. 65, 419–439.

Condit R, Hubbell, S P and Foster R B 1996a Assessing the response of plant functional types to climatic change in tropical forests. J. Veg. Sci. 7, 405–416.

Condit R, Hubbell S P and Foster R B 1996b Changes in tree species abundance in a Neotropical forest: Impact of climate change. J. Trop. Ecol. 12, 231–256.

Deka R N, Wairiu M, Mtakwa P W, Mullins C E, Veenendaal E M and Townend J 1995 Use and accuracy of the filter-paper technique for measurement of soil matric potential. Eur. J. Soil Sci. 46, 233–238.

Denslow J S 1980 Gap partitioning among tropical rainforest trees. Biotropica 12 (Supplement), 47–55.

Dietrich W E, Windsor D M and Dunne T 1982 Geology, climate and hydrology of Barro Colorado Island. *In* The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Eds. E G Leigh Jr., A S Rand and D M Windsor. pp. 21–46. Smithsonian Institution Press, Washington, DC.

Felton G K and Nieber J L 1991 Four soil-moisture characteristic curve functions evaluated for numerical modelling of sand. Trans. ASAE 34, 417–422.

Grubb P J 1977 The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.

Hall J B and Swaine M D 1976 Classification and ecology of closed canopy forest in Ghana. J. Ecol. 64, 913–951.

Harms K E 1997 Habitat-specialization and seed dispersal-limitation in a Neotropical forest. PhD thesis, Princeton University, Princeton, NJ.

Helvey J D 1971 Predicting soil moisture in the southern Appalachians. MSc. thesis, University of Georgia, Athens, GA.

Hewlett J D and Hibbert A R 1963 Moisture and energy conditions within a sloping soil mass during drainage. J. Geophys Res. 68, 1081–1087.

Hubbell S P and Foster R B 1983 Diversity of canopy trees in a neotropical forest and implications for conservation. *In* Tropical Rain Forest: Ecology and Management. Eds. S L Sutton, T C Whitmore and A C Chadwick. pp. 25–41. Blackwell Scientific Publications, Oxford.

Hubbell S P and Foster R B 1986 Biology, chance, and history and the structure of tropical rain forest tree communities. *In* Community Ecology. Eds. J Diamond and T J Case. pp 314–329. Harper and Row, New York, NY.

Knapp B J 1978 Infiltration and storage of soil water. *In* Hillslope Hydrology Ed. MJ Kirkby. pp. 43–72. Wiley, Chichester.

Kobe R K 1999 Light gradient partitioning among tropical tree species through differential seedling mortality and growth. Ecology 80, 187–201.

Leigh E G Jr., Rand A S and Windsor D M, Eds. 1982 The Ecology of a Neotropical Forest: Seasonal Rhythms and Longer-term Changes. Smithsonian Institution, Washington, D.C.

Leigh E G Jr. 1999 Tropical Forest Ecology: A View from Barro Colorado Island. Oxford University Press, Oxford.

Mahdi R, Law R and Willis A J 1989 Large niche overlaps among coexisting plant species in a limestone grassland community. J. Ecol. 77, 386–400.

Marshall T J Holmes J W and Rose C W 1996 Soil Physics. 3rd edn. Cambridge University Press, Cambridge.

Mullins C E 2000 Matric potential. *In* Soil and Environmental Analysis: Physical Methods. Eds K A Smith and C E Mullins. pp 65–93. Marcel Dekker, Inc., New York, NY.

Odum H T 1970 Rain forest and mineral cycling homeostasis. *In* A Tropical Rainforest. Eds. H T Odum and R F Pigeon. pp H-1–H-52. U.S. Atomic Energy Commission, Oak Ridge, Tenn.: Division of Technical Information.

Opler P A, Frankie G W and Baker H G 1980 Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 68, 167–188.

Picket S T A and Bazzaz F A 1978 Organization of an assemblage of early successional species on a soil moisture gradient. Ecology 59, 1248–1255.

Ricklefs R E 1977 Environmental heterogeneity and plant species diversity: A hypothesis. Am. Nat. 111, 376–381.

Silvertown J, Dodd M E, Gowing D J G and Mountford J O 1999 Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400, 61–63.

Tilman D 1982 Resource Competition and Community Structure. Monographs in population Biology, Princeton University Press, NJ.

Tilman G D 1984 Plant dominance along an experimental nutrient gradient. Ecology 65, 1445–1453.

Townend J, Reeve M J and Carter A 2000 Water release characteristics. *In* Soil and Environmental Analysis: Physical Methods. Eds K A Smith and C E Mullins. pp.95-140. Marcel Dekker Inc., New York, NY.

Veenendaal E M, Swaine M D, Blay D, Yelifari N B and Mullins C E 1996 Seasonal and long-term soil water regime in West African tropical forest. J. Veg. Sci. 7, 473–482.

Werling J A Jr. and Tajchman S J 1983/84 Soil thermal and moisture regimes on forested slopes of an Appalachian watershed. For. Ecol. Manag. 7, 297–310.

Williamson M H 1957 An elementary theory of interspecific competition. Nature 180, 422–425.

Windsor D M 1990 Climate and Moisture Availability in a Tropical Forest: Long-term Records from Barro Colorado Island, Panamá. Smithsonian Contributions to the Earth Sciences, no. 29. Smithsonian Institution Press, Washington, DC.

Wright S J 1992 Seasonal drought, soil fertility and the species density of tropical forest plant communities. Trends Ecol. Evol. 7, 260–263.

Yavitt J B and Wieder R K 1988 Nitrogen, phosphorous, and sulfur properties of some forest soils on Barro Colorado Island, Panama. Biotropica 20, 2–10.

Young H J and Young T P 1983 Local distribution of C_3 and C_4 grasses in sites of overlap on Mount Kenya. Oecologia (Berl.) 58, 373–377.

Section editor: P. M. Attiwill