

# Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees

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## ABSTRACT

**In the present study the linkage between hydraulic, photosynthetic and phenological properties of tropical dry forest trees were investigated. Seasonal patterns of stem-specific conductivity ( $K_{SP}$ ) described from 12 species, including deciduous, brevi-deciduous and evergreen species, indicated that only evergreen species were consistent in their response to a dry-to-wet season transition. In contrast,  $K_{SP}$  in deciduous and brevi-deciduous species encompassed a range of responses, from an insignificant increase in  $K_{SP}$  following rains in some species, to a nine-fold increase in others. Amongst deciduous species, the minimum  $K_{SP}$  during the dry season ranged from 6 to 56% of wet season  $K_{SP}$ , indicating in the latter case that a significant portion of the xylem remained functional during the dry season. In all species and all seasons, leaf-specific stem conductivity ( $K_L$ ) was strongly related to the photosynthetic capacity of the supported foliage, although leaf photosynthesis became saturated in species with high  $K_L$ . The strength of this correlation was surprising given that much of the whole-plant resistance appears to be in the leaves. Hydraulic capacity, defined as the product of  $K_L$  and the soil–leaf water potential difference, was strongly correlated with the photosynthetic rate of foliage in the dry season, but only weakly correlated in the wet season.**

*Key-words:* fluorescence; hydraulic conductivity; phenology; photosynthesis; tropical dry forest.

## INTRODUCTION

Higher plants possess a vascular system that connects their water source, generally within the soil, to the sites of evaporation in the leaf mesophyll. The physical characteristics of this conducting system are responsible for the resistance encountered by water flowing between the soil and leaf, and this in turn determines the drop in water pressure, or potential, from the soil to the leaf. Hence the relationship between soil water potential ( $\Psi_S$ ), transpiration, and leaf water potential ( $\Psi_L$ ) is dictated by the conductivity of the vascular system. An interesting aspect of this relationship

is that the hydraulic conductivity of a plant's vascular system must therefore govern to a large degree the maximum rate of transpiration and photosynthesis of the foliage it supplies. This comes about because the leaves of higher plants tend to operate within a fairly narrow range of water potentials (generally  $-1$  to  $-5$  MPa), and a decrease in  $\Psi_L$  below a certain limit (defined by the mechanical and osmotic characteristics of the epidermal and guard cells) results in stomatal closure. The most compelling evidence for an influence of xylem conductivity on stomatal conductance ( $g_s$ ) and  $\Psi_L$  comes from experimental manipulations of the vascular system. In these manipulations, reductions in xylem conductivity induced by processes such as embolism injection (Sperry & Pockman 1993; Hubbard *et al.* 2001), root chilling (Brodribb & Hill 2000), and root pruning (Teskey, Hinckley & Grier 1983; Meinzer & Grantz 1990), cause rapid decreases in  $g_s$  or  $\Psi_L$ .

Among plant species there is an enormous range in xylem conductivity, to the extent that co-occurring species can exhibit orders of magnitude differences in the conductivity of their xylem (Tyree & Ewers 1991; Brodribb & Feild 2000; Feild & Brodribb 2001). Considering this, as well as the effects of reduced xylem conductivity by natural embolism induced by drought (Kolb & Davis 1994; Alder, Sperry & Pockman 1996) and frost (Wang, Ives & Lechowicz 1992; Nardini *et al.* 2000), it is probable that photosynthesis and growth in natural systems are constrained by the water transport characteristics of individual species. The concept that photosynthesis in natural systems may be limited by hydraulic qualities of the xylem is of particular importance, as it promises to provide new insights into the factors controlling plant productivity and death. The great majority of hydraulic work in natural systems, however, has focused on embolism (Alder *et al.* 1996; Vogt 2001), with dynamics in hydraulic conductivity described by 'percentage loss in conductivity' (PLC) (Tyree & Sperry 1989). This ratio defines the proportional increase in stem conductivity after a high-pressure flush of water is applied to excised stems or roots in order to dissolve embolisms in the wood. Unfortunately this method provides no information about the absolute conductivity of the xylem, and hence conveys little information about possible co-ordination between photosynthesis in leaves and xylem hydraulics.

Seasonally dry forest provides perhaps the best opportunity for scrutinizing the interaction between hydraulic sup-

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ply to leaves and realized photosynthetic rates. These forests are characterized by a variety of leaf habits, phenologies, and growth forms (Borchert 1994; Machado & Tyree 1994; Holbrook, Whitbeck & Mooney 1995; Medina 1995; Eamus & Prior 2001) all apparently linked to the seasonal availability of water. Although some work has focused on the hydraulic properties of seasonally dry forest species (Sobrado 1993, 1997; Prior & Eamus 2000) little attention has been paid to hydraulic co-ordination between the xylem and photosynthesis, or the effects of seasonal transitions on xylem hydraulic capacity.

In a recent article, Brodribb & Field (2000) showed that the photosynthetic capacity of leaves of tropical rainforest species was correlated with the leaf-specific hydraulic conductance ( $K_L$ ) of supporting branches. Their study used independent measures of hydraulic and photosynthetic capacities thus avoiding problems of autocorrelation associated with calculating xylem conductance from leaf transpiration and  $\Psi_L$  (Comstock 2000). In the present study we examined the co-ordination of photosynthesis and hydraulic conductivity in tropical forest exposed to large seasonal fluctuations in water availability. We compared species from a range of phylogenetic groups, which span leaf habit classes from evergreen through brevi-deciduous to fully deciduous. The diversity of phenological behaviour allowed us to assess the relation between xylem intrinsic conductivity ( $K_{SP}$  wood conductivity per unit cross-sectional area) and factors such as leaf to sapwood area ratio (Huber value), photosynthetic rate, and leaf water potential. We commenced measurements during the middle of the dry season and monitored hydraulic conductivity, photosynthesis and water potential through into the wet season, thus encompassing leafless and leafy phases of deciduous species. Our aims were to examine the questions: how are xylem hydraulics and photosynthesis co-ordinated in tropical dry forest? Does this relationship change when moving from dry to wet season? Do species with different leaf habits and phenologies illustrate different relationships between wood hydraulics and leaf photosynthesis.

## MATERIALS AND METHODS

### Study site

This investigation was undertaken in the Santa Rosa National Park, located on the Northern Pacific coast of Costa Rica (10°52' N, 85°34' W, 285 m above sea level). The mean annual rainfall in the park is 1528 mm however, more than 90% of this falls between the months of May and December, resulting in a pronounced dry season. The dry season is accompanied by strong trade winds, low relative humidity and high irradiance, all of which contribute to generate a high evaporative demand. Diurnal and seasonal temperature ranges are relatively small, with a mean annual temperature of 28 °C.

The vegetation in the park comprises a heterogeneous mosaic consisting of various stages of regeneration from former pastures as well as some small areas of primary

forest. Evergreen and deciduous species can be found at all successional stages, however, the percentage cover by evergreen species is greatest in the mature forest, and deciduous species tend to be more dominant in earlier successional stages.

### Plant material

Twelve species were chosen, five of which were deciduous, three were evergreen, and four were classified as brevi-deciduous. In brevi-deciduous species an annual exchange of leaves occurs, at which time all leaves are shed and a flush of new leaves immediately follow. The deciduous species were: *Bursera simaruba* (Burseraceae), *Calycophyllum candidissimum* (Rubiaceae), *Enterolobium cyclocarpum* (Fabaceae) *Gliricidia sepium* (Fabaceae), and *Rhedera trinervis* (Verbenaceae). Evergreen species were: *Curatella americana* (Dilleniaceae), *Simarouba glauca* (Simaroubiaceae), *Quercus oleoides* (Fagaceae) and brevi-deciduous species: *Byrsonima crassifolia* (Malpighiaceae), *Hymenaea courbaril* (Fabaceae), *Swietenia macrophylla* (Meliaceae) and *Manilkara chicle* (Sapotaceae). All sample trees were less than 5 m tall and located in open sites, giving good access to fully illuminated branches.

### Hydraulic conductivity

Hydraulic conductivity was measured on segments excised from the distal ends of the branches in all species. The size of excised segments was standardized such that diameters fell in the range 2–5 mm with the bark removed and lengths were 0.15–0.35 m. Care was taken to ensure that stem segments contained no through vessels (i.e. vessels that were open at both ends). The vessel lengths were measured by injecting air at 0.1 MPa into the cut end of segments and cutting the distal end of the segment back until air bubbles were first seen to emerge from xylem vessels. Vessel lengths were surveyed every month in all species. Using segments that included the junction from stem to petiole was the safest way to ensure that all vessels contained at least one end-wall.

Branches were collected approximately every 30 d between 1030 and 1130 h and cut under water to ensure no embolisms were introduced into the measured segment. Branches were selected with a cluster of leaves at the tip such that when leaves were removed, the cut ends of the petioles were equidistant from the initial cut (this allowed the length of the segment to be simply expressed). Branches were then transferred to the laboratory where they were re-cut under water, leaves removed and bagged, and stems attached to a flowmeter for measurement of hydraulic conductivity. The flowmeter was similar to that described in Brodribb & Field (2000), and worked on the principal of measuring the decrease in water pressure across a capillary tube of known resistance connected in series with the segment to be measured. Water flowed from a head pressure of around 0.01 MPa resulting in delivery pressures to the stem of approximately half this value. To

avoid problems with ions affecting conductivity measurements (Zwieniecki, Melcher & Holbrook 2001) the stem perfusing solution was filtered (0.1  $\mu\text{m}$ ) and KCl was added to make a concentration of 0.01 M. Once the stems were attached to the flowmeter they were allowed to equilibrate (generally requiring less than 5 min) and the head pressure and delivery pressure recorded. From these two figures and the length of segment, its conductivity could be calculated ( $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}$ ). The stems were then perfused with safranin dye to visualize the conductive wood area. Measurement of the leaf area using a digital camera (Epson, Oregon, USA) and image analysis software (Scion Image, National Institute of Health, Bethesda, MD, USA), as well as the determination of stem cross-sectional area immediately proximal to the cut petioles, enabled stem conductivity to be expressed as the intrinsic conductivity of the wood ( $K_{\text{SP}}$ ;  $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ ) and leaf-specific conductivity ( $K_{\text{L}}$ ;  $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ ).

### Chlorophyll fluorescence

We used chlorophyll fluorescence to measure the photosynthetic activity of leaves. The quantum yield of photosystem II electron transport ( $\phi_{\text{PSII}}$ ) was determined in the light using a miniPAM portable fluorometer (Waltz, Effeltrich, Germany) operated in the field as described by Bilger, Schreiber & Buck (1996). Preliminary measurements made throughout the day indicated that  $\phi_{\text{PSII}}$  determined at a PPFD of 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  peaked between 1000 and 1200 h, and there was no evidence of strong midday depression of  $\phi_{\text{PSII}}$  (T.J. Brodribb, unpubl. results). Measurements were carried out at least every 30 d within 60 min of 1030 h and on cloudless days. We selected fully expanded leaves from exposed, undamaged branches and  $\phi_{\text{PSII}}$  was determined by measuring the increase in chlorophyll fluorescence during the application of a single saturating flash of light (Genty, Briantais & Baker 1989) to leaves illuminated by the internal actinic light set to produce 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at the leaf surface (PPFD in full sun at Santa Rosa was between 1900 and 2200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Saturation pulses were applied for 0.8 s at an intensity of 3500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Photosynthetic rates were expressed as electron transport rates (ETR). The ETR was calculated using Eqn 1:

$$\text{ETR} = \phi_{\text{PSII}} I \alpha / 2 \quad (1)$$

where  $I$  is the incident PPFD (in the waveband 400–700 nm);  $\alpha$  is the leaf absorbance, taken here as 0.84 (Björkman & Demmig 1987); and the factor of 2 accounts for the fact that two photons are required per electron passed through PSII, assuming linear electron flow, and even distribution of absorbed quanta between PSII and PSI. Green leaves have been shown to be conservative in their leaf absorbance characteristics hence we used a value of 0.84 for  $\alpha$  as determined by Björkman & Demmig (1987), and it was assumed that the excitation energy was evenly distributed between PSII and PSI (Loreto, Domenico & Di Marco 1995; Bilger *et al.* 1996). The units

of ETR are  $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$ , although it should be noted that values of ETR may not be precise due to small variations in  $\alpha$ .

### Water potential

Pre-dawn and midday (1100 h) leaf water potentials were measured monthly using a pressure chamber (PMS Instruments, Oregon, USA). We assumed that the mean soil water potential at the root level of each species was equal to the pre-dawn  $\Psi_{\text{L}}$ . Midday water potentials were measured on transpiring leaves as well as others that had been covered to prevent water loss allowing us to calculate how much of the water potential gradient between soil and leaf occurred due to the hydraulic resistance of the leaf itself. Five leaves of each species were covered with plastic wrap and aluminium foil in the early morning. These covered leaves and five adjacent uncovered leaves were collected for midday water potential measurements. Water potential of the wrapped (non-transpiring) leaves was assumed to equal the xylem water potential at the petiole ( $\Psi_{\text{X}}$ ).

### Sampling protocol

We sampled  $K_{\text{SP}}$ ,  $K_{\text{L}}$ , ETR and  $\Psi_{\text{L}}$  at least every 30 d for each of the 12 species. Trees were sampled between April and August 2001 spanning a period from mid-dry season to mid-wet season. Branches for hydraulic measurements were collected from four individual trees of each species and  $\Psi_{\text{L}}$  and ETR measurements were made from equivalent branches from the same trees. Mean  $\Psi_{\text{L}}$  for trees was calculated from a sample of five leaves, and mean ETR was calculated from 15 to 20 measurements on each tree. Measurements of  $K_{\text{L}}$ ,  $\Psi_{\text{L}}$  and ETR were all made within 90 min of 1130 h on a single day for each species.

At three times of the year (mid-late dry season, end of the dry season and early wet season)  $\Psi_{\text{S}}$  was measured from the pre-dawn water potential of eight leaves (two leaves from each of four trees) of each species, enabling calculation of the water potential gradient from the soil to transpiring leaves ( $\Delta\Psi$ ). This enabled us to examine both the relationship between the intrinsic conductivity of the stems ( $K_{\text{L}}$ ) and photosynthetic potential of the foliage, as well as the interaction between realized hydraulic and photosynthetic potential. Assuming the Ohm's law analogy for water flow in plants (van den Honert 1948)  $g_{\text{s}}$  should be related to  $K_{\text{p}}$ , the whole-plant leaf-specific conductivity, by Eqn 2 during steady-state flow, when the effects of stem capacitance are minimal.

$$g_{\text{s}} = K_{\text{p}} \Delta\Psi / D \quad (2)$$

where  $\Delta\Psi = \Psi_{\text{S}} - \Psi_{\text{L}}$ , and  $D$  is the vapour pressure deficit. Because stomatal optimization leads to a linear relationship between  $g_{\text{s}}$  and assimilation (Cowan & Farquhar 1977; Wong, Cowan & Farquhar 1985), and variation in  $D$  at 1030 h (the time of sampling) was small during the dry season, the realized hydraulic capacity can be expressed as ( $K_{\text{p}} \Delta\Psi$ ). Hence we examined the interaction between

mean ( $K_L \Delta\Psi$ ) and mean ETR among species, assuming branch conductivity was uniformly scaled to whole-plant conductivity (Nardini & Salleo 2000).

## Statistics

Linear regressions were fitted to data relating ETR and hydraulic capacity. Comparisons of regressions for deciduous, evergreen and brevi-deciduous were made using the general linear models procedure of SAS (SAS Institute, Cary, NC, USA). Where regressions were found to be significantly different, an analysis of covariance was made to compare regression means and  $y$ -intercepts.

## RESULTS

### Seasonal patterns

Distinct patterns of  $K_{SP}$  dynamics from dry to wet season were apparent in the different species, however, hydraulic behaviour was not uniquely related to phenology (Fig. 1). In three of the five deciduous species, minimum  $K_{SP}$  was  $<0.5 \text{ kg s}^{-1} \text{MPa}^{-1} \text{ m}$ , whereas the other two species had dry season values of approximately  $1 \text{ kg s}^{-1} \text{MPa}^{-1} \text{ m}$ . In all but one of the deciduous species, large (up to nine-fold) increases in  $K_{SP}$  were observed near the time of the first rainfall of the wet season, yielding the highest  $K_{SP}$  values measured in this study ( $3.5\text{--}3.8 \text{ kg s}^{-1} \text{MPa}^{-1} \text{ m}$ ). The value of  $K_{SP}$  in *Enterolobium cyclocarpum* increased significantly before the rains began (Fig. 1), coinciding with the dry season leaf expansion that is so pronounced in this species (Daubenmire 1972; Janzen 1983). *Gliricidia sepium* also showed some increase in  $K_{SP}$  prior to the onset of the rainy season. Early leaf flushing also occurs in this species, although to a lesser extent than in *Enterolobium cyclocarpum*. *Calycophyllum candidissimum* dif-

fered from the other deciduous species by having  $K_{SP}$  remain essentially constant ( $\sim 1 \text{ kg s}^{-1} \text{MPa}^{-1} \text{ m}$ ) throughout the study period.

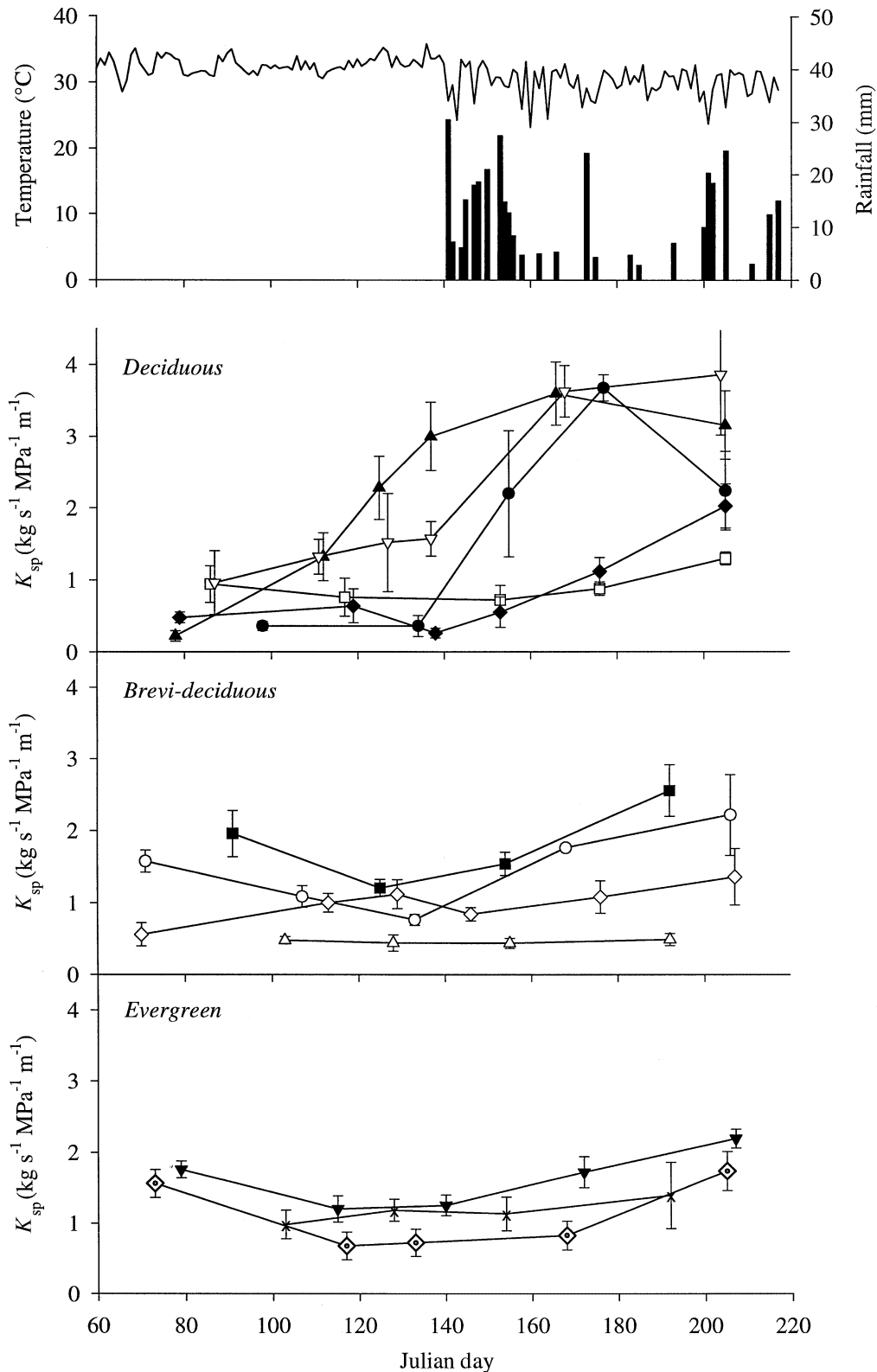
In contrast to deciduous trees, the three evergreen species were somewhat conservative in their response of  $K_{SP}$  to seasonal change (Fig. 1). The value of  $K_{SP}$  remained basically constant in one species (*Curatela americana*), whereas the other two evergreen species exhibited moderate increases in  $K_{SP}$  following the onset of the rains. The minimum values of  $K_{SP}$  in evergreen species ranges between 0.8 and  $1.3 \text{ kg s}^{-1} \text{MPa}^{-1} \text{ m}$ , whereas maximum values were  $<2 \text{ kg s}^{-1} \text{MPa}^{-1} \text{ m}$ . Brevi-deciduous species were intermediate between deciduous and evergreen both in terms of variability and the magnitude of  $K_{SP}$ .

Although the maximum  $K_{SP}$  and  $K_L$  (July) were highest in deciduous species followed by evergreen and lowest in brevi-deciduous species (Table 1), only the  $K_{SP}$  of deciduous and evergreen species could be differentiated at a significant level  $P < 0.05$  ( $t$ -test). The large amount of variation in maximum  $K_{SP}$  and  $K_L$  amongst brevi-deciduous species meant that they were not significantly different to either of the other two leaf phenological groups. A similar pattern was noted for the ratio of sapwood to leaf area, with deciduous species on average dedicating less sapwood per unit leaf area than other species (Table 1), although again only deciduous and evergreens were statistically distinguishable at the  $P < 0.05$  level ( $t$ -test).

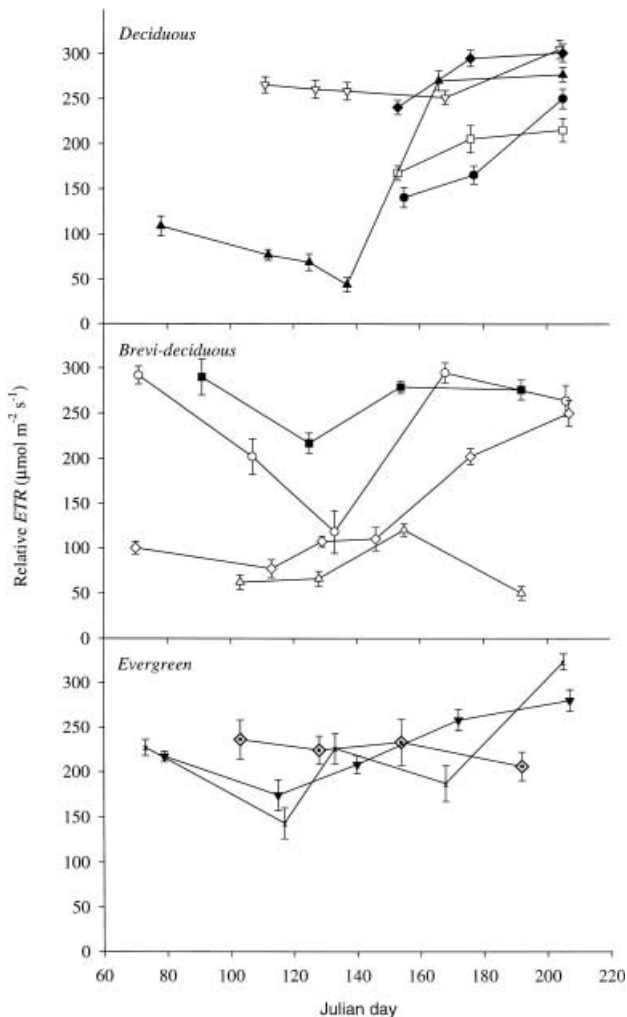
The mean ETR was extremely variable among species prior to the first rainfall of the wet season, although within 60 d of the first rainfall, photosynthesis in all but one species had converged to similar rates (Fig. 2). The single exception was *Manilkara chicle*, which maintained a low mean ETR during the entire study period. In this species leaf shedding occurs during the rainy season, and thus leaves measured in July were close to being shed. There was no trend in the mean ETR between the three phenological

**Table 1.** Hydraulic parameters for the 12 species used in this study. All parameters were measured during the early wet season (July), except minimum leaf water potential which spans the entire period of the study. Means and standard errors are shown for leaf-specific conductivity ( $K_L$ ;  $\text{kg s}^{-1} \text{MPa}^{-1} \text{ m}$ ), the ratio of sapwood to leaf area (Huber value), midday leaf water potential ( $\Psi_L$ ; MPa), the water potential drop from stem xylem to bulk leaf ( $\Psi_L - \Psi_X$ ; MPa), and the minimum leaf water potential ( $\Psi_{\min}$ ; MPa)

Species	$K_L \times 10^{-4}$	Huber value $\times 10^{-4}$	Midday $\Psi_L$ (July)	$\Psi_L - \Psi_X$	Annual min. $\Psi_{\min}$
Evergreen					
<i>Curatela americana</i>	1.27 $\pm$ 0.18	1.08 $\pm$ 0.11	-1.34 $\pm$ 0.06	-0.75 $\pm$ 0.04	-1.79 $\pm$ 0.06
<i>Quercus oleoides</i>	1.99 $\pm$ 0.35	1.18 $\pm$ 0.14	-1.01 $\pm$ 0.15	-0.43 $\pm$ 0.06	-3.48 $\pm$ 0.07
<i>Simarouba glauca</i>	3.66 $\pm$ 0.20	1.70 $\pm$ 0.08	-1.46 $\pm$ 0.07	-0.61 $\pm$ 0.04	-2.01 $\pm$ 0.06
Deciduous					
<i>Bursera simaruba</i>	2.14 $\pm$ 0.46	0.54 $\pm$ 0.07	-1.02 $\pm$ 0.05	-0.35 $\pm$ 0.05	-1.62 $\pm$ 0.02
<i>Calycophyllum candidissimum</i>	1.37 $\pm$ 0.16	0.95 $\pm$ 0.14	-1.36 $\pm$ 0.07	-0.39 $\pm$ 0.05	-2.37 $\pm$ 0.03
<i>Enterolobium cyclocarpum</i>	4.26 $\pm$ 0.54	1.27 $\pm$ 0.19	-0.96 $\pm$ 0.16	-0.12 $\pm$ 0.04	-1.98 $\pm$ 0.02
<i>Gliricidia sepium</i>	2.75 $\pm$ 0.19	0.67 $\pm$ 0.10	-1.29 $\pm$ 0.10	-0.44 $\pm$ 0.04	-1.79 $\pm$ 0.05
<i>Rhedeia trinervis</i>	2.62 $\pm$ 0.60	1.22 $\pm$ 0.20	-1.36 $\pm$ 0.06	-0.53 $\pm$ 0.02	-2.96 $\pm$ 0.16
Brevi-deciduous					
<i>Byrsonima crassifolia</i>	2.25 $\pm$ 0.57	0.83 $\pm$ 0.11	-1.68 $\pm$ 0.05	-0.75 $\pm$ 0.05	-2.38 $\pm$ 0.05
<i>Hymenaea courbaril</i>	1.69 $\pm$ 0.22	1.07 $\pm$ 0.15	-1.98 $\pm$ 0.03	-0.64 $\pm$ 0.01	-3.11 $\pm$ 0.02
<i>Manilkara chicle</i>	0.48 $\pm$ 0.08	1.02 $\pm$ 0.20	-2.34 $\pm$ 0.05	-0.78 $\pm$ 0.08	-4.59 $\pm$ 0.09
<i>Sweitenia macrophylla</i>	1.44 $\pm$ 0.20	0.84 $\pm$ 0.11	-2.16 $\pm$ 0.06	-0.88 $\pm$ 0.03	-2.69 $\pm$ 0.05



**Figure 1.** Rainfall and noon temperature during the study period at Santa Rosa National Park are illustrated in the top panel. Lower panels show patterns of mean  $K_{sp} \pm \text{SE}$  ( $n = 4$ ) in the 12 species studied. The first of these shows the deciduous species: *Bursera simarouba* (●), *Enterolobium cyclocarpum* (▲), *Calycophyllum candidissimum* (□), *Rhedera trinervis* (◇), and *Gliricidia sepium* (▽). The middle panel shows the brevi-deciduous species: *Byrsonima crassifolia* (○), *Hymenaea courbaril* (■), *Sweitenia macrophylla* (◇), and *Manilkara chicle* (△). In the lower panel, the evergreen species *Curatella americana* (×), *Simarouba glauca* (◇), and *Quercus oleoides* (▼) are shown.



**Figure 2.** Changes in mean midday electron transfer rate (ETR)  $\pm$  SE ( $n = 15$ ) for leaves of the five deciduous, four brevi-deciduous and three evergreen species throughout the study period. Species are labelled as in Fig. 1. A dotted line is shown to represent the date of the first rainfall of the wet season.

classes. The two deciduous species that expanded their leaves prior to the onset of the rains differed markedly in measured ETR. The value of ETR in recently expanded leaves of *Enterolobium* decreased with time until the onset of the rains, at which point they markedly increased. In contrast, ETR in young *Gliricidia* leaves were equally high in both the weeks preceding and following the onset of the rainy season (Fig. 2).

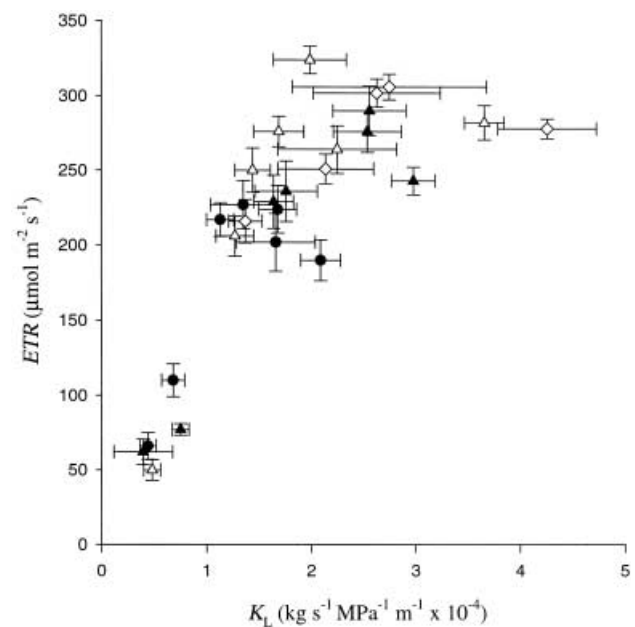
### Photosynthetic–hydraulic co-ordination

Mean leaf-specific hydraulic conductivity of excised stems was clearly related to the mean ETR in all species (Fig. 3). The data appear to show an initial strong dependence of ETR upon  $K_L$ , which saturated at values of  $K_L$  above  $3 \times 10^{-4} \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$ . All measurements, both across seasons and among species conformed to this pattern.

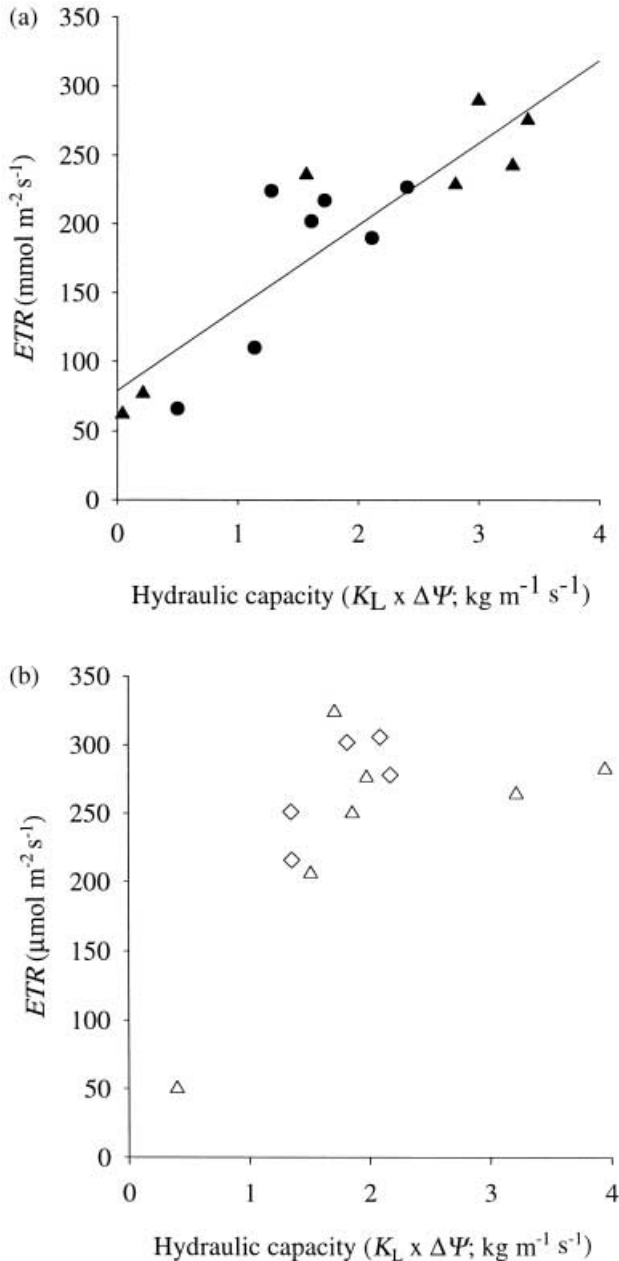
The ETR and hydraulic capacity were strongly correlated during the dry season (during which time only evergreen and brevi-deciduous species bore leaves) with a highly significant linear regression ( $r^2 = 0.87$ ;  $P < 0.001$ ) describing the relationship between these parameters (Fig. 4a). The y-intercept for the regression in Fig. 4a of an ETR of  $80 \mu\text{mol m}^{-2} \text{ s}^{-1}$  was close to the mean ETR measured in detached leaves of the evergreen species with closed stomata (T.J. Brodribb, unpubl. results).

During the wet season, the relation between ETR and hydraulic capacity in non-deciduous species was weaker ( $r^2 = 0.44$ ) although the slope and intercept of the linear regression were not significantly different to those for the dry season data (Fig. 4b). Amongst deciduous species alone, the relationship between photosynthetic and hydraulic capacities was somewhat stronger although barely significant ( $r^2 = 0.78$ ;  $P < 0.05$ ). This regression suggests that deciduous species in the rainy season realized higher photosynthetic rates than non-deciduous species with equivalent hydraulic capacities in the dry season (ANOVA;  $P < 0.01$ ).

There were significant differences in water potential gradients between the deciduous and non-deciduous species measured during the rainy season (July). The mean difference between xylem and bulk leaf water potential in deciduous species was significantly lower than in non-deciduous species measured in the rainy season ( $P < 0.05$ , Student's  $t$ -test; Table 1). However, mean  $\Delta\Psi$  from xylem to leaf in



**Figure 3.** Mean leaf-specific hydraulic conductivity  $\pm$  SE ( $K_L$ ) versus mean photosynthetic capacity (electron transfer rate)  $\pm$  SE for branch tips of the 12 species investigated [non-deciduous species measured in the mid (▲) and late (●) dry season and wet season in July (△), and deciduous species measured in July (◇)]. A strong initial response of ETR to  $K_L$  appears to become saturated when  $K_L$  was in excess of approximately  $3 \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$ .



**Figure 4.** Co-ordination between mean stem hydraulic capacity ( $K_L$  multiplied by  $\Psi_s - \Psi_L$ ) and mean photosynthetic rate (electron transfer rate of PSII; ETR) at three times during the study period. (a) Photosynthetic-hydraulic co-ordination was strong in non-deciduous species measured in the mid ( $\square$ ) and late ( $\bullet$ ) dry season ( $R^2 = 0.87$ ;  $P < 0.001$ ). (b) Deciduous species in the wet season ( $\diamond$ ) also showed correlation between mean hydraulic and mean photosynthetic capacities ( $R^2 = 0.78$ ;  $P < 0.05$ ), in contrast, non-deciduous species during the wet season ( $\Delta$ ) showed no significant correlation with hydraulic capacity.

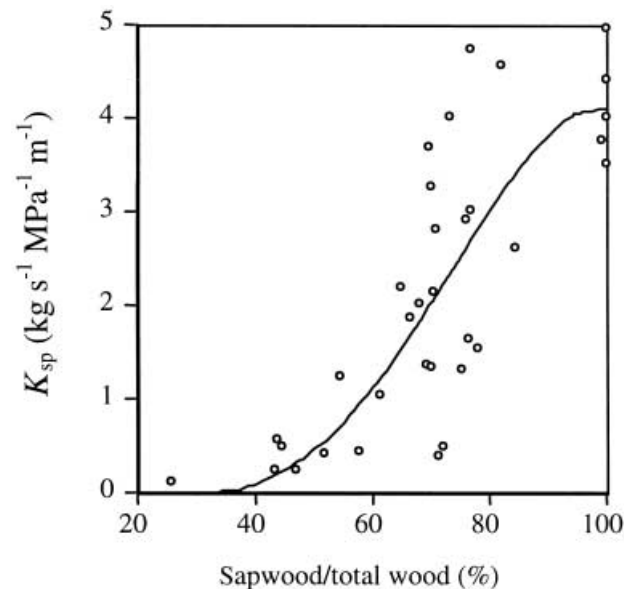
each species was strongly correlated with  $\Delta\Psi$  across the whole plant ( $r^2 = 0.72$ ;  $P < 0.001$ ), and contributed the largest component of the whole-plant  $\Delta\Psi$  (between 50 and 80%) except in *Enterolobium* where it comprised only 19%.

## DISCUSSION

In this study we have shown that hydraulic 'behaviour' was highly variable between species from the Santa Rosa tropical dry forest. However despite this variability, co-ordination between hydraulic and photosynthetic characters in the field was maintained across a strong seasonal transition, and among species with different leaf phenologies and seasonal xylem dynamics.

### Hydraulics and phenology

An enormous range of wood conductivities was observed in the 12 species measured, with deciduous species producing both the minimum and maximum values of mean  $K_{SP}$  before and after leaf flushing, respectively. Unlike some previous studies in tropical dry forest (e.g. Sobrado 1993), a range of patterns in seasonal xylem hydraulics were observed among the deciduous species, probably illustrating different leaf loss strategies. Two of the deciduous species, *Enterolobium cyclocarpum* and *Bursera simaruba* for example, underwent nearly a tenfold increase in  $K_{SP}$  from dry to wet season (Fig. 1), and in these species the  $K_{SP}$  of branches during the dry season was close to zero. Figure 5 illustrates the increase in  $K_{SP}$  of 2-year-old-shoots of *Enterolobium cyclocarpum* immediately prior to the end of the dry season, showing the rapid increase in stem conductivity as new wood was developed. In neither of these species was



**Figure 5.** Changes in the conductivity of wood in 2-year-old branches of *Enterolobium cyclocarpum* during a 3 month period at the end of the dry season. The percentage sapwood illustrates the proportion of total wood area represented by new sapwood. Data illustrate that wood from the previous wet season was completely embolized, with  $K_{SP}$  increasing in response to new wood development. Most new wood was added prior to the beginning of the wet season.

there evidence of re-use of the previous year's xylem when stems were infused with dye, presumably indicating that this xylem tissue had been blocked by air or tyloses. The question remains as to whether the complete embolism of xylem in the branch tips in the dry season preceded leaf drop, or was caused by leaf abscission; this is the subject of continuing research.

Remarkably, we found that the conductivity of branches in another deciduous species, *Calycophyllum candidissimum* did not change significantly from dry to wet season (Fig. 1). Dye infusion in branches of this species confirmed that a large proportion of xylem remained functional during the dry season, despite the fact that these trees were leafless for up to 6 months. In this species it seems that leaf senescence occurs without the embolism of associated xylem, and that xylem remains hydrated but inactive until the return of wet season rainfall.

Interspecific variation was also observed in the xylem dynamics of brevi-deciduous species, although the magnitude of this variation was much lower than that of deciduous species. Thus there was no unifying vascular trait identified that could be used to define deciduous or brevi-deciduous species, or distinguish the two. Evergreen species appeared much more conservative in their seasonal xylem dynamics, although there was still some overlap in the range of  $K_{SP}$  between deciduous and evergreen species. The inability to clearly differentiate xylem behaviour in dry forest species with different phenological patterns has been noted previously (Sobrado 1997), and appears to be associated with a combination of different rooting strategies as well as variation in the degree to which leaf senescence, xylem cavitation and soil water potential are linked. Our conclusion from the data presented here is that some deciduous species avoid drought-induced embolism prior to leaf shedding, whereas in others leaf shedding and xylem embolism are closely linked.

### Vascular and photosynthetic co-ordination

The branch hydraulic conductivity ( $K_L$ ) was related to photosynthetic capacity despite considerable seasonal and interspecific variation in the water potential gradient through individual plants (Fig. 3). Other factors being equal, one would expect that species with larger branch hydraulic conductivity would attain higher potential stomatal conductance and ETR than species with a less efficient hydraulic supply. However, the response of ETR to  $K_L$  in Fig. 3 appears to be saturating, suggesting that the higher values of  $K_L$  served more to decrease the water potential gradient across the plant rather than enhance the leaf photosynthetic rate.

The regression between hydraulic and photosynthetic capacity in the dry season was stronger than between  $K_L$  and ETR (Fig. 4a), indicating that hydraulic conductivity alone did not determine leaf photosynthetic capacity. This relationship was not significantly different to that described for evergreen conifers and angiosperm species in New Caledonia (Brodribb & Feild 2000). The linear regression

shown in Fig. 4a illustrates that hydraulic flux, assimilation rate and diffusive stomatal conductance were all co-ordinated in accordance with the Ohm's law analogy. This also indicates that in the non-deciduous species, the ratio between conductivity of the distal parts of branches and of the whole plant is conserved (Nardini & Salleo 2000; Bucci 2001). The strength of this relationship is impressive considering the fact that up to 80% of the plant's hydraulic resistance may be found in the leaf itself (Table 1; Nardini 2001), and hence that the relative proportion of total plant hydraulic resistance represented in the excised stem segments measured here must have been small.

During the wet season, co-ordination of hydraulic and photosynthetic parameters was much weaker than during the dry season (Fig. 4b). This variation cannot be attributed to differences in evaporative demand because variation in vapour pressure deficit at the time of measurement was small. This leaves three other possible explanations. First, that different mesophyll  $CO_2$  concentrations or photorespiratory rates in leaves could have affected the relationship between ETR and  $g_s$ . Second, that the ratio of branch to whole-plant conductivity might have been more variable in the wet season during leaf stem and shoot growth. Third, there may have been a decline in the optimality of stomatal regulation with respect to assimilation when soil and atmospheric moisture was abundant (Thomas, Eamus & Bell 1999).

To test the first explanation we carried out a survey of ETR and  $g_s$  in the species used here and found that there was no systematic difference between ETR versus  $g_s$  regressions in the deciduous and non-deciduous species (T. J. Brodribb, unpublished results). In examining the second explanation we note that the variation in  $\Delta\Psi$  across the leaf was closely correlated with variation in  $\Delta\Psi$  across the whole plant in all species ( $r^2 = 0.72$ ;  $P < 0.001$ ). As a result, leaf and whole-plant conductivities remained in proportion, with leaves (excepting *Enterolobium*) representing 50–80% of the whole-plant resistances. This figure falls within the range of measured leaf resistances described in other studies (Yang & Tyree 1994; Nardini 2001). The possibility remains that seasonal root growth or filling of embolisms in some species (Nardini, Lo Gullo & Salleo 1999) may result in increases in root conductivity relative to whole-plant conductivity in the wet season compared with the dry season. Root characteristics of dry tropical forest species are known to be highly variable, both seasonally (Kummerow *et al.* 1990) and between species (Sobrado & Cuenca 1979; Cuevas 1995). The final possibility is that regulation of stomatal conductance relative to photosynthesis was less optimal in the wet season, although several studies have shown this not to be the case.

A number of recent articles have illustrated linkages between the control of leaf water loss and the hydraulic supply of water under laboratory conditions or during manipulations of trees (Sperry, Alder & Eastlack 1993; Salleo *et al.* 2000; Hubbard *et al.* 2001). The data presented here demonstrate co-ordination between hydraulic conductivity of branch tips and the photosynthetic rate of leaves



under stable natural conditions (i.e. within the dry season). Some breakdown of this linkage was observed during the seasonal transition from dry to hydrated soil. We hypothesize that this may be associated with changes in the proportional contribution of branches, roots and leaves to whole-plant resistance. The surprising result that the majority of whole-plant resistance resides in the leaf may help explain why the phenology of many seasonal dry forest species appear to be synchronized more to atmospheric conditions than soil hydration or leaf age (Wright & Cornejo 1990; Myers *et al.* 1998).

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