Selbyana 16(2): 201–211

SAP FLOW RATE AND SAP NUTRIENT CONTENT OF A TROPICAL RAIN FOREST CANOPY SPECIES, *DRYOBALANOPS AROMATICA*, IN BRUNEI

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ABSTRACT. We describe a study involving simultaneous measurements of sap flow rate and sap nutrient content in three canopy and four sub-canopy trees of *Dryobalanops aromatica* Gaertn. f. (Dipterocarpaceae). Sap flow rate was measured using a heat pulse technique. Sap nutrient content was determined for potassium, calcium, total Kjeldahl nitrogen and phosphorus from samples collected diurnally in the tree crowns. Sap concentration for all nutrients at each 2-h sampling period was unrelated to tree size, except for K during the 1600–1800 h period. Relative concentrations of the four nutrients followed the general pattern of N > K > Ca > P; greatest rates of delivery (mmol h^{-1}) to tree crowns tended to occur at mid-day for each of the four nutrients. Distinct diurnal patterns of sap flow and nutrient content were apparent in most trees. Sap nutrient concentration was often positively correlated with the rate of sap flow. We discuss possible explanations for this unexpected correlation in terms of within-tree nutrient cycling, and also the postulated osmotic role of xylem sap solutes. We conclude that combining measurements of sap flow and sap nutrient content, a technique apparently not previously used in a tropical rain forest study, has considerable potential in ecophysiology.

INTRODUCTION

Many tropical rain forest trees are subject to nutrient limitation and experience periods of reduced transpiration. Transpiration rates can be reduced by high relative humidity or by low soil moisture, and tropical rain forest trees frequently experience both of these conditions. Even for tropical rain forests growing on relatively fertile soils, it has been argued that transpiration rate is a major factor in nutrient uptake (Leigh 1975). However, there has been much debate, still not satisfactorily resolved, concerning the relative effects of reduced nutrient and reduced water uptake on tree growth (Grubb 1977, 1989, Anderson 1981, Whitmore 1989, Medina *et. al.* 1990). Central to the resolution of the debate is the need for a clear understanding of the extent to which water and nutrient uptake processes are independent. Water is required for nutrient uptake and transport but its flow rate does not necessarily determine nutrient uptake rates by plants (Viets 1972). It is possible, for example, that nutrient uptake is affected by transpiration only if the nutrient status of both plant and soil are high, i.e. when active processes do not contribute substantially to uptake processes (Russell & Shorrocks 1959). Movement of soil nutrients to the root surface is generally accepted to be by two processes, diffusion and mass flow, of which only the latter is strongly associated with transpiration. Recent work has indicated that plant growth is largely independent of transpiration; the authors conclude that transpiration is not essential for the long-distance transport of minerals from root to shoot (Tanner & Beevers 1990).

The relative importance of water and nutrient shortage in tropical rain forests is the subject of continuing speculation, and Grubb (1989) identified a clear need for further experimental evidence to directly address this question. Previous combined investigations of nutrient transport and transpiration rate have, as far as we can tell, entirely neglected trees, although the long-standing need for water and solute flux data from mature trees has been recognized (Glavac *et. al.* 1990). There have been relatively few sap flow studies in the wet tropics (but see Jordan & Kline 1977, Yoshikawa et. al. 1986, Granier et. al. 1992, Meinzer et. al. 1993), and apparently no analysis of sap nutrients in mature tropical rain forest trees.

Distribution of nutrients in tree crowns can be investigated by either xylem sap or foliar sampling. Xylem sap nutrient content measurements can provide information on short-term, dynamic responses of nutrient distribution to changes in flow rate of the transpiration stream. In contrast, foliar nutrient concentrations represent the net result of longer-term cumulative effects of delivery and re-mobilization processes. Once researchers are in the canopy, xylem sap can easily be collected and subsequently analysed. In the present study, we attempt to evaluate the relationship between xylem sap flow and sap nutrient

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concentrations in a dominant canopy species, utilizing methods apparently not previously employed in combination in tropical rain forest investigations. We tested the hypothesis that diurnal xylem sap nutrient concentrations are independent of sap flow rates.

Study Site

Measurements were made in a lowland, mixed dipterocarp forest in a 0.96 ha research plot at Andulau Forest Reserve, Brunei Darussalam, Borneo (4.66 °N, 114.52 °E, 60 m above mean sea level). The study was conducted during a moderately wet season in August/September 1993; annual rainfall is *c.* 3000 mm, wet season monthly median rainfall > 100 mm (Becker 1992). Soil psychrometry measurements (data not shown) indicated that soil water varied between saturation and field capacity during the study. Soil at the site is a haplic acrisol, derived from interlaminated clay and sandstone (Ashton 1964).

Methods

The species used was *Dryobalanops aromatica* Gaertn. f. (Dipterocarpaceae), chosen because it is the most important canopy species (basal area 7% of total for trees ≥ 5 cm dbh) in the 0.96 ha research plot. The plot contained 1,484 trees ≥ 5 cm dbh, having a total basal area of 38.6 m^2 ha^{-1}. Study trees were from the emergent or canopy and subcanopy or understory components of the forest; there were respectively 4 and 3 trees in each of these two broad height groups (further details are given in the caption for FIGURE 1). Canopy (c. 30 – 40 m high) and emergent (c. 40–60 m) trees had fully-exposed crowns, whilst those of the sub-canopy were overtopped by a single crown layer. The study trees ranged in size from 9.3- 97.1 cm diameter at breast height (dbh), with projected crown area 5.3 – 239.5 m^2, and represented all major size classes in the forest apart from seedlings and saplings.

Sap flow and sap nutrients.–Sap flow rate was measured by a heat pulse velocity technique (Greenspan Technology, Warwick, Qld., Australia); probes were implanted into trees at 1.3 m height. Heat pulse velocity was recorded at four sapwood depths every 30 min. throughout each sampling day. Xylem sap collections were made on separate days from each tree; five of the seven trees were sampled again on a second, non-consecutive day, to provide replicate days. Repeat days on the remaining two trees were not possible due to insufficient sample material (smallest tree) or equipment failure. Repeat days for each tree were separated by 8-17 d; we avoided measurements on consecutive sampling days because such measurements would be more likely to be autocorrelated.

Sap sampling was conducted diurnally during five, 2-h intervals from 0800 to 1800 h. Previous studies with temperate trees have shown that canopy height (Stark *et. al.* 1985) and aspect (Moreno & Garcia-Martinez 1980) can affect xylem sap concentrations, therefore sap was collected from distal branches (c. 0.8–1.5 cm diam., 40–60 cm long), cut from the upper central part of tree crowns. Canopy access was by rope climbing (Dial & Tobin 1994); branches which could not be reached directly were cut with a pole-pruner. Sap was obtained from approximately eight branches during each 2-h sampling period, to integrate across the 2-h period, to collect sufficient volume for analysis, and to ameliorate possible branch heterogeneity effects (see Selvendran & Sabaratnam 1971). Sample branches always included newly-expanded leaves. Xylem sap was extracted using the vacuum technique described by Peoples (1989). Freshly-cut branches (with lateral branches and leaves removed) were prepared by trimming away c. 1.5 cm of bark at one end and rinsing with ethanol, to prevent possible comtamination from phloem sap (Osnubi *et. al.* 1983). This proximal end of the branch was inserted into a close-fitting rubber sleeve, connected to syringe needle which in turn was inserted through the rubber stopper of a 5 ml glass vial ('Vacutainer'; Becton Dickinson, Rutherford, NJ, USA). A second syringe needle inserted into the vial was connected to a hand-held vacuum pump (Nalgene, Rochester, NY, USA), developing a vacuum of 50–80 kN m^{-2}. The first few drops of extract were discarded, in case of contamination from cut surfaces. Sections of c. 4 cm were progressively cut from the distal end of each branch during extraction, to maintain flow. Additional branches were used as required throughout each 2-h collection period. Collection vials were surrounded by ice during extraction and temporary storage, and then were frozen in the laboratory (within 10 h) until analysis. Sap samples were analysed for total Kjeldahl N and P, and for K and Ca, using a Lachat QuickChem AE Automated Ion Analyzer (Lachat Instruments, Milwaukee, WI, USA). Each analytical run included internal reference sap samples to check reproducibility. Mean coefficients of variation for the internal reference samples in N= 2 analytical runs were respectively 16.7 %, 5.6 % and 14.6 % for N, K and Ca (n = 5), and 28.5 % for P (n = 4–5). The relatively high coefficient for P probably is related to its low concentrations and associated low signal-to-noise ratios.

We tested for effects of tree size on sap nutrient

concentration using linear regressions, with tree dbh or basal area as the independent variable. Each sampling period within the sampling day was evaluated separately. We assumed that data from collection periods within a given day for each tree were autocorrelated. We also assumed that sap nutrient concentration for any one collection period was the best estimate of sap nutrient concentration across the four 30-min. intervals within the collection period. To test whether diurnal patterns in sap nutrient concentration were related to patterns of sap flow, we conducted cross-correlation analysis for each tree on a given day. The analysis tested real-time correlations (i.e. lag = 0) and also the effect of negative and positive lags of 30 min. (i.e. lag = $\pm$ 0.5 h) and 60 min. (i.e. lag= $\pm$ 1.0 h), to reveal possible phase-shift relations; positive lags 'moved' sap nutrient concentration data 'ahead' of sap flow data, and vice versa for negative lags. Sap flow data measured at 30-min. intervals were sytematically compared with sap nutrient concentration data measured at 2-h intervals. To provide matching time intervals, we assumed that values obtained for nutrient concentrations were representative of those which would have been obtained at 30-min. measurment intervals.

Mean sap flow rates for each 2-h sap collection period were calculated for each tree. Nutrient supplying potential (NSP) was calculated for each nutrient, as the product of sap flow ($L\ h^{-1}$) $\times$ sap concentration ($mmol\ L^{-1}$) (Hocking *et. al.* 1978, Stark *et. al.* 1985). Mean NSP and SEs for all trees (n = 7) were calculated, for each of the five sap-sampling periods; only one randomly-chosen replicate day was included for each tree.

Results

Sap nutrient concentrations were consistent with those reported in temperate tree studies (e.g. Moreno & Garcia-Martinez 1980, Stark *et. al.* 1985) (FIGURE 1). For most of the four nutrients in the study, and during most of the five collection periods, no tree size-related statistically-significant ($P \leq 0.05$) relations were found; the only exception was for K, during the 1600–1800 h sampling period, which was negatively linearly related for tree size expressed as dbh ($P = 0.003$, $R^2 = 0.60$, $F = 15.22$) or basal area ($P = 0.008$, $R^2 = 0.52$, $F = 11.0$).

Diurnal patterns were apparent for both sap flow and sap nutrient concentrations for most trees and days. Relative concentrations of the four nutrients showed a general trend of N > K > Ca > P. Cross-correlation analysis revealed correlations for all trees, including replicate days, for at least one of the four nutrients (TABLE 1). For most trees and days, correlation was positive and contemporaneous (lag = 0), i.e. patterns of sap nutrient concentration and sap flow were synchronous in real-time. In many cases, positive and negative lag times of 30 min. or 60 min. also resulted in positive correlations.

Nutrient supplying potential (NSP) values showed diurnal trends for each of the four nutrients in the study, peaking at mid-day (FIGURE 2). The relatively large standard errors reflect the fact that large sap flow rate differences in trees of different sizes are not accompanied by corresponding differences in sap nutrient concentrations (e.g. compare sap flow of large and small trees in 'a' and 'd' respectively, in FIGURE 1). Individual trees showed large diurnal amplitudes in NSP (data not shown).

Discussion

We simultaneously studied diurnal sap flow and sap nutrient concentration patterns in tropical rain forest canopy trees, an approach which has apparently not been used previously. Our results are interpreted in terms of within-tree processes, including crown nutrient delivery and possible localized nutrient movements.

Our study revealed the general absence of a relation between tree size (as measured by dbh) and sap nutrient concentration at a given time. This is not surprising, given the frequent observation that xylem cross-sectional area of the stem is proportional to the mass of leaves that are supported by the stem (Ewers & Cruiziat 1991). Thus, a tree's diameter should not directly affect the concentration of sap being delivered to a given part of the crown. In this context, leaves are important both as transpiring surfaces which may, potentially at least, affect sap flow rate, and also as major sinks for sap nutrients. Xylem sap concentrations have been shown to be higher in young (presumably smaller), compared with older, temperate trees (Stark *et. al.* 1985), but we are not aware of previously-reported relationships of tree diameter with sap concentration. Results for sap K content during the 1600–1800 h sampling period indicate that tree size cannot be ignored as a factor. In this case, the larger trees generally have lower K concentrations than smaller trees, perhaps due to lower delivery rates in the crown.

There were distinct diurnal patterns of xylem sap nutrient concentrations in most trees. This has been observed in several other studies (e.g. Hocking *et. al.* 1978, Moreno & Garcia-Martinez 1980, Andersen & Brodbeck 1989), though Osnubi *et. al.* (1983) found no such variation. Afternoon (c. 1500 h) peaks for Ca and K, observed in our study, have been reported previously (Stark *et. al.* 1985). Also apparent in our data are mid-day peaks for N (c.f. Moreno & Garcia-Martinez

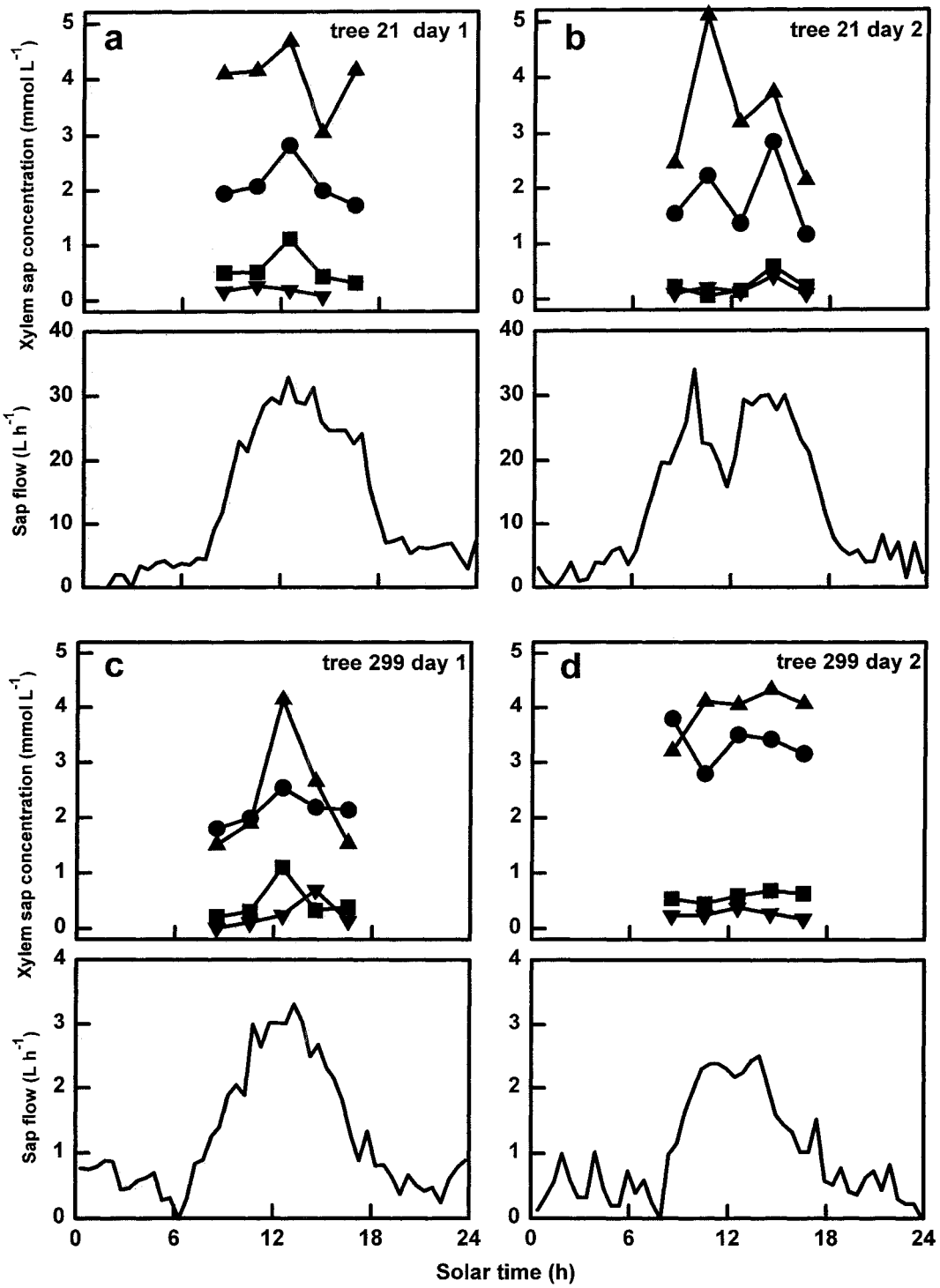
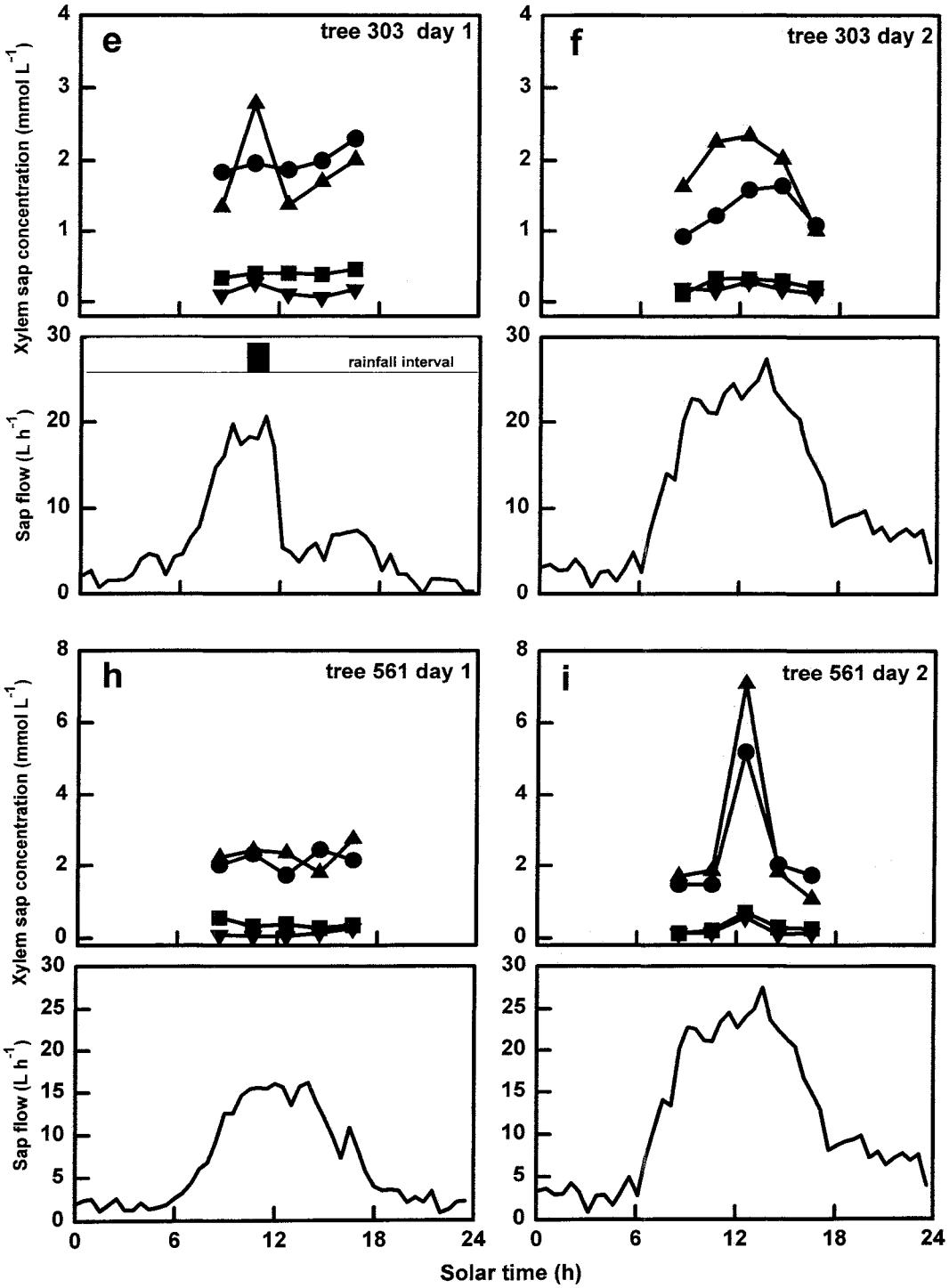


FIGURE 1 (*a* to *m*). Diurnal xylem sap nutrient concentrations of N (▲), P (▼), K (●) and Ca (■) (mmol l^{-1}) (top panels) and sap flow (L h^{-1}) (bottom panels) for seven *Dryobalanops aromatica* trees on single days. Rainfall episodes are indicated when they occurred. Tree sizes for dbh (cm), height group and (in parentheses) mean projected crown area (m^2) were as follows: tree 21= 79.5, emergent or canopy, (208.5); tree 299= 23.0, sub-



canopy or understory, (27.5); tree 303= 75.3, emergent or canopy, (234.5); tree 561= 55.5, sub-canopy or understory, (98.0); tree 9999= 46.2, canopy or sub-canopy, (77.0); tree 134= 78.7, emergent or canopy, (239.5); tree 318= 9.3, sub-canopy or understory, (5.3).

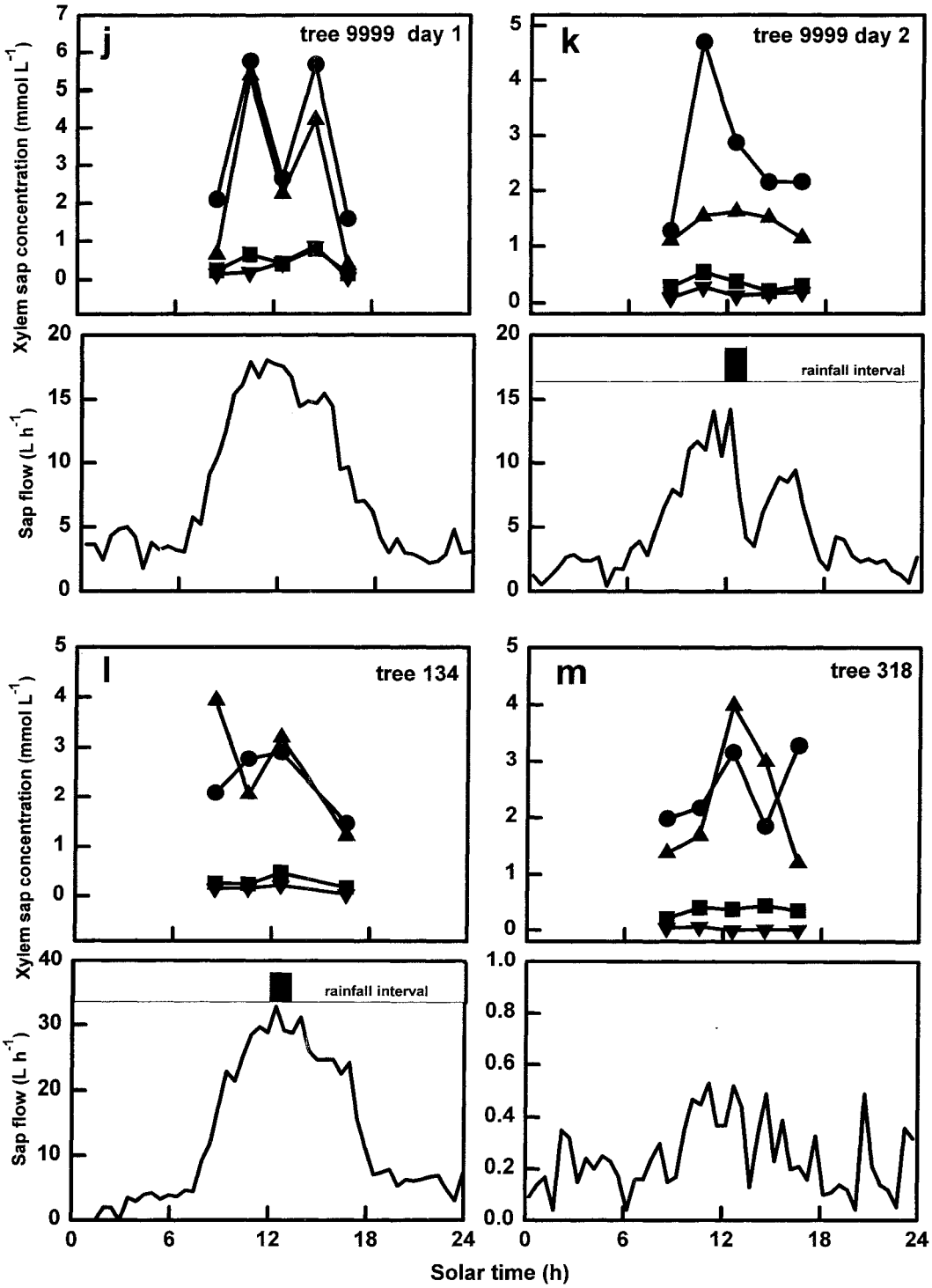


FIGURE 1. Continued.

TABLE 1. Cross-correlation data for sap nutrient concentration in relation to sap flow. Lag numbers refer to phase-shifting of sap concentration and sap flow data in relation to each other: Positive lag values indicate sap concentration data moved 'ahead' of sap flow data by 30 min (lag = 0.5 hr) or 60 min (lag = 1.0 hr). Negative lag values indicate sap concentration data moved 'behind' sap flow data by 30 min (lag = −0.5 hr) or 60 min (lag = −1.0 hr). Lag = 0, shown in bold, indicates no lag shift (i.e., contemporaneous correlation). Only significant correlation coefficients (corr.) are shown, and are positive unless otherwise indicated.

Tree	Day	Ca Lag	Ca corr.	K Lag	K corr.	N Lag	N corr.	P Lag	P corr.
21	1	0.5	0.485	**0**	**0.536**				
				0.5	0.564				
21	2							−1.0	0.496
								−0.5	0.495
				0	**0.525**			**0**	**0.558**
134	1	−1.0	0.538						
		−0.5	0.516						
		0	**0.545**	**0**	**0.562**				
				0.5	0.558				
				1.0	0.486				
299	1			−1.0	0.630	−1.0	0.580	−1.0	0.584
		−0.5	0.482	−0.5	0.635	−0.5	0.647	−0.5	0.573
		0	**0.613**	**0**	**0.690**	**0**	**0.780**		
		0.5	0.547	0.5	0.538	0.5	0.665		
						1.0	0.495		
299	2					−1.0	0.558	−1.0	0.572
						−0.5	0.616	−0.5	0.592
						0	**0.580**	**0**	**0.563**
303	1			−1.0	−0.486				
								−0.5	0.550
								0	**0.556**
								0.5	0.566
303	2	−1.0	0.547	−1.0	0.614				
		−0.5	0.645	−0.5	0.700	−0.5	0.547		
		0	**0.666**	**0**	**0.702**	**0**	**0.724**		
		0.5	0.500	0.5	0.486	0.5	0.597	0.5	0.557
						1.0	0.594	1.0	0.543
318	1					−0.5	0.499		
561	1	−0.5	−0.486						
		−1.0	−0.584						
		0	**−0.567**					**0**	**−0.496**
								0.5	−0.527
								1.0	−0.490
561	2	−1.0	0.505						
		−0.5	0.559						
		0	**0.599**	**0**	**0.518**	**0**	**0.515**	**0**	**0.498**
9999	1	−0.5	0.542			−0.5	0.590		
		0	**0.687**	**0**	**0.645**	**0**	**0.744**		
						0.5	0.557		
9999	2	−1.0	0.486						
		−0.5	0.587						
		0	**0.674**	**0**	**0.657**			**0**	**0.492**

1980, Andersen & Brodbeck 1989) and K (c.f. Hocking 1980); this was sometimes accompanied by decreased sap flow, during which sap concentrations were relatively high. One source of between-day differences appeared to be variations in rainfall. Rainfall tends to substantially depress transpiration rates in larger trees, e.g. those shown in FIGURE 1, *e* and *k*; this phenomenon is further complicated by the fact that any effects of rainfall on sap flow or sap nutrient concentration may not be immediate.

In our study, there was a generally close association between sap flow and sap nutrient concentrations, further suggested by the fact that nutrient supplying potential (NSP) values frequently showed trends similar to those of sap concentrations (NSP data for individual trees not shown). Stark *et. al.* (1985) found the net result of NSP

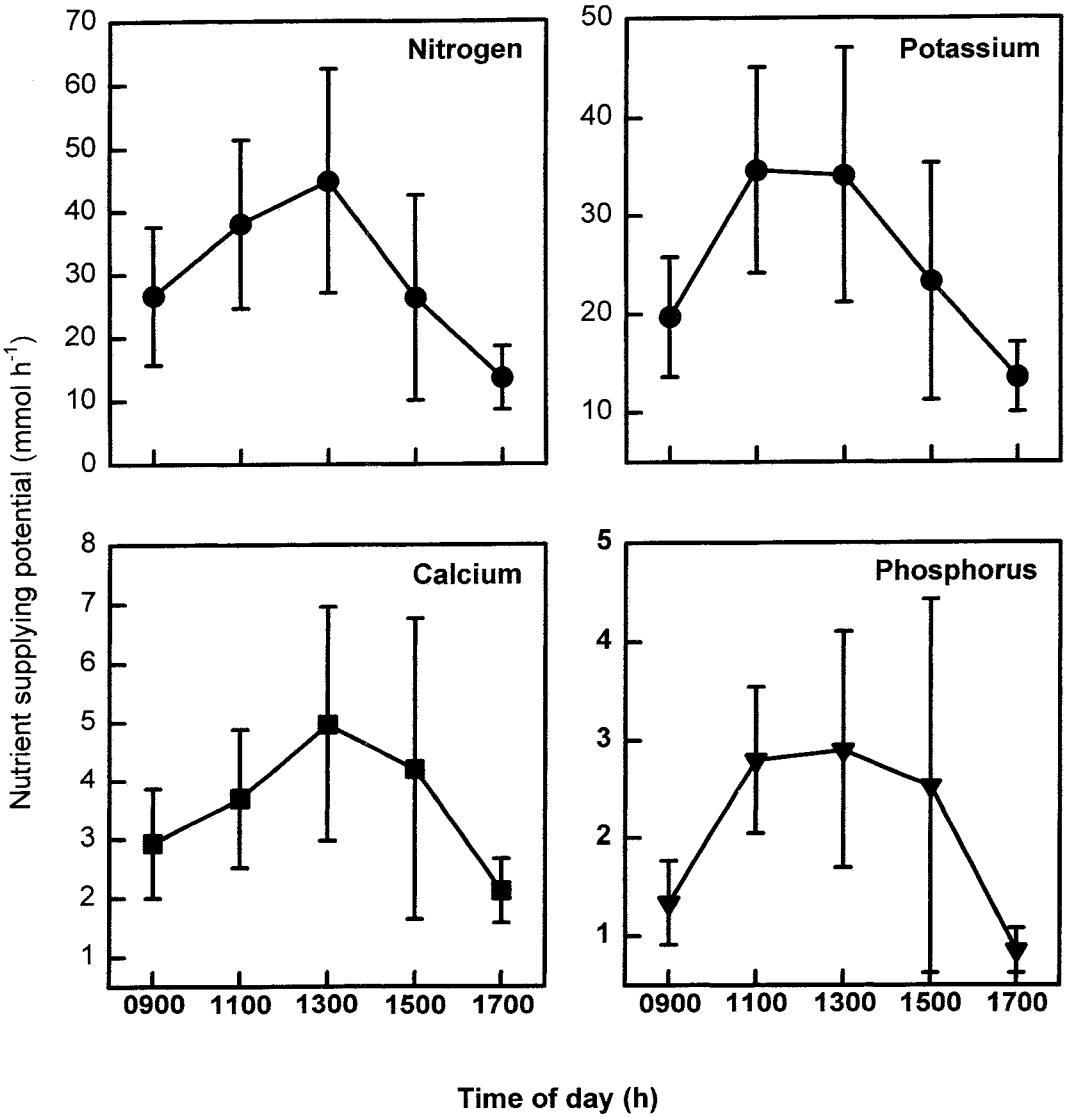


FIGURE 2. Mean NSP (mmol h^{-1}) and 2 × SEs for all trees (n = 7), for each of the five sap-sampling periods. Abscissa values are median times during each sampling period. Only one randomly-chosen replicate day was included for each tree.

is statistically equivalent to direct comparison of sap concentrations. If sap flow and sap nutrient concentration were not correlated, NSP would be expected to at least partly ameliorate diurnal trends in each variable. The large amplitudes in total diurnal NSP values indicate that delivery of nutrients to the canopy does not occur at a constant rate.

We found positive correlation of sap flow and sap nutrient concentration, for at least one nutrient, for most trees, including replicate days. In many of these cases, correlation occurs synchronously (i.e. lag = 0; TABLE 1). The most obvious interpretation of this result is that sap nutrient concentration and sap flow are in some way linked, either by a direct causal relationship, or by both being simultaneously influenced by other factors. We briefly examine the 'direction' of this relationship before turning to possible functional implications for the trees.

For several trees in this study, correlation was often maintained when sap flow and sap nutrient concentration patterns were phase-shifted by 30 min. or 60 min., indicating that asynchronous

relations may also be important. When the sap concentration data are 'moved ahead' of sap flow data by 30 min. (i.e. lag = 0.5 h) or 60 min. (lag = 1.0 h), any correlation suggests that sap concentration is *influencing* sap flow, with a corresponding 30 or 60 min. delay in the effect. There are several examples of this phenomenon in our data, particularly for K and N. Conversely, correlations were also observed when sap nutrient concentration data was 'moved back' in relation to sap flow data (i.e. lag = −0.5 h, or −1.0 h), suggesting that sap concentration is *being influenced by* sap flow; this pattern was particularly apparent with Ca. P shows a more mixed response to positive or negative lag times.

The positive correlation between sap flow and sap nutrient concentrations may have a functional basis which deserves further consideration, particularly with reference to within-plant processes. We should emphasize that this study did not attempt to examine nutrient uptake processes by roots. Though transpiration can influence nutrient uptake directly in certain circumstances, the precise mechanisms are complex (Schulze & Bloom 1984). Xylem sap nutrients, particularly N and P, are often in organic form (Bollard 1960, Herridge *et. al.* 1988, Andersen & Brodbeck 1989), and so clearly they do not enter the transpiration stream directly following root uptake. Furthermore, nutrients present in xylem sap may have been re-mobilized from pools within the plant (Glavac *et. al.* 1990, Dambrine *et. al.* 1992), or transferred from the phloem (Bollard 1960). With respect to this, we do not suspect phloem sap contamination of our samples in our study, particularly as phloem tissue was removed in the region of extraction; other workers indicate that this is not, in any case, likely to be a serious problem (Herridge *et. al.* 1988, M. Peoples, personal communication). Concentrations of xylem sap nutrients in the distal parts of the shoot system are, additionally, likely to be affected by the relative demand of nearby sinks (Bollard 1960), or by local tissue water potentials (Moreno & Garcia-Martinez 1980). Finally, high sap nutrient concentrations may simply reflect low nutrient usage (Stark 1992).

Notwithstanding these complications, our results do often reveal distinct flow-related trends in xylem sap nutrient concentrations. In this study, sap flow measurements and sap collections were made respectively at the base and crown of trees. However, we see no reason to suppose that sap flow rates in a tree crown should be substantially different from those measured (for practical convenience) at the base of the same tree, and separate experiments have shown similar diurnal patterns, with no appreciable time lag, in simultaneous tree base and crown measurements (P. Becker, unpublished data).

Experimental work on the relationship between transpiration and nutrient transport has been, as far as we are aware, exclusively conducted on herbaceous species. Working with maize, Tanner & Beevers (1990) demonstrated that, for a wide range of transpiration rates (e.g. differing by factors of two to four), supply of nutrients to shoots was fairly constant. The authors postulated non-transpirational mechanisms for xylem mass flow, by the 'pull' of water entering the phloem ('Münch counterflow'), and by the consumption of water in growth. Smith (1991) argued that it 'seems intrinsically unlikely' that these mechanisms could account for observed nutrient fluxes, and suggested instead that experimental observations could be the result of an inverse relationship between transpiration rate and xylem sap solute concentrations; i.e. the production of more concentrated xylem sap to offset the effects of reduced transpiration rate, for which there is some evidence (Moreno & Garcia-Martinez 1980). An alternative scenario, which assumes fairly constant loading of xylem sap with nutrients, is that increased transpiration rates simply 'dilute' the xylem sap (Anderssen 1929). In either case, increased sap flow should be accompanied by decreased xylem sap concentrations; our results do not provide any clear indication of these patterns. In any case, changes in sap flow rate are not accompanied by consistent changes in concentration of all four nutrients under consideration. This relative independence in the behavior of individual nutrients suggests that observed patterns are not simply the effect of sap flow rate changes on constantly-loaded nutrients.

If increases in sap flow *are* accompanied by increases in sap concentration in our study, even as an occasional phenomenon, then a mechanism needs to be invoked. Uptake of nutrients at the roots is by a combination of mass flow and diffusion. Increases in mass flow, whilst primarily influenced by transpiration rate, can only account for increased uptake rates of relatively mobile nutrients, e.g. N and Ca, but not less mobile nutrients such as K and P, whose uptake is mainly by diffusion or active transport (Viets 1972, Nye & Tinker 1977). However, diffusion and active transport may be indirectly affected by transpiration rates. Broyer and Hoagland (1943) postulate that accelerated removal by the transpiration stream of nutrients in root tissue could disturb dynamic equilibria and hence stimulate increased rates of active uptake into roots. A further possibility, briefly reviewed by Lopushinsky (1964), is that root cells become more permeable to ions as transpiration rates

increase. Similar mechanisms might also operate involving the remobilization of stored nutrients from root or shoot tissues. Our investigation examined crown delivery of nutrients, and we emphasize that this probably represents the net result of numerous processes including nutrient uptake, assimilation, local transport and re-mobilization. We make no attempt here to elucidate the specific contribution of each of these processes, and the extent to which they are directly or indirectly influenced by sap flow rates.

Strong arguments have been proposed in support of the independence of transpiration and long-distance nutrient supply (Broyer & Hoagland 1943, Grubb 1977, Schulze & Bloom 1984, Tanner & Beevers 1990, Smith 1991). The general contention is that transpiration per se is not required for the long-distance transport of nutrients, and we do not challenge the basis of this assertion. However, the possibility remains that transpiration de facto is responsible for at least part of the delivery by mass flow of nutrients from roots to shoots. Indeed, Broyer & Hoagland (1943) suggested that it may be essential in tall plants. Certainly we have difficulty accepting that transpiration does not play a direct and perhaps critical role in nutrient delivery to the crowns of large canopy trees. This assumption does not, of course, imply that rates of transpiration must be high to sustain nutrient demand, nor that trees growing in the humid tropics are at a disadvantage because of low transpiration rates. Indeed, more concentrated sap may be produced when transpiration rates are low, including at nighttime.

Much of the debate concerning the relationship between sap nutrient content and sap flow has sought either to reject the relationship, or to argue that delivery of sap nutrients to tree crowns is affected by sap flow rates. A further intriguing possibility exists, that sap solutes may influence sap flow by their osmotic activity (Zimmermann *et. al.* 1994). It has been suggested that the presence of xylem sap solutes could promote osmosis-driven sap flow in trees, including tropical trees, as an alternative to transpirationally-driven sap flow (Braun 1983). There is tentative evidence for such a mechanism in our results; positive correlations with positive lag times (lag = 0.5, 1.0), suggesting that sap flow could be 'pulled' by factors affected by sap concentration. This pattern was observed particularly for K and N, both of which could occur as osmotically-active sap solutes, and which occur at relatively high concentrations. Furthermore, highest sap concentrations for all solutes tend to occur during the mid-day period, when transpiration is often low in tropical trees (M. Barker, unpublished data), and is presumably accompanied by corresponding reductions in leaf water potential, which drives sap flow. Clearly, further research is needed to study the relationship between sap flow, sap nutrient content and transpiration.

We conclude that simultaneous determinations of sap flow and xylem sap nutrient concentration in tropical canopy trees is an informative and practically feasible technique, provided sampling methods are consistent between trees. Furthermore, we feel that this approach provides an important opportunity to fully investigate the relative independence of water and nutrient uptake. This information is particularly necessary in evaluating the factors limiting forest growth at sites subjected to nutrient or water deficiencies. Results from this study indicate that sap flow and sap delivery to the crown are frequently associated, suggesting a causal relationship between them, which may be dependent or independent of transpiration rates. We believe that a simple model is unlikely to be adequate to describe the relationship between sap flow and sap delivery to the tree crowns, which is likely to be the product of several within-tree processes.

Acknowledgements

We gratefully acknowledge funding from the Universiti Brunei Darussalam, and the generous provision of facilities by the Department of Forestry, Brunei Darussalam. We thank Hj Ruslan bin Kurus for assistance with fieldwork. We received valuable critical comments on earlier drafts of the paper from M. Carrington, N. Comerford, P. Grubb, E. Medina, R. Ostertag, M. Pinard, F. Putz, C. Woodward and an anonymous reviewer.

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