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Hydraulic architecture and water use of selected species from a lower montane forest in Panama

Abstract Plant water relations of nine woody species were studied in a lower montane rain forest in Panama. These data provide a partial test of the hypothesis that hydraulic architecture of lower montane species might limit transpiration and thus leaf size or nutrient transport (as suggested by J. Cavelier and E. G. Leigh, respectively). Diurnal variation in leaf transpiration was closely correlated with changes in net radiation. Peak transpiration rates (7×10^{-5} kg s^{-1} m^{-2}) were as high as peak transpiration rates from tropical lowland forests but mean daily water use [0.39 ± 0.08 (SEM) kg m^{-2} day^{-1}] were mostly lower than comparable data from tropical lowland forests. Thus transpiration rates are sufficiently high for sufficiently long periods to make it unlikely that nutrient transport is limited by transpiration. Another objective of this study was a comparison of two different methods to measure hydraulic conductance (K_h = flow rate per unit pressure gradient) and leaf specific conductance of stem segments ($K_L = K_h$/leaf area distal to the segment). The results obtained with the traditional conductivity apparatus and the high pressure flow meter method, yielded similar results in six out of seven cases.

Key words Hydraulic architecture · Transpiration · Lower montane forest · Cloud forest

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Introduction

Tropical montane forests are among the least understood of humid tropical forest ecosystems as far as the water and nutrient dynamics are concerned (Whitmore 1990; Bruijnzeel and Proctor 1995). For example, although it has long been suggested that a suppression of transpiration due to high humidity and cloud cover and a consequent limitation of mineral supply could explain the reduced forest height with altitude (Beard 1944; Leigh 1975), available *in situ* observations of transpiration and leaf water relations are rare and contradictory: Weaver et al. (1973) reported very low transpiration rates among elfin forest species in Puerto Rico, while Cavelier (1990) found no evidence for reduced transpiration rates among cloud forest tree species in Colombia. Our lack of knowledge of the water relations of montane forest tree species is even more striking in relation to their hydraulic architecture. Recently, Cavelier (1996) proposed that cloud forest species might differ from lowland species in their hydraulic architecture and that this might lead to limitations of transpiration under sunny conditions. Cavelier (1996) has suggested that hydraulic conductance of cloud forest trees "may not be high enough to compensate for the high water losses that occur during sunny periods in montane forests. A water supply limited by the hydraulic conductance of stems would impose a reduction in leaf size and leaf area index." The well documented decline in leaf size with increasing altitude in tropical mountains has defied definitive explanation. However, there is not a single study which might provide information to test this notion. Pertinent studies have focused exclusively on lowland species (Patiño et al. 1995; Tyree and Ewers 1996).

The primary objectives of this study were therefore to compare woody species of a Panamanian cloud forest to lowland forest species in two measures of water relations: (1) diel transpiration per unit leaf area and (2) quantitative measures of hydraulic architecture such as leaf area per unit stem cross-section, hydraulic conductance, K_h, and leaf specific conductance, K_L, of stem segments.

A secondary objective of this study was to compare two different methods of measuring hydraulic conductance, K_h, and leaf specific conductance, K_L, of stem segments. The first (traditional) method (Sperry et al. 1987) is to measure K_h on excised stem segments with a wide range of diameters using a conductivity manifold while keeping tract of leaf area distal to each segment measured (for calculation of K_L). The second (faster) method is to use a high pressure flowmeter (HPFM) to measure whole shoot resistance of large shoots with leaves attached, then measuring the resistance of distal portions of the shoot by selective removal of leaves, followed by the removal of stems of different diameter size classes (Tyree et al. 1993, 1995).

Materials and methods

Field site

Our study was performed in the lower montane rain forest of the Fortuna watershed (Cordillera Central, Republic of Panama, approx. 8° 43' N, 82° 14' W) in April and May of 1994. The study site was at about 1100 m above sea level at the Centro de Investigaciones Tropicales Jorge L. Arauz of the Instituto de Recursos Hidraulicos y Electrificacion (IRHE). The forest at Fortuna had a rather open canopy. Trees were generally 20–30 m tall. A preliminary species list of phanerogamic species is supplied by Adames (1977). Only a brief description of the vegetation is available (Cavelier 1992). The physiognomic characteristics suggest that the forest is a lower montane rain forest *sensu strictu* (Grubb 1977).

Species

We chose a wide array of different species and life-forms, e.g., several pioneer and late-successional tree species, *Citharexylum macradenium* Greenm. (Verbenaceae), *Croton draco* Schlecht. (Euphorbiaceae), *Ficus macbridei* Standl. (Moraceae), *Inga punctata* Willd. (Leguminosae), *Parathesis amplifolia* Lund. (Myrsinaceae), three woody hemiepiphytes *Blakea foliacea* Gleason (Melastomataceae), *Clusia stenophylla* Standl. (Clusiaceae), *Dendropanax arboreus* (L.) Dec. & Planch. (Araliaceae), and a very common shrub in disturbed areas around the research station [*Baccharis pedunculata* (Mill.) Cabr.; Asteraceae]. All species names follow D'Arcy (1987). The parameters described below were not measured on all nine species due to limitations in available time for the field project.

Field measurements of transpiration, net radiation, temperature and humidity

Daily courses of water uptake (W', kg s^{-1}) were measured on excised branches bearing 1 to 3 m^2 of leaves, with a computer-controlled potometer described by Tyree et al. (1991). In brief, water was delivered to the branches through a water-filled plastic pipe from a 2-l container resting on a digital balance (range, 5 kg; readability ± 0.01 g). Water use was measured simultaneously on three shoots (each a different species) on any given day. Shoots were replaced every 2–3 days, and one shoot was always a reference species, *Baccharis pedunculata*. All shoots were placed in a clearing next to the field station, but water use was primarily a function of net radiation, i.e., was more during sunny than cloudy periods. The use of a reference species permitted ranking of water use of *B. pedunculata* relative to other test species given the day-to-day variation in cloud cover. At the end of

each experiment leaf area (A_L) of each branch was measured with a LI-3100 leaf area meter (Li-Cor, Lincoln, Neb.) and water uptake was expressed per unit leaf area ($E = W'/A_L$).

Simultaneously, basic climatic data were collected with a data logger (Datataker DT100; ZI-TECH Institute, Mountain View, Calif.), e.g., net radiation with an Eppley-type net radiometer (Radiation Energy Balance Systems, Seattle, Wash.), and air temperature and relative humidity with a custom-made, aspirated psychrometer. Measurements were made every 20 s and recorded as means every 300 s.

Hydraulic architecture measurements

Shoots (0.02 to 0.06 m basal diameter) were excised from plants in the early morning. The bases were immediately put into a bucket of water and recut under water to remove some of the embolisms sucked into vessels when they were cut in the air. The shoots were returned to the laboratory and either attached to a high pressure flowmeter (HPFM, see below) or were placed under water and stem segments of 0.002 to 0.04 m wood diameter and 0.1 to 0.3 m length were excised under water and attached to a conductivity apparatus. Maximum vessel lengths were estimated by air-injection methods and sufficient material was removed from the base of each branch to exclude embolisms induced by the excision of branches in the field. Record was kept of leaf area distal to each stem segment excised and leaf areas were measured with a model LI-3100 leaf area meter.

The conductivity apparatus is described elsewhere (Sperry et al. 1987). Briefly, it is a manifold constructed from stopcocks and water-filled tubing that permits parallel mounting of 10–15 stem segments. The stopcocks are used to direct water flow through one segment at a time. Water flow is from a high to a low reservoir. The typical height difference of the reservoirs are adjusted to provide a pressure difference (ΔP) across the stem segments of 4–8 kPa (= 0.4–0.8 m height difference). The lower reservoir was positioned on a four-place digital balance. Flow rate (F) is calculated by a computer programmed to read weights at specified time intervals (typically 10–20 s intervals).

The HPFM is described in detail in Tyree et al. (1995) and its use for the determination of leaf and stem hydraulic resistance is discussed in Yang and Tyree (1994) and Tyree et al. (1993). Briefly, the HPFM is a device used to perfuse water into the base of large shoots at pressures up to 700 kPa while simultaneously measuring water flow rate. The pressure applied is adjusted to provide a flow rate into the base of the shoot that exceeds the rate of transpiration from leaves, consequently the mesophyll air spaces in the leaf blades infiltrate with water and water drips from stomates. The flow rate (F) and applied pressure (P) is used to compute the hydraulic conductance or resistance of the shoot (see below). Since air bubbles in vessels are compressed to a small fraction of their original volume and partly dissolved during measurement, the HPFM is not very influenced by xylem embolism and potentially could overestimate hydraulic conductance.

Hydraulic conductance of stem segments

All hydraulic measurements were made with tap water filtered through a 0.2 μm filtration membrane. The hydraulic conductance, K_h, of stem segments in the conductivity apparatus was computed from $K_h = LF/\Delta P$ where L is the length of the stem segment. Values of K_h could also be calculated from HPFM measurements, but it required more complicated measurements and calculations as outlined below.

Whole shoots (with leaves) were perfused with water while monitoring flow rate (F) and the pressure (P) applied to the base until leaves were infiltrated with water and stable values were obtained. The whole-shoot hydraulic resistance with leaves present, R_{+L}, was calculated from $R_{+L} = P/F$. The leaves were then removed and leaf areas determined. Removal of leaves caused an increase of flow. The shoot resistance without leaves, R_{-L}, was computed from the new values of P and F. The total area of leaves removed (A_L) was measured and the hydraulic resistance of leaves were computed from $R_L = A_L$ ($R_{+L}-R_{-L}$).

Stem segment resistance to water flow were computed from successive removal of distal stem segments by diameter size class.

Fig. 1 Diel changes of water
uptake per unit leaf area (E) from
potometer measurements, relative
humidity (RH), and net radiation
on two sunny days in May 1994.
A Water uptake for *Clusia steno-
phylla* (*solid line*), *Croton draco*
(*dotted line*), **B** Water uptake for
Baccharis pedunculata, **E** Water
uptake for *Dendropanax arboreus*
(*solid line*), *Clusia stenophylla*
(*dotted line*), **F** Water uptake for
B. pedunculata, **C & G** relative
humidity, **D & H** net radiation. To
allow easy comparison with the
literature, water uptake per unit
area is given in kg s^{-1} m^{-2} $\times$ 10^{-5}
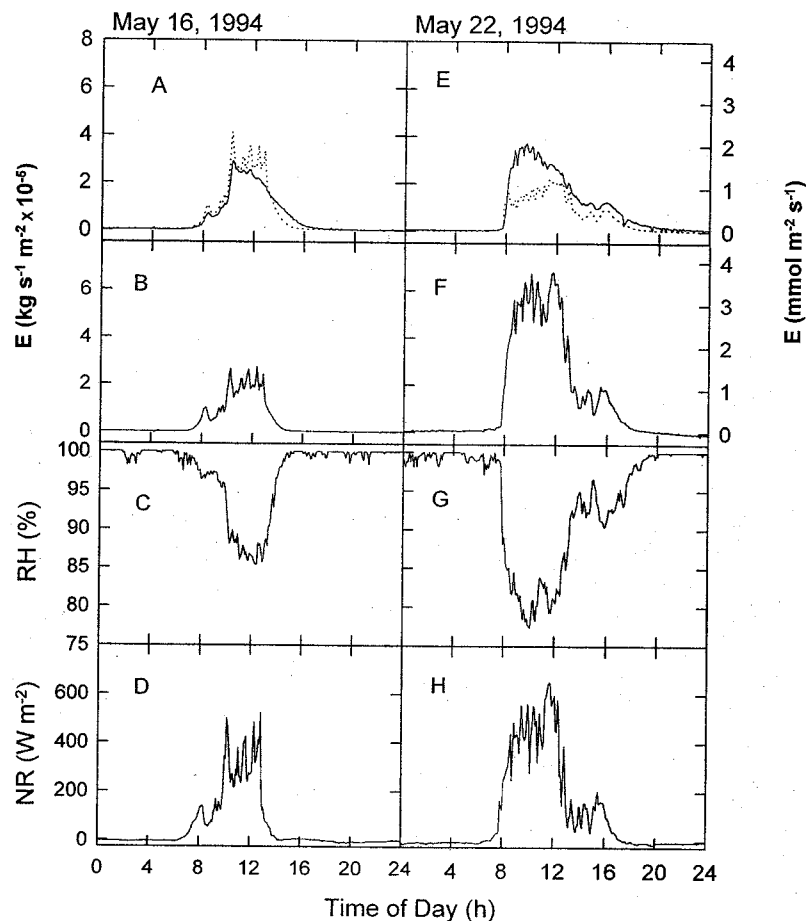and mmol s^{-1} m^{-2}; RH is in%,
and net
radiation is in W m^{-2}

Table 1 Important leaf characteristic of nine species with different life-form (T = tree, S = shrub, H = hemiepiphyte). Given are leaf area (LA, cm^2), leaf thickness (cm), water content (g m^{-2}), and specific leaf area (SLA, cm^2 g$_{DW}^{-1}$). Data are means $\pm$ SD (n)

Species	Family	Life-form	LA	Thickness	WC	SLA
Citharexylum macradenium	Verbenaceae	T	47 $\pm$ 14 (41)	0.23 $\pm$ 0.02 (10)	190 $\pm$ 21 (8)	96 $\pm$ 24 (8)
Baccharis pedunculata	Asteraceae	S	36 $\pm$ 3 (21)	0.26 $\pm$ 0.02 (10)	187 $\pm$ 13 (8)	164 $\pm$ 12 (8)
Parathesis amplifolia	Myrsinaceae	T	237 $\pm$ 88 (41)	n.d.	281 $\pm$ 22 (8)	121 $\pm$ 18 (8)
Blakea foliacea	Melastomataceae	H	42 $\pm$ 18 (22)	0.26 $\pm$ 0.01 (11)	163 $\pm$ 10 (8)	137 $\pm$ 29 (8)
Ficus macbridei	Moraceae	T/H	444 $\pm$ 99 (41)	0.29 $\pm$ 0.02 (15)	354 $\pm$ 32 (8)	62 $\pm$ 4 (8)
Inga punctata	Fabaceae	S/T	53 $\pm$ 27 (26)	0.23 $\pm$ 0.02 (10)	134 $\pm$ 6 (8)	89 $\pm$ 4 (8)
Croton draco	Euphorbiaceae	T	269 $\pm$ 65 (20)	0.20 $\pm$ 0.02 (10)	131 $\pm$ 7 (8)	161 $\pm$ 10 (8)
Dendropanax arboreus	Araliaceae	T/H	214 $\pm$ 118 (34)	0.57 $\pm$ 0.06 (10)	416 $\pm$ 39 (8)	49 $\pm$ 6 (8)
Clusia stenophylla	Clusiaceae	H	155 $\pm$ 87 (41)	0.47 $\pm$ 0.05 (12)	529 $\pm$ 26 (8)	38 $\pm$ 3 (8)

The first stem segments to be removed were all leaf bearing stems (LBS). The LBS were excised 2–4 mm basal of the last attached leaf. A record was kept of the length, L$_i$, and basal diameter of the wood, D$_i$, of each LBS. The resistance of all the LBS in parallel was calculated from R$_{LBS}$ = (P$_i$/F$_i$)–(P$_o$/F$_o$), where the subscript i refers to the initial value before removal of the stems and o refers to the final value after removal of the stems. The average K$_h$ of the stem segments removed was computed from K$_h$ = L$_R$/(n R$_{LBS}$), where n = the number of stem segments removed (and thus n R$_{LBS}$ is the average resistance of any given stem segment removed) and L$_R$ is a resistance-averaged length of the stem segments, i.e.,

L$_R$ = n/[(1/L$_1$) + (1/L$_2$) + ... + (1/L$_n$)],

where the subscripts 1 to n refer to stem segments 1 to n.

The reason for using resistance-averaged length, rather than the simple average, is that the resistance of any segment removed is proportional to its length. However, the segments removed can all be

viewed as resistances in parallel, and resistances in parallel relate to the total parallel resistance in a similar inverse fashion as in the above equation.

After removal of LBS, other stems based on basal-diameter size-class were removed. Size-classes selected were based on shoot morphology, but a typical sequence might be removal of all stems < 8 mm followed by all stems < 12, < 16 mm etc. Formulas similar to those for LBS were used to calculate K$_h$ for each size class.

Leaf specific hydraulic conductance

Leaf specific hydraulic conductance, K$_L$, was calculated by dividing K$_h$ by the leaf area distal of the stem segment for data collected with the conductivity apparatus. For K$_h$ values derived from HPFM measurements, K$_L$ was calculated from:
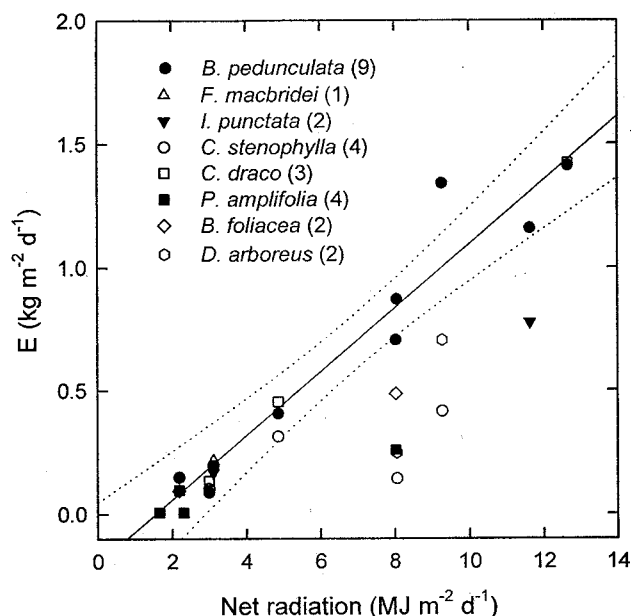
K$_L$ = K$_h$/(A$_T$/n),

Fig. 2 Correlation of daily water use of leaves (E*, kg m^{-2} day^{-1}) and net radiation (NR, MJ m^{-2} day^{-1}). Data are from potometer experiments with eight woody cloud forest species. The number of days per species is given in parenthesis. The regression line (with 95% confidence intervals) is for *Baccharis pedunculata* (E* = –0.20 + 1.29 10^{-7} NR; r^2 = 0.92)

where A_T is the total area of leaves cut from the shoot during measurement of K_h and n is the number of stem segments removed in each basal-diameter size-class.

Miscellaneous measurements

For the determination of leaf characteristics, branches similar to those used in the potometer measurements were collected. Leaf area was measured of all the leaves of these branches with a LI-3100 leaf area meter, whereas only a subset was used to determine leaf thickness, WC (leaf water content = fresh weight – dry weight, g H$_2$O m^{-2}), and SLA (specific leaf area, m^2 g$_{DW}^{-1}$). To obtain the leaf dry weight, samples were dried for 48 h at 60°C.
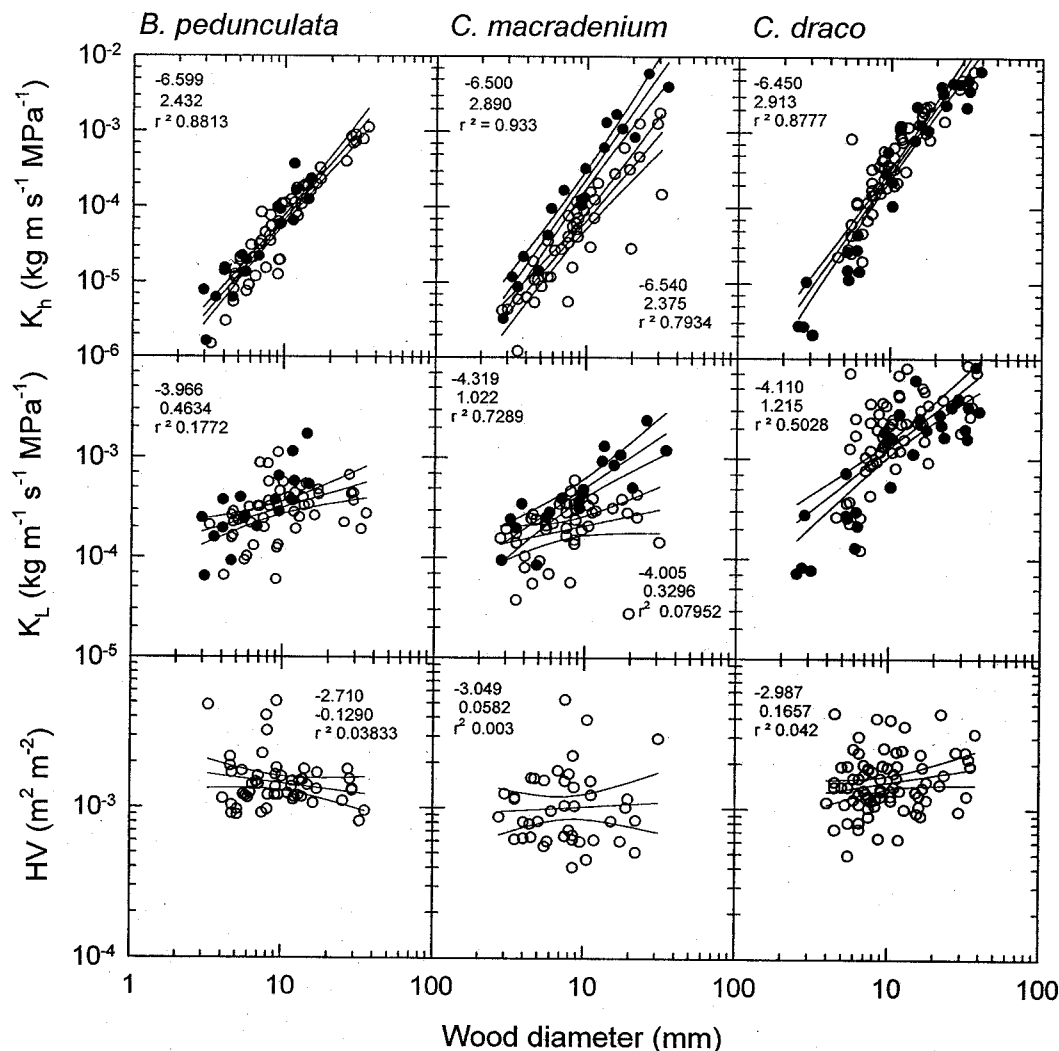
Results and discussion

The leaves of the nine species of this study show a large variation in important characteristics (Table 1). Average leaf size ranged over one order of magnitude with small mesophyll leaves in *Baccharis pedunculata* (average size: 36 cm^2) and large, macrophyll leaves in *Ficus macbridei* (average size: 444 cm^2, nomenclature *sensu* Vareschi 1980). Leaf thickness varied much less (range 0.23–0.57 mm). The values of the specific leaf area (SLA) indicate both sclerophylls (e.g. *Clusia stenophylla*, SLA = 38 cm^2 g^{-1}) and malacophylls (e.g. *Baccharis pedunculata*, SLA = 164 cm^2 g^{-1}).

Sunny days are infrequent in a cloud-forest environment, but E values are likely to be maximal on such days (Weaver 1975). The data in Fig. 1 give E, relative humidity and net radiation on the few, mostly-sunny days which occurred while measuring the uptake flux on four species. The E values during sunny periods were comparable to those observed for fast-growing, early colonizer species of trees in the lowland rainforest of Panama. Peak E values in Fig. 1 ranged from 3 to 7 × 10^{-5} kg s^{-1} m^{-2} compared to 6 × 10^{-5} for *Schefflera morototoni* (Tyree et al. 1991) and 4 to 6 × 10^{-5} for *Ochroma pyramidale* and *Pseudobombax septenatum*, respectively (Machado and Tyree 1994), and are in excess of the E values observed for many temperate trees (Tyree et al. 1991). Studies in montane tropical forests often reported much lower transpiration rates (Weaver et al. 1973; Weaver 1975). Other studies, however, e.g. Cavelier (1990) or Odum et al. (1970), show that our observations are not exceptional. Cavelier (1990) documents E values above 5 × 10^{-5} kg s^{-1} m^{-2} for several tree species of an elfin forest in Colombia, and Odum et al. (1970) report transpiration rates of approximately 2 × 10^{-5} kg s^{-1} m^{-2} for sun leaves of *Dacryodes excelsa* growing in a lower montane rain forest in Puerto Rico.

Difficulties arise in comparing E values between species since the climatic conditions varied on the different days when E was measured, but there was a strong correlation between net radiation and E. An analysis of our data revealed that >80% of the short term variation in E could be accounted for by short-term variation in net radiation (based on 30 min running means of E and net radiation) for each species (data not shown r^2 ≥ 0.8 df ≥ 20). Figure 2 correlates the total day-time water use (E*, kg m^{-2} day^{-1}) with the total net radiation (NR, MJ m^{-2} day^{-1}). In our reference species, the shrub *B. pedunculata*, the correlation was very tight (regression equation: E* = –0.2 + 1.29 NR, r^2 = 0.92). There were insufficient data for other species to see if E* followed the same trend as in *B. pedunculata*. A comparable correlation was found by Weaver (1975) in trees growing in elfin forests of Puerto Rico, but not by Cavelier (1990) in similar forests in Colombia. The latter author found no differences in daily transpiration rates on cloudy and sunny days.

Integrated net radiation was as high as 12.6 MJ m^{-2} day^{-1} with instantaneous rates reaching up to 653 W m^{-2} (Fig. 1). The highest 24-h transpiration rates (~1.4 kg m^{-2} day^{-1} = 78 mol m^{-2} day^{-1}) were observed in *C. draco* and *B. pedunculata*, the control species. For most other species daily water use was >50% of the highest values. The mean daily water use of *B. pedunculata* was 0.70 ± 0.17 (SEM) kg m^{-2} day^{-1} based on 9 days of observations, while the value for the other species ranged from 0.09 (*Parathesis amplifolia*) to 0.67 (*Croton draco*) kg m^{-2} day^{-1}. The mean daily water use of all eight species was 0.39 ± 0.08 (SEM) kg m^{-2} day^{-1} based on 26 days of observations (Fig. 2). These numbers are lower than the daily water use of lowland tree species such as *Ficus insipida* (2.0 ± 0.1 kg m^{-2} day^{-1}, n = 3), *Ceiba pentandra* (1.1 ± 0.1 kg m^{-2} day^{-1}, n = 7), *Virola surinamensis* (0.7 ± 0.2 kg m^{-2} day^{-1}, n = 3), or *Anacardium excelsum*

Fig. 3 Correlations of hydraulic architecture parameters and wood diameter of stem segments. K_h = hydraulic conductivity of stem segments (flow per unit pressure gradient), K_L = leaf specific conductivity (K_h/A), Huber Value = sapwood cross section/A_L, where A_L = total leaf area apical of the stem segment. Hydraulic conductance was measured with the traditional method (*open symbols*) and the HPFM (*closed symbols*), respectively. In *Baccharis pedunculata* and *Croton draco*, regression lines and 95% confidence intervals are for pooled data because when analyzed separately no significant difference was found. In *Citharexylum macradenium* each data set was analyzed separately. Numbers in each graph are regression coefficients for Y = b + m X, where Y = Log of the ordinate values and X = Log of the abscissa values. The top number is b, the second number is m followed by the r^2 value

(0.7 ± 0.1 kg m^{-2} day^{-1}, n = 3) during the wet season in lowland moist forest of Panama (data are means ± SEM, and are recalculated from Zotz 1992; Zotz and Winter 1994a; Zotz et al. 1995). The two lowland species with the lowest averages (*Virola surinamensis, Anacardium excelsum*) are comparable to the species of the present study with the highest 24-h water use, the shrub *B. pedunculata*. Hemiepiphytic species, however, may have considerably lower transpiration rates also in lowland forests, e.g., exposed leaves of *Clusia uvitana* lost only 0.2 ± 0.01 kg m^{-2} day^{-1} (n = 37) in the wet season on Barro Colorado Island (Zotz and Winter 1994b).
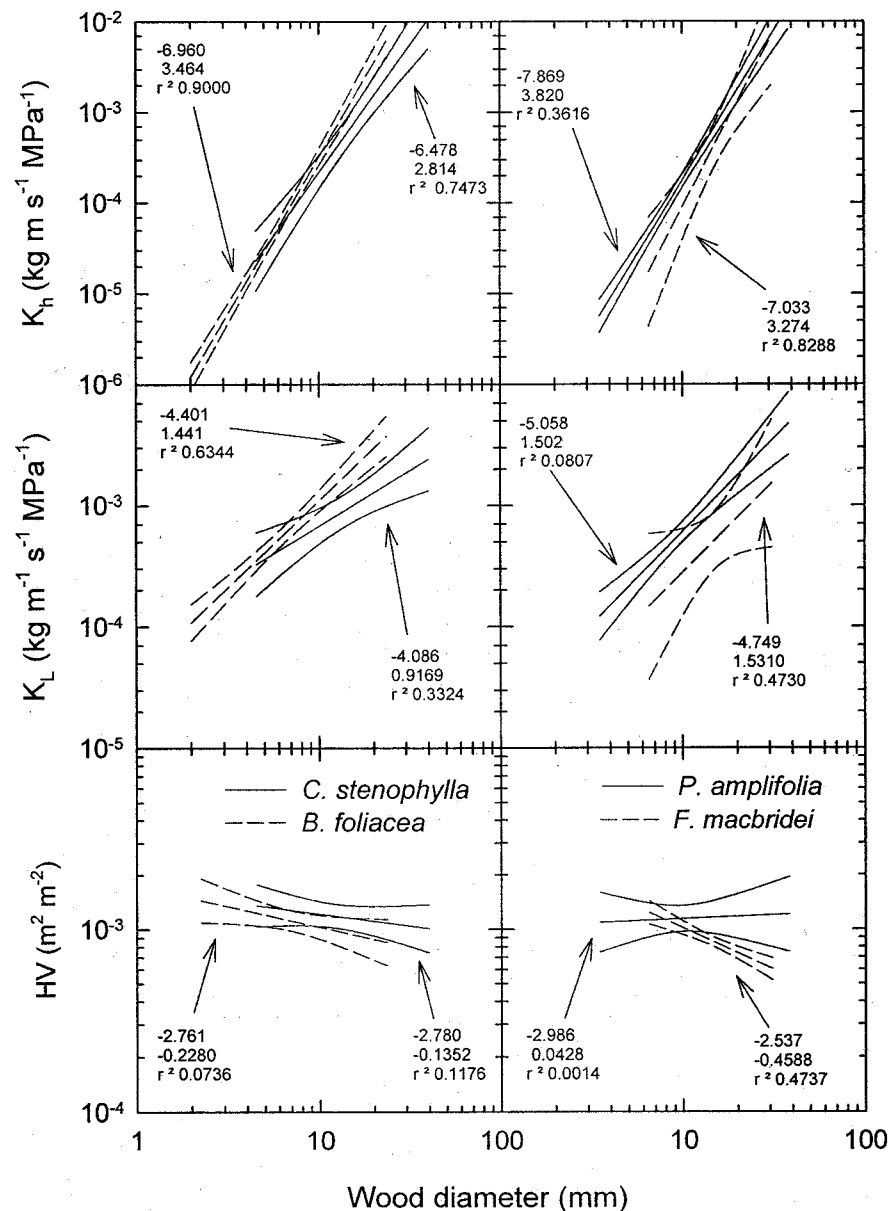
There is an apparent contradiction between diel water use rates and instantaneous water use rates. Peak rates were more comparable between the montane forest (Fortuna) site and the lowland sites, but diel water use tended to be higher in the lowland sites. The difference is probably due to the larger number of hours of high light per day observed in lowland sites compared to the Fortuna site.

Measurements of K_h and K_L were obtained using the traditional conductivity apparatus and the HPFM method, respectively. Both methods gave similar values for six out of seven species (Figs. 3, 4). In the exceptional species,

Citharexylum macradenium (Fig. 3), the two data sets were analyzed separately. For the other species data were pooled for regression analysis. We have no explanation why the HPFM method gave different results in one species. More comparisons are needed to evaluate whether the two methods are compatible. Our results give the first evidence that this may be the case in all but the exceptional case. The HPFM method is faster than the traditional method and should be evaluated in future comparative studies.

Fig. 4 Correlations of hydraulic architecture parameters and wood diameter of stem segments. Hydraulic conductance was measured with the traditional method and the HPFM method. Shown are regression lines and 95% confidence intervals for four species. Scatter of points was similar to Fig. 3. For further details see Fig. 3. Regression values are given as in Fig. 3

K_h (kg m s^{-1} MPa^{-1})

-6.960
3.464
r^2 0.9000

-6.478
2.814
r^2 0.7473

-7.869
3.820
r^2 0.3616

-7.033
3.274
r^2 0.8288

K_L (kg m^{-1} s^{-1} MPa^{-1})

-4.401
1.441
r^2 0.6344

-4.086
0.9169
r^2 0.3324

-5.058
1.502
r^2 0.0807

-4.749
1.5310
r^2 0.4730

——— C. stenophylla
– – – B. foliacea

——— P. amplifolia
– – – F. macbridei

HV (m^2 m^{-2})

-2.761
-0.2280
r^2 0.0736

-2.780
-0.1352
r^2 0.1176

-2.986
0.0428
r^2 0.0014

-2.537
-0.4588
r^2 0.4737

Wood diameter (mm)

Huber values (HV) in this study ranged from 7 to 16 × 10^{-3} m^2 wood cross-section per m^2 of leaves. This is in the upper range of lowland tropical trees which range from 1 to 16 × 10^{-3} for 15 mm diameter branches (Patiño et al. 1995). The K_L values in this study ranged from 2 to 20 × 10^{-4} kg s^{-1} m^{-1} MPa^{-1} which is at the lower end of the range of lowland tropical trees which ranged from 8 to 140 × 10^{-2} for 15 mm diameter branches (Patiño et al. 1995).

There is evidence that low K_L values can limit E under high-light conditions. The mechanism to explain this follows from the Ohm's Law analogue for water flow in whole plants (Yang and Tyree 1992). Qualitatively, the argument is as follows: the value of E is determined by the product of stomatal conductance (g$_s$) and driving force of water vapor diffusion (= difference in mole fraction across stomates), and g$_s$ is a function of leaf water potential (Ψ_L), i.e., g$_s$ tends to be maximal in high light when Ψ_L is above a

threshold value and begins to decline with declining Ψ_L when Ψ_L is below the threshold value. However, the value of Ψ_L depends on K_L; at any given E the value of Ψ_L decreases with decreasing K_L because a low value of K_L increases the drop in Ψ between the soil and leaf. Hence if K_L is too small the value of Ψ_L is always below the threshold value in high light. In our study, E values in high light rival those of lowland tropical species, hence there is no evidence of any more limitation of E in our lower montane site than in lowland sites due to differences hydraulic architecture between sites. However, the issue of how hydraulic architecture might 'limit' E in species needs more comprehensive studies than currently found in the literature. Relationships between E and stem K_L are likely to be misleading since whole plant conductance could be limited more by non-vascular conductances of roots and leaves than by vascular conductances measured by K_L. Until more comprehensive hydraulic data become avail-

able, we are limited to judging limitations imposed on transpiration by the values of E between forest sites. One approach might be to compare E values measured on intact plants to E values on excised branches measured in the same location so that net radiation, humidity and temperature are the same. In the former case E could be lower than in the latter since Ψ_L will be less in intact plants than in the excised branch because the excised branches have less stem resistance and no root resistance.

Odum (1970) and Leigh (1975) suggested that small trees of montane forests result when the transpiration is low without interruption because this would reduce transport of minerals in the transpiration stream. Arguments against these ideas have been proposed by Grubb (1977) and Medina et al. (1981). There is no evidence of transpiration-limited mineral transport at our study site, but mineral transport, in our opinion, should not be dependent on transpiration in any circumstance. Even in non-transpiring trees, there will be a continuous recirculation of Münch water which could be sufficient to transport minerals. Münch water is the water loaded into sieve tubes in leaves for the translocation of carbohydrtes to roots. In the roots the Münch water is unloaded and must return to the leaves via the xylem for reloading. The energy for this recirculation of water is provided by the energy required to load sucrose and the pressure for recirculation is osmotically driven. In non-transpiring trees the concentration of minerals in the xylem stream will be higher and the velocity of transport (m s^{-1}) will be lower than in transpiring trees but mineral transport will occur at the same rate (mol s^{-1} m^{-2}) as in transpiring trees as long as there is photosynthesis and transport of carbohydrates to roots for storage, growth and respiration.

In conclusion, we have found that: (1) The species in this study can have peak E values during sunny periods that rival those of lowland forest species, but the typical daily water use values (E*) are lower than in lowland forests because of higher cloud cover. (2) Leaf areas supported per unit stem cross-section tends to be higher in the study site than in lowland forests. (3) K_L values tend to be lower. (4) We find no evidence to support Cavelier's hypothesis (Cavelier 1996) that hydraulic architecture might lead to limitation of transpiration under sunny conditions, i.e., no more so in lowland montane than in lowland tropical forests.

References

Adames AJ (1977) Evaluacion ambiental y efectos del proyecto hidroelectrico Fortuna. Rev Lot 254–256: 1–538

Beard JS (1944) Climax vegetation in tropical America. Ecology 25: 127–158

Bruijnzeel LA, Proctor J (1995) Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? In: Hamilton LS, Juvik JO, Scatena FN (eds) Tropical montane cloud forests. (Ecological studies, vol 110). Springer, Berlin Heidelberg New York, pp 38–78

Cavelier J (1990) Tissue water relations in elfin cloud forest tree species of Serrania de Macuira, Guajira, Colombia. Trees 4: 155–163

Cavelier J (1992) Fine-root biomass and soil properties in a semideciduous and lower montane rain forest in Panama. Plant Soil 142: 187–201

Cavelier J (1996) Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman & Hall, New York, pp 399–439

D'Arcy WG (1987) Flora of Panama: checklist and Index. Missouri Botanical Gardens, St. Louis

Grubb PJ (1977) Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. Annu Rev Ecol Syst 8: 83–107

Leigh EG Jr (1975) Structure and climate in tropical rainforest. Annu Rev Ecol Syst 6: 67–86

Machado J-L, Tyree MT (1994) Patterns of hydraulic architecture and water relations of two tropical trees with contrasting leaf phenologies: Ochroma pyramidale and Pseudobombax septenatum. Tree Physiol 14: 219–240

Medina E, Cuevas E, Weaver PL (1981) Composición foliar y transpiración de especies leñosas del Pico del este, Sierra de Luquillo, Puerto Rico. Acta Cient Venez 32: 159–165

Odum HT (1970) Rainforest structure and mineral cycling homeostasis. In: Odum HT, Pigeon RF (eds) A tropical rainforest. U.S. Atomic Energy Commission, Division of Technical Information, Oak Ridge, Tenn., pp 103–164

Odum HT, Lugo A, Cintrón G, Jordan C F (1970) Metabolism and evapotranspiration of some rain forest plants and soil. In: Odum HT, Pigeon RF (eds) A tropical rainforest. U.S. Atomic Energy Commission, Division of Technical Information, Oak Ridge, Tenn., pp 103–164

Patiño S, Tyree MT, Herre EA (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic Ficus species from Panama. New Phytol 129: 125–134

Sperry JS, Donnelly JR, Tyree MT (1987) A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ 11: 35–40

Tyree MT, Ewers FW (1996) Hydraulic architecture of woody tropical plants. In Tropical Forest Plant Ecophysiology. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman & Hall, New York, pp 217–243

Tyree MT, Snyderman DA, Wilmot TR, Machado J-L (1991) Water relations and hydraulic architecture of a tropical tree (Schefflera morototoni). Plant Physiol 96: 1105–1113

Tyree MT, Sinclair B, Lu P, Granier A (1993) Whole shoot hydraulic resistance in Quercus species measured with a new high-pressure flowmeter. Ann Sci For 50: 417–423

Tyree MT, Patiño S, Bennink J, Alexander J (1995) Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. J Exp Bot 46: 83–94

Vareschi V (1980) Vegetationsökologie der Tropen. Ulmer, Stuttgart

Weaver PL, Byer MD, Bruck DL (1973) Transpiration rates in the Luquillo Mountains of Puerto Rico. Biotropica 5: 123–133

Weaver PL (1975) Transpiration rates in the elfin forest of the Luquillo Mountains of Puerto Rico. Carib J Sci 15: 21–30

Whitmore TC (1990) An introduction to tropical rain forests. Oxford University Press, Oxford

Yang S, Tyree MT (1992) Hydraulic resistance in *Acer saccharum* shoots and its influence on leaf water potential and transpiration. Tree Physiol 12: 231–242

Yang S, Tyree MT (1994) Hydraulic architecture of *Acer saccharum* and *A. rubrum*: comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. J Exp Bot 45: 179–186

Zotz G (1992) Photosynthese und Wasserhaushalt von Pflanzen verschiedener Lebensformen des tropischen Regenwalds auf der Insel von Barro Colorado, Panama. Ph.D. thesis, Würzburg

Zotz G, Königer M, Harris G, Winter K (1995) High rates of photosynthesis in the tropical pioneer tree, *Ficus insipida* Willd. Flora 190: 265–272

Zotz G, Winter K (1994a) Photosynthesis of a tropical canopy tree, *Ceiba pentandra*, in a lowland tropical forest in Panama. Tree Physiol 14: 1291–1301

Zotz G, Winter K (1994b) A one-year study on carbon, water and nutrient relationships in a tropical C_3-CAM hemiepiphyte, *Clusia uvitana*. New Phytol 127: 45–60