

Gas exchange and water balance of a mistletoe species and its mangrove hosts

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Summary. The gas exchange and water relations of the hemiparasite *Pthirusa maritima* and two of its mangrove host species, *Conocarpus erectus* and *Coccoloba uvifera*, were studied in an intertidal zone of the Venezuelan coast. Carbon uptake and transpiration, leaf osmotic and total water potential, as well as nutrient content in the xylem sap and leaves of mistletoes and hosts were followed through the dry and wet season. In addition, carbon isotope ratios of leaf tissue were measured to further evaluate water use efficiency. Under similar light and humidity conditions, mistletoes had higher transpiration rates, lower leaf water potentials, and lower water use efficiencies than their hosts. Potassium content was much higher in mistletoes than in host leaves, but mineral nutrient content in the xylem sap of mistletoes was relatively low. The resistance of the liquid pathway from the soil to the leaf surface of mistletoes was larger than the total liquid flow resistance of host plants. Differences in the daily cycles of osmotic potential of the xylem sap also indicate the existence of a high resistance pathway along the vascular connection between the parasite and its host. *P. maritima* mistletoes adjust to the different physiological characteristics of the host species which it parasitizes, thus ensuring an adequate water and carbon balance.

Key words: Mistletoes – Mangrove trees – Gas exchange – Water relations – Carbon isotope ratios

Mistletoes are vascular parasites of higher plant species. Although capable of photosynthesis, these hemi-parasites obtain mineral nutrients and water via haustorial connections to the internal tissues of their host. Due to their reliance on the host vascular system, mistletoes are able to grow without either roots or an extensive support system, but must modify their internal water relations in order to maintain a sufficient movement of water and nutrients from the host (Glatzel 1983). This study examines gas exchange, water uptake, and nutrient relations of a mistletoe species and two mangrove host species.

Mistletoe leaves generally exhibit higher rates of water loss than those of their host. Schulze and coworkers (1984) have proposed that the unusually high stomatal conductances and transpiration rates are, in part, a mechanism to obtain sufficient nitrogen from the host xylem stream. This hypothesis assumes that nutrients move mostly passively from the host into the mistletoe along with the mass flow of xylem water and that a continuous pathway exists between the xylem of host and mistletoe. However, a recent anatomical and physiological study challenges the assumption of xylem continuity between host and mistletoe (Lamont 1983). This poses the question of which route(s) nutrients enter the mistletoes and whether mineral uptake by mistletoes is a simple transpiration-stream phenomenon.

Host plants do not obtain carbon or nutritional benefit from mistletoes because the phloem tissues of the two species are usually not connected. On the contrary, the parasite may affect the carbon uptake and the water economy of the host. For example, Ehleringer et al. (1986) observed that infected stems experienced lower leaf water potentials, net assimilation rates, and leaf nitrogen concentrations than uninfected host stems. This may diminish growth, increase branch loss, and induce premature mortality of the infected plant (Hawksworth 1983). In some cases, however, long-term survival of the mistletoe and host has been observed. In these apparently stable host-parasite systems, a coordination of water and nutrient control mechanisms by the mistletoe may occur, allowing survival of both parasite and host (Ullmann et al. 1985).

Many mangrove tree species in the caribbean coast of Venezuela are heavily infected by mistletoes. Mangroves is used, in this work, to refer to the constituent tropical trees and shrubs restricted to intertidal and adjacent communities (Tomlinson 1986). It is well known that mangroves, which grow in the saline and anaerobic substrates of the intertidal zone, have mechanisms to cope with low soil water potentials and high levels of salt in the interstitial soil water (Clough et al. 1982). In order to maintain a positive water balance, mangroves must have very negative leaf water potentials. The question arises as to how mistletoes of mangrove trees behave under such circumstances, given that to divert water and nutrients from the host, mistletoe leaf water potentials must be even lower than those of their host.

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The purpose of this work was to investigate some water, carbon, and nutrient relations of the hemiparasite species *Pthirusa maritima* (Loranthaceae) and two of its principal tropical intertidal host species *Conocarpus erectus* L. (Combrretaceae) and *Coccoloba wifera* Jacq. (Polygonaceae). Specifically, we compare water use efficiency, nutrient content of leaves, xylem sap, and hydraulic resistance between mistletoes and hosts. The principal question that this study addresses is the coordination of water and nutrient economy of the mistletoe in relation to the physiological behavior of the host species.

Materials and methods

Site characteristics and plant material

The study site was located in the coast of the Morrocoy National Park in Falcon, a northern Venezuelan state (10° 50' N, 68° 14' W). The annual precipitation is approximately 1050 mm and has a highly seasonal distribution. During the principal dry season (May August), the soil water potential can decrease 1.0 MPa, as a consequence of increasing levels of interstitial soil water salinity. Thus, even though mangroves are rooted in substrates that are partially saturated with water, they can experience increased water deficit during the rainless season. The mean annual temperature is 26.5° C with very little seasonal variation.

The host species chosen for this study were *Conocarpus erectus* and *Coccoloba wifera*. The first species grows near the seaward end of the salinity gradient in sandy substrates that are not permanently flooded, and can be considered a "true" mangrove, although it lacks some of the morphological features, such as vivipary, that characterize true mangroves. It is tolerant of high salinities, but it also grows

near fresh water (Tomlinson 1986). *C. wifera* grows further inland, at the inward end of the gradient where soil salinity is lower. This species is not a strict or true mangrove, however dense populations of this species are conspicuous constituents of the intertidal communities in the study area. The hemiparasite species *Pthirusa maritima* has opposite leaves and long-slender stems, which gives the plant the appearance of a vine.

Field and laboratory studies

A fully portable system operating in the open mode was used to measure gas exchange in the field (LCA-2 System, The Analytical Development Co. Ltd., Hoddesdon, Herts, England). The system consisted of leaf chamber, air supply unit, and infrared gas analyzer. The infrared gas analyzer was calibrated with a gas mixture containing 326 $\mu\text{mol/mol}$ of CO_2 . The air supply unit was fitted with a variable area flow meter that was also calibrated with a soap-bubble flowmeter. Gas exchange rates were determined from flow rates, projected leaf surface area sealed within the cuvette, and water vapor and CO_2 concentration differences between reference and analysis air. Gas exchange calculations were conducted according to von Caemmerer and Farquhar (1981).

A pressure chamber was used to measure leaf water potentials (Ψ_l). Leaf temperatures were measured with 36 gauge copper-constantan thermocouples attached to the lower leaf surface. Air humidity was monitored with ventilated wet and dry bulb psychrometers installed at 1.5 m, and photon flux density was measured with a quantum sensor contained in the leaf cuvette.

Xylem sap was extracted every 2–3 h on each sampling day from host and mistletoe shoots with the pressure chamber. After the balancing pressures were obtained with each shoot, a 0.3 to 0.4 MPa pressure increase was applied

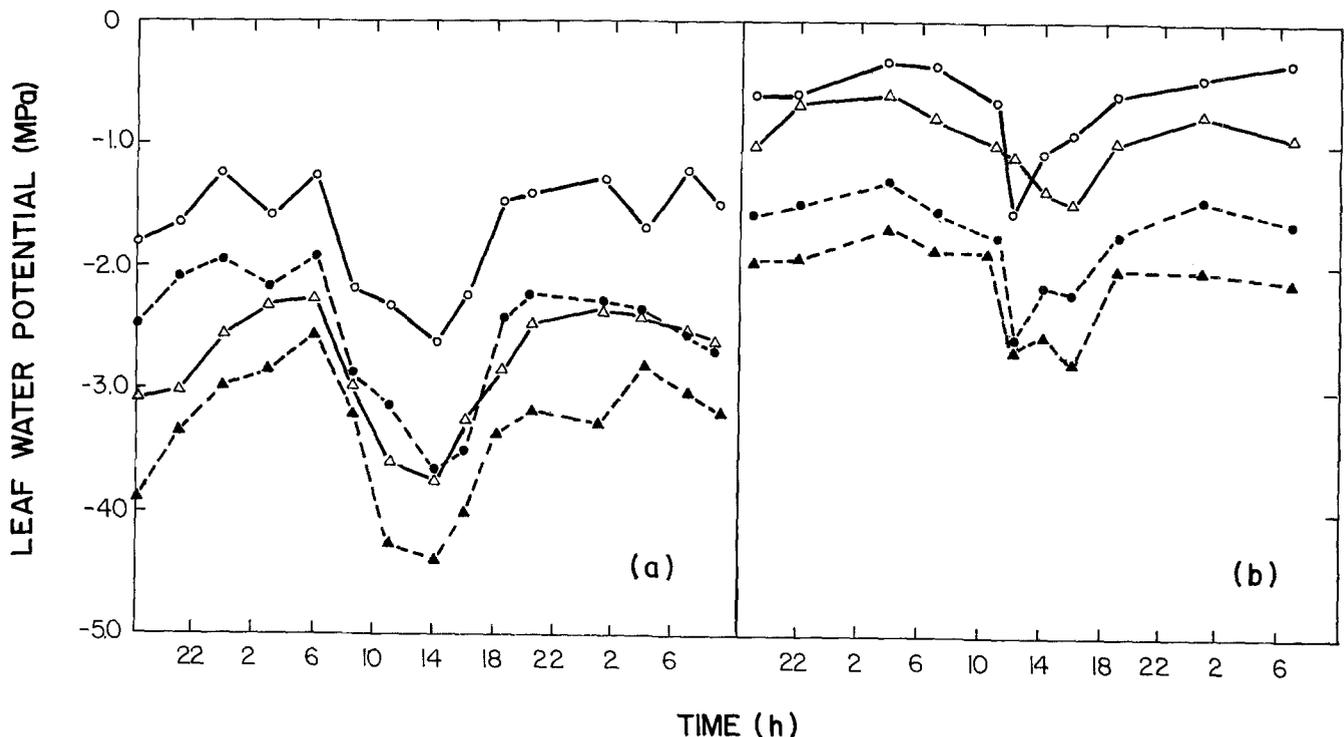


Fig. 1a, b. Daily courses of leaf water potential during a representative (a) dry season day and (b) a representative wet season days for *Pthirusa maritima* mistletoe (●) and its host *Coccoloba wifera* (○), and for *Pthirusa maritima* mistletoe (▲) and its host *Conocarpus erectus* (△)

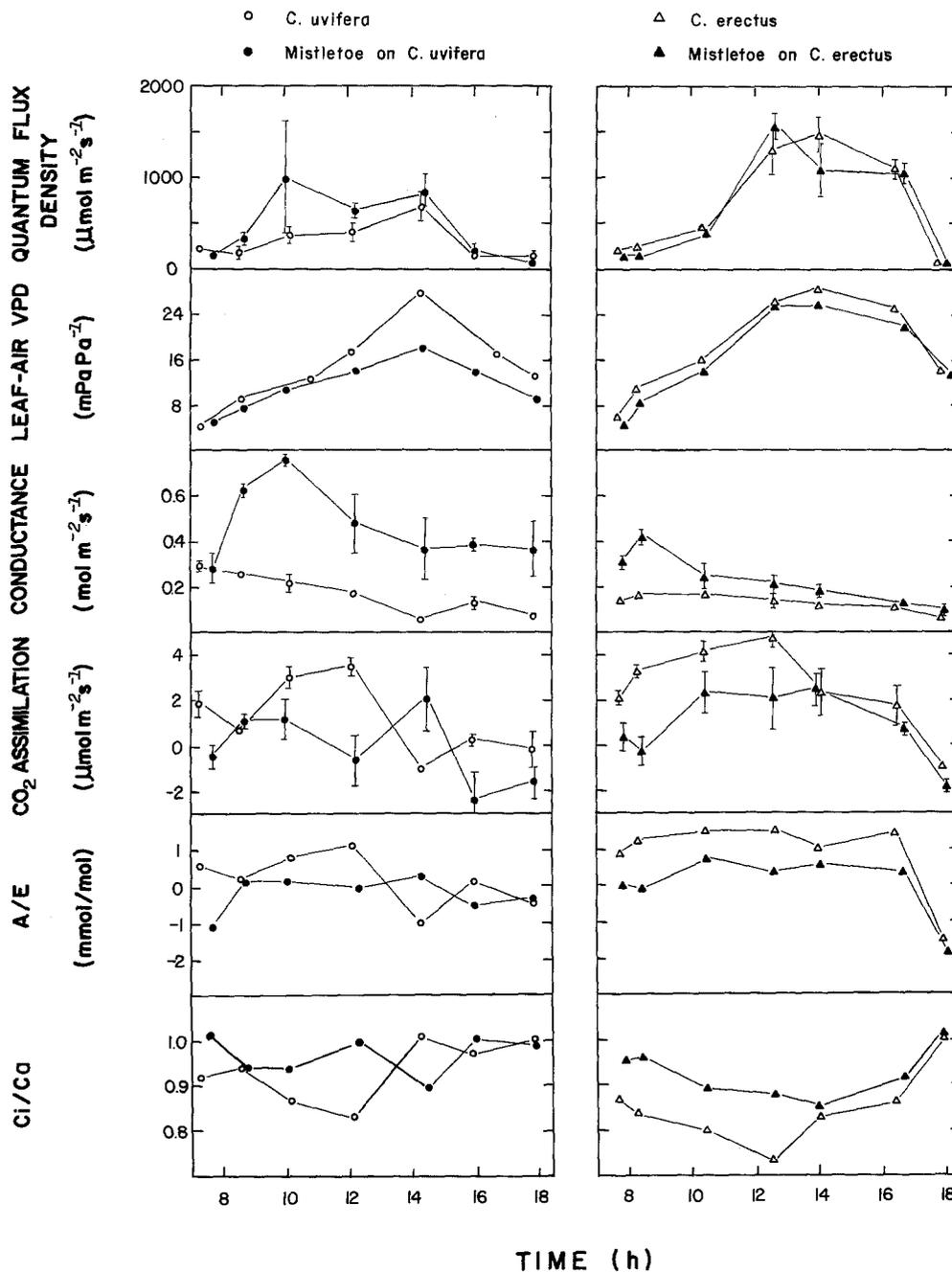


Fig. 2. Diurnal courses during a wet season day of quantum flux density, Leaf-Air VPD, leaf conductance, CO_2 assimilation, water use efficiency (A/E), and the ratio of internal to external CO_2 concentration (c_i/c_a) for the mistletoe *Pthirusa maritima* (●) and its host *Coccoloba uvifera* (○), and for the mistletoe *Pthirusa maritima* (▲) and its host *Conocarpus erectus* (△)

in order to extract sufficient volumes of xylem sap without causing sap dilution (Hamze 1985). The exudate samples were carefully collected with a micropipette to avoid bark and phloem contamination.

Osmotic potentials of the xylem water were determined psychrometrically with a dew point microvoltmeter (HR-33 Wescor) fitted with C-52 Wescor chambers. Calcium, K, Mg, and Na content were also determined in xylem water by atomic absorption spectroscopy. Total soluble carbohydrates were determined in the sap exudate using the anthrone method described by Allen (1974).

Fully expanded leaves collected in the field were transported to the laboratory on ice and oven dried at 65°C . The leaf samples were obtained at 0800 h, 1300 h and 1900 h on each sampling day. For chemical analysis the samples were ground and acid digested (Horwitz 1980), with K, Na,

Ca, and Mg levels determined by flame emission and atomic absorption spectroscopy.

Leaf tissues of fully expanded leaves from the three species studied here were dried at 50°C in an oven and ground to a fine powder in a Wiley mill. Five to eight milligrams of dried leaf material was combusted with 1 g cupric oxide and 1 g of copper in an evacuated sealed Vycor ampule at 800°C . Carbon dioxide was cryogenically distilled from the combustion products and used for mass spectrometry analysis. Carbon isotope ratios are reported in δ units where

$$\delta(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) 10^3 \quad (1)$$

and R represents $^{13}\text{C}/^{12}\text{C}$ for sample and standard respectively. δ values are reported relative to PDB standard with a precision of $\pm 0.2\text{‰}$.

Results

Throughout the day, leaf water potentials were consistently lower in the mistletoe than in the host (Fig. 1). On a seasonal basis, leaf water potentials of all the species were on the order of 1.0 MPa higher during the wet season than during the dry season. This difference was similar to the seasonal changes observed in the osmotic potential of the water substrate (Rada and Goldstein, unpublished work). An increase in osmotic potential during the rainy season occurs because a large input of rainfall water decreases the interstitial soil water salinity. *C. erectus*, rooted in soil substrates with relatively high salinity levels, and its mistletoe, exhibited the most negative potential values throughout the day. A similar pattern was observed for osmotic potentials (data not shown).

Time courses of gas exchange measurements in the two host species and their parasites, on a day when the air temperature varied between 27.5 and 36.0°C and the vapour pressure deficit reached 28 mPa Pa⁻¹, are shown in Fig. 2. The mistletoes had higher stomatal conductances than their hosts. Mistletoe CO₂ uptake rates, however, were generally lower than those of the host leaves. This led to higher water-use efficiencies (W.U.E.) and lower intercellular/external CO₂ concentration ratios (c_i/c_a) in the hosts leaves relative to their parasites. *C. uvifera*, exhibited lower rates of carbon assimilation than *C. erectus*, and negative photosynthetic rates during the last three measured hours. Negative photosynthetic rates may be a result of a heavy load of mistletoes imposing water stress on the branches used for field measurements.

Carbon isotope ratios of plant tissue were measured to further evaluate differences in water use efficiency. In all cases mistletoe leaf tissues had $\delta^{13}\text{C}$ values more negative than that of their hosts (Fig. 3). $\delta^{13}\text{C}$ values of approximately -31‰ measured here were consistent with previous measurements of other mistletoe species (Ehleringer et al. 1985). $\delta^{13}\text{C}$ values were highly correlated to the wet season weighted average c_i/c_a ($Y = -11.4 - 21.3x$, $r = 0.93$) and weighted average W.U.E. values ($Y = -32.4 + 2.7x$, $r = 0.92$) shown in Fig. 3a, b. It is important to derive the weighted average of W.U.E. and c_i/c_a values (Francey et al. 1985) since evidently these parameters will have the greatest impact on the carbon isotope ratios of plant matter during the period of the highest carbon dioxide uptake. For this same reason we only relate $\delta^{13}\text{C}$ values to W.U.E. and c_i/c_a values derived from wet season gas exchange measurements, when productivity is the highest. $\delta^{13}\text{C}$ values of *C. erectus* and its parasite were greater than those for *C. uvifera* and its parasite respectively, indicating that differences in interstitial salinity, in which these species occur, are not only affecting the water use efficiency of host plants but of their respective parasites.

The resistance of the liquid pathway from the soil to the leaf surface was estimated from transpiration-water potential relationships (Jarvis 1975) (Fig. 4). To reduce the confounding effect of the hysteresis, only the morning hour values of two daily courses are included. In order to determine the influence of the mistletoe on parasitized branches, transpiration flux density was multiplied by the surface area of all leaves above the hasutorium. Several parasitized branches throughout the crown were sampled for each host tree to account for microenvironmental effects. Total transpiration of the mistletoes, in each branch, was determined using the same procedure. A linear function was fitted to

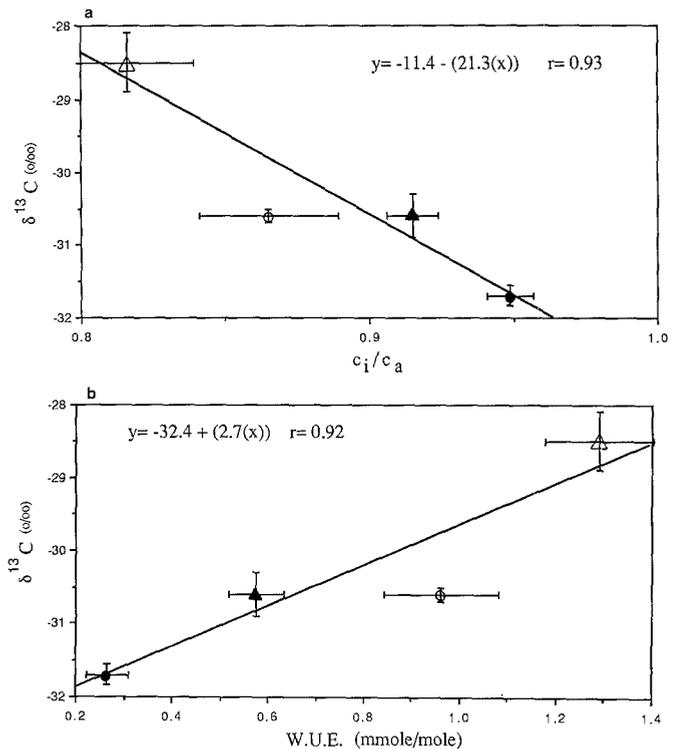


Fig. 3a, b. Relation between (a) carbon isotope ratio ($\delta^{13}\text{C}$) and weighed average intercellular/external CO₂ concentration ratios (c_i/c_a), and (b) carbon isotope ratio ($\delta^{13}\text{C}$) and weighed average water use efficiency (W.U.E.) for *Conocarpus erectus* host (Δ), *Coccoloba uvifera* host (\circ), *Pthirusa maritima* mistletoe on *Conocarpus erectus* (\blacktriangle), and *Pthirusa maritima* mistletoe on *Coccoloba uvifera* (\bullet). Bars are $1 \pm \text{SE}$ of the mean

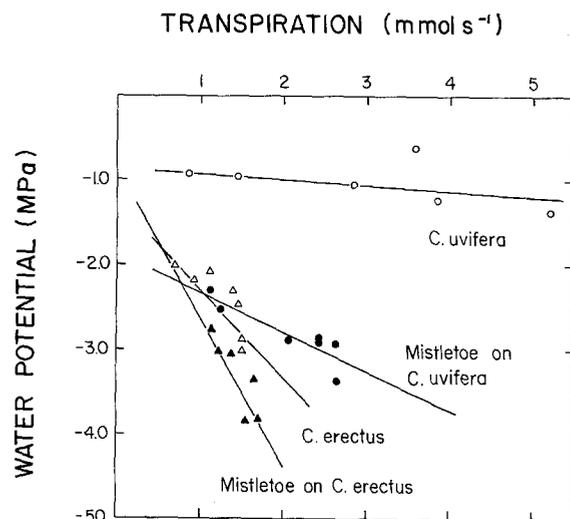


Fig. 4. Relationships between leaf water potential and total transpiration rates (E). Total transpiration rates were obtained by multiplying mean transpiration flux density of a sample of leaves by total leaf area. The slopes are linear regressions fitted to each set of data and represent the hydraulic conductance of the whole water pathway from soil through leaves. The regression lines are: *Coccoloba uvifera* $\Psi_L = -0.25 - 0.73 E$, $r = 0.50$; Mistletoe on *Coccoloba uvifera* $\Psi_L = -18.67 - 4.68 E$, $r = 0.89$; *Conocarpus erectus* $\Psi_L = -12.77 - 10.22 E$, $r = 0.84$; Mistletoe on *Conocarpus erectus* $\Psi_L = -8.92 - 17.10 E$, $r = 0.85$

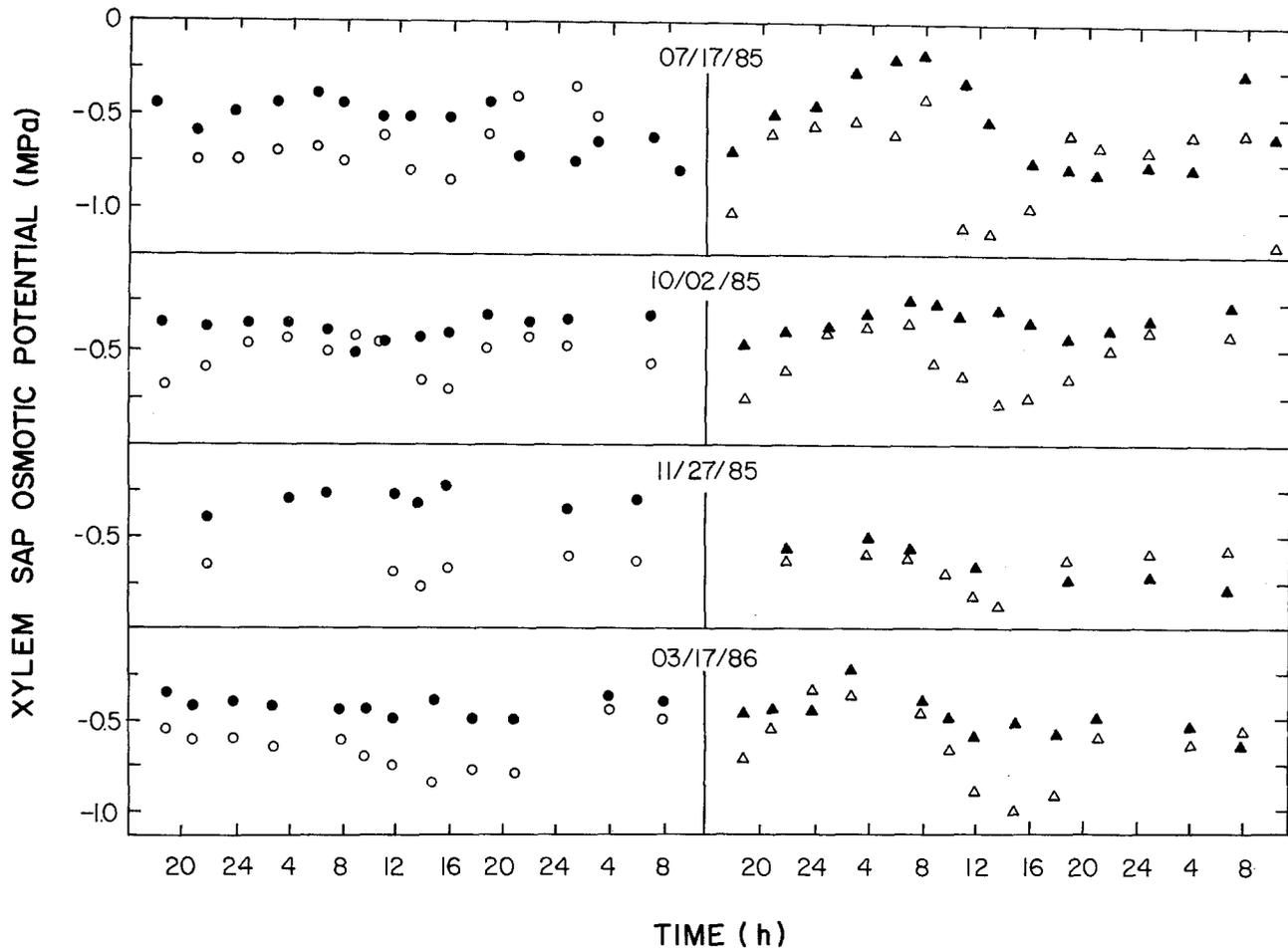


Fig. 5. Daily courses of xylem sap osmotic potential for the mistletoe *Pthirusa maritima* (●) and its host *Cocoloba wifera* (○), and for the mistletoe *Pthirusa maritima* (▲) and its host *Conocarpus erectus* (△). The data were obtained during wet and dry season days

Table 1. Daily average inorganic solute content in the xylem sap of the mistletoe (*Pthirusa maritima*) and its two hosts (Nov. 26, 1986). The sap samples were obtained at 7:00, 13:00 and 17:30 h. Values in mg l^{-1} are means \pm one standard error. The standard error is a measure of daily variations in solute content

Species	Na (mg l^{-1})	K (mg l^{-1})	Ca (mg l^{-1})	Mg (mg l^{-1})
<i>Conocarpus erectus</i>	12.60 ± 7.2	73.82 ± 3.1	48.56 ± 5.0	16.32 ± 1.9
Mistletoe on <i>C. erectus</i>	4.71 ± 0.5	58.82 ± 8.7	35.60 ± 6.6	4.46 ± 1.2
<i>Cocoloba wifera</i>	42.12 ± 3.0	96.77 ± 25.6	71.42 ± 10.2	29.86 ± 13.5
Mistletoe on <i>C. wifera</i>	17.86 ± 18.4	78.61 ± 38.6	55.84 ± 8.2	13.90 ± 0.9

Table 2. Soluble carbohydrate content and its contribution to the osmotic potential in xylem sap samples for the two hosts and their mistletoes (*Pthirusa maritima*)

Species	Soluble carbohydrate content (mg l^{-1})	Calculated osmotic potential contribution (%)
<i>Conocarpus erectus</i>	7.01	0.17
Mistletoe on <i>C. erectus</i>	6.35	0.16
<i>Cocoloba wifera</i>	5.52	0.14
Mistletoe on <i>C. wifera</i>	4.23	0.10

each set of data because we were interested in comparing the average hydraulic properties of the total transport system. The mistletoes had steeper transpiration/ Ψ_L slopes than their hosts, indicating that the hydraulic resistance of the water pathway from soil to the mistletoe's leaf was relatively high.

The osmotic potential of the xylem sap of mistletoe and hosts was monitored during several wet and dry season days (Fig. 5). Three patterns were observed. First, hosts tended to have lower osmotic potentials than did the hemiparasites; second, the osmotic potential of the xylem sap exhibited diurnal variation with a tendency, better seen in *C. erectus* and its mistletoe, of more negative potentials at

Table 3. Daily average inorganic nutrient content in leaves of the mistletoe (*Pthirusa maritima*) and its two hosts (Nov. 26, 1986). Values are means \pm one standard error for $n=5$. Leaf samples were taken at different times during the day and are given in mg g^{-1} dry weight

Species	Na (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})
<i>Conocarpus erectus</i>	85.70 \pm 59.4	2.2 \pm 0.7	12.4 \pm 4.5	14.0 \pm 1.5
Mistletoe on <i>C. erectus</i>	104.80 \pm 48.0	26.7 \pm 7.6	7.6 \pm 4.6	10.9 \pm 3.8
<i>Coccoloba wifera</i>	4.10 \pm 0.9	6.1 \pm 2.4	16.00 \pm 7.9	6.4 \pm 1.7
Mistletoe on <i>C. wifera</i>	18.60 \pm 7.0	24.5 \pm 4.2	16.00 \pm 2.4	5.6 \pm 1.1

midday or early afternoon hours when transpiration rates and water fluxes were higher; and third, this fluctuation was less pronounced in the mistletoe and tended to lag a few hours behind the change in the sap osmotic potential of the host.

The lower osmotic potentials observed in the xylem sap of the host can be partially attributed to the higher concentrations of several important inorganic osmotically active ions (Table 1). In all instances ion concentrations of the xylem sap were higher in the host than in the mistletoes. Soluble carbohydrates were also estimated in exudates of the shoot xylem to verify that the xylem sap samples were not contaminated with phloem exudates. The soluble carbohydrates concentrations varied from 4 to 7 mg l^{-1} (Table 2) and represent less than 0.2% of all of the osmotically active solutes found in the xylem sap. The contribution of organic solutes to the observed sap osmotic potentials (calculated from the Boyle Van't Hoff relationship), were insufficient to explain either the absolute values or the daily variation in osmotic potentials.

In contrast to the inorganic ion concentration in the xylem, K and Na content of mistletoe leaves greatly exceeded those of the host leaves (Table 3). Calcium and Mg contents, on the other hand, were quite similar. From a nutritional point of view K levels in the leaf tissue of the host plants were very low (Ulrich 1952).

Discussion

The mistletoe is indeed a profligate user of water; *P. maritima* transpires from 2 to 3 times as much water as its host at similar VPD's and irradiance levels. High rates of water loss is one of the most consistent physiological features of vascular mistletoes from temperate and tropical regions (Glatzel 1983; Schulze and Ehleringer 1984; Ullmann et al. 1985). High transpiration rates contribute to the lower leaf water potentials observed in the mistletoe, and to the creation of a hydrostatic gradient that facilitates the movement of water and nutrients from host to mistletoe. It is interesting to note that even during the night the water potentials of the mistletoe were lower than those of its host. If rates of water loss from the host and mistletoe leaves were negligible by the end of the dark period, one would expect similar water potential values. The consistent differences in nighttime leaf water stress may be partially explained by more negative osmotic potentials and higher nocturnal transpiration rates.

Mistletoes had higher stomatal conductances but a much lower capacity to fix carbon (Fig. 2). As a consequence, they have a low water use efficiency and a relatively high intercellular CO_2 concentration. The rates of carbon uptake by the leaves of the mangrove species were relatively

low because heavily parasitized individuals were used in this study. The differences in water use efficiency between host and mistletoes would have been higher if a comparison of gas exchange behaviours were made between mistletoes and non-parasitized trees (Goldstein and Rada, unpublished).

Carbon isotope ratios of leaf tissue is primarily determined by $\delta^{13}\text{C}$ values of atmospheric CO_2 and isotopic fractionations associated with diffusion resistance and the carboxylation reaction. This relationship can be approximated by the following equation (Farquhar et al. 1982).

$$\delta^{13}\text{C}_{\text{PLANT}} = \delta^{13}\text{C}_{\text{ATM}} - a((c_a - c_i)/c_a) - b(c_i/c_a) \quad (2)$$

where $\delta^{13}\text{C}_{\text{PLANT}}$ and $\delta^{13}\text{C}_{\text{ATM}}$ are the $\delta^{13}\text{C}$ values of plant material and atmospheric CO_2 (about -7.8‰) respectively, c_i and c_a are the intercellular and ambient CO_2 concentrations respectively, and a and b are the isotopic fractionation factors associated with stomatal diffusion (about 4.4‰) and the isotopic fractionation by the RubP carboxylase reaction (29‰, Roeske and O'Leary 1984) respectively. Equation 2 is usually simplified to

$$\delta^{13}\text{C}_{\text{PLANT}} = -12.2 - (24.6(c_i/c_a)) \quad (3)$$

When equation 3 is merged with the water use efficiency equation,

$$\text{W.U.E.} = \frac{\Delta c}{\Delta w 1.56} = \frac{c_a \left(1 - \frac{c_i}{c_a}\right)}{\Delta w 1.56}, \quad (4)$$

the following equation expressing the relationship between $\delta^{13}\text{C}$ values of plant tissue and water use efficiency is derived:

$$\text{W.U.E.} = \frac{c_a \left(1 - \frac{\delta^{13}\text{C}_{\text{PLANT}} + 12.2}{-24.6}\right)}{\Delta w 1.56} \quad (5)$$

Which can be simplified to,

$$\frac{\text{W.U.E.} \Delta w 1.56}{c_a} = 1 + \frac{\delta^{13}\text{C}_{\text{PLANT}} + 12.2}{24.6} \quad (6)$$

Further simplification of this equation leads to the following:

$$\text{W.U.E.} \frac{\Delta w 38.4}{c_a} - 36.8 = \delta^{13}\text{C}_{\text{PLANT}} \quad (7)$$

thus the relationship between $\delta^{13}\text{C}$ values of plant matter and W.U.E is linear, having a slope of $(\Delta w 38.4/c_a)$ and an intercept at -36.8 . On a qualitative basis our instantaneous gas exchange measurements agrees quite well with carbon isotope ratio measurements; i.e. low W.U.E. values concurrent with low carbon isotope ratios. We further tested

the relationship between $\delta^{13}\text{C}$ values of plant tissue versus c_i/c_a and W.U.E. values by deriving a weighted average of wet season W.U.E. and c_i/c_a values for the three species studied here during positive net carbon dioxide uptake (Fig. 3). There is a highly significant relationship between $\delta^{13}\text{C}$ values and the measured c_i/c_a values and this relationship agrees quite well with equation 3. The small deviation may be due to inaccuracies in integrating our short period of gas exchange measurements to the seasonal average and small deviations found between the actual fractionation and theoretical predictions due to the PEP carboxylase reaction (Evans et al. 1986). Carbon isotope ratio of plants are also related to water use efficiency and the vapor pressure deficit as shown on equation 7. There is a highly significant relationship between these two parameters as observed on Fig. 3b. This relationship was somewhat different than that observed by Ehleringer et al. (1985). This could be due to the fact that gas exchange measurements were taken on parasitized stems of hosts, or because measurements taken by Ehleringer et al. were done under different vapor pressure deficit conditions. W.U.E. values for nonparasitized stems taken concurrently with the measurements presented here were much higher. Since the slope of the relationship between $\delta^{13}\text{C}$ and W.U.E. is a function of Δw , c_a , and a constant (equation 7), it is possible to approximate the average vapor pressure deficit when tissue is synthesized in these two hosts species and their respective parasites. A slope of 2.7 as reported in Fig. 3 yields a vapor pressure deficit of 23.4 mPa Pa⁻¹ in excellent agreement with our psychrometer estimation of Δw .

The hydraulic resistance at the host-parasite interface and/or within the mistletoe xylem was considerably larger than the liquid flow resistance in the host. Schulze et al. (1984), however, did not find significant slope differences between transpiration flux density and leaf water potentials in a different host/mistletoe system, and therefore concluded that the observed differences in water potential between parasite and host were mainly a consequence of the differences in transpiration rates at similar liquid flow resistances. The use of the transpiration flux density-water potential relation as an estimate of the hydraulic properties of the vascular system, however, includes a tacit assumption that the species being investigated have a similar relationship between total leaf surface area and cross sectional area of the conducting pathway (Jarvis 1975). In this work we plot water potential as a function of total transpiration (transpiration per unit leaf area times the total surface area of all leaves hydraulically connected to the branches of either the mistletoe or the host). The slopes are a measure of the intrinsic efficiency of the whole water pathway from soil through leaves. The hydraulic conductances, which are expressed in units of mmol MPa⁻¹ s⁻¹, are lower (steeper slopes) in the mistletoe than in the host water pathway. This may have important consequences not only for the water relations of both group of species, but also for the nutrient movement into the mistletoe.

The lower ion concentration observed in the xylem sap of the mistletoe suggests that there are no direct xylem to xylem connections between the water pathways of *P. maritima* and its hosts. Indeed, there are studies with very different host-mistletoe systems reporting anatomical or physiological evidence that xylem continuity does not exist (see review in Lamont 1983). It is likely that in the haustorium the mineral ions move passively from the host xylem (via host

parenchyma) into the mistletoe xylem (via mistletoe parenchyma). If this were the case, a relatively "tortuous" pathway for minerals movement across the haustorium will exist that could partially explain the differences in xylem sap concentration of minerals ions observed between host and mistletoes. The haustorium could be considered as an ion-exchange column, where ionizable functional groups attached to the cell walls could provide ion exchange sites, and/or a site of mineral salts removed by absorption along the way. Biddulph et al. (1961) have suggested that a similar translocation mechanism, involving an exchange process, could explained the ascent of Ca in the xylem tissue of bean plants more successfully than a mechanism based purely on mass flow. Regardless of the model that describes the observed xylem sap pattern, our results indicate that nutrient budgets of mistletoes calculated with the assumption that the xylem sap composition of the mistletoe and its host are identical, have to be considered with caution.

Another pattern observed during this work was daily cycling in xylem sap osmotic potential of both mistletoe and host. The decrease in xylem sap osmotic potential, which is a consequence of increases in mineral salt concentration of the xylem, occurs at midday in the host plants when the rate of water transport is high. This may be the result of a decrease in the permeability of the root system to certain minerals salts, when the daily peak of water potential gradient is developed. Waisel et al. (1986) found that the salt concentration in the xylem sap also varied during the day, but in a different pattern as compared to transpiration. These results were surprising as Scholander (1966) did not find diurnal variations in the salt concentration of the xylem sap in four different mangrove species. Further investigation on the mechanisms of nutrient uptake and transport in mangrove species is necessary.

A midday decline in the osmotic potential of the xylem is also exhibited by the mistletoe growing on *C. erectus*, however, the variations in the xylem sap osmotic potential tend to lag a few hours from the time they occur in the host (Fig. 5). The daily variations in the concentration differences of osmotically active solutes indicates that there is a high resistance pathway to nutrient movement between host and mistletoe.

P. maritima mistletoes tend to adjust their physiological behaviour to that of the parasitized organism in terms of water relations and gas exchange. Leaf water potential of the mistletoe are always 0.5 to 0.7 MPa lower than the water potential of its host indicating that mistletoes are able to adjust their water potential components depending on the water relations of the plants on which they grow. The apparent hydraulic conductivity of the mistletoe is a function of the hydraulic properties of the host species. The mistletoe growing on *C. wifera*, with an efficient water transport system, has a much higher hydraulic conductivity than the same mistletoe species growing on *C. erectus* which has a relatively low water transport efficiency (Fig. 4). The same pattern of physiological acclimation is exhibited by the mistletoes in terms of its water use efficiency (Fig. 3). This ability of *P. maritima* to adjust to the different water and gas exchange characteristics of the host plant allows mistletoe organisms to maintain an adequate water and carbon balance, thus ensuring their survival.

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References

- Allen SE, Grimshaw HM, Parkinson JA, Quarmby C (1974) Chemical Analysis of Ecological Materials. Blackwell Scientific Publications, Oxford, p 565
- Biddulph O, Nakayama FS, Cory R (1961) Transpiration stream and ascension of calcium. *Plant Physiol* 36:429–436
- Bradford KJ, Sharkey TD, Farquhar GD (1983) Gas exchange, stomatal behavior and C values of the flaca tomato mutant in relation to abscisic acid. *Plant Physiol* 72:245–258
- Caemmerer S von, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153:376–387
- Clough DF, Andrews TJ, Cowan IR (1982) Physiological processes in mangroves. In: BF Clough (ed) *Mangroves Ecosystems in Australia*. Austr Nat Univ Press, pp 193–210
- Downton WJS, Grant WJR, Robinson SP (1985) Photosynthetic and stomatal response of spinach leaves to salt stress. *Plant Physiol* 78:85–88
- Ehleringer JR, Schulze E-D, Ziegler H, Lange OL, Farquhar GD, Cowan IR (1985) Xylem mistletoes: water or nutrient parasites? *Science* 227:1479–1481
- Ehleringer JR, Cook CS, Tieszen LL (1986) Comparative water use and nitrogen relationships in a mistletoe and its host. *Oecologia* 68:279–284
- Evans JR, Sharkey TD, Berry JA, Farquhar GD (1986) Carbon isotope discrimination measured concurrently with gas exchange to investigate CO₂ diffusion in leaves of higher plants. *Austr J Plant Physiol* 13:281–292
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Austr J Plant Physiol* 9:121–137
- Francey RJ, Gifford RM, Sharkey TD, Weir B (1985) Physiological influences on carbon isotope discrimination in huon pine (*Lagarostrobos franklinii*). *Oecologia* 66:211–218
- Glatzel G (1983) Mineral nutrition and water relations of hemiparasitic mistletoes: a question of partitioning. Experiments with *Loranthus europaeus* on *Quercus petraea* and *Quercus robur*. *Oecologia* 58:310–321
- Hamze M (1985) Xylem sap extraction from citrus seedlings using a modified pressure chamber method. *J Plant Nutr* 8(3):219–232
- Hawksworth FG (1983) Mistletoes as forest parasites. In: M Calder, P Bernhardt (eds) *The Biology of Mistletoes*. Academic Press, New York, pp 185–204
- Hollinger DY (1983) Photosynthesis and water relations of the mistletoe, *Phoradendron villosum*, and its host, the California valley oak, *Quercus lobata*. *Oecologia* 60:396–400
- Horwitz W (1980) Official Methods of Analysis of the Association of Official Analytical Chemists. 13th Edit., Association of Official Analytical Chemists., Washington
- Jarvis PG (1975) Water transport in plants. In: DA deVries, HH Afgan (eds) *Heat and Mass Transfer in the Biosphere*. John Wiley and Sons, New York, pp 369–394
- Lamont BB (1983) Minerals nutrition of mistletoes. In: M Calder, P Bernhardt (eds) *The Biology of Mistletoes*. Academic Press, New York, pp 185–204
- Roeske CA, O'Leary MH (1984) Carbon isotope effects on the enzyme-catalized carboxylation of ribulose bisphosphate. *Biochemistry* 23:6275–6284
- Scholander PF, Bradstreet ED, Hammel HT, Hemmingsen EA (1966) Sap concentrations in halophytes and some other plants. *Plant Physiol* 41:529–532
- Schulze E-D, Ehleringer JR (1984) The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. *Planta* 162:268–275
- Schulze E-D, Turner NC, Glatzel G (1984) Carbon, water and nutrient relations of two mistletoes and their hosts: a hypothesis. *Plant, Cell Environm* 7:293–299
- Tomlinson PB (1986) *The botany of mangroves*. Cambridge University Press, Cambridge, p 413
- Ulrich A (1952) Physiological bases for assessing the nutritional requirements of plants. *Ann Rev Plant Physiol* 3:207–228
- Ullmann I, Lange OL, Ziegler H, Ehleringer JR, Schulze E-D, Cowan IR (1985) Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia. *Oecologia* 67:577–587
- Weisel Y, Eshel A, Agami M (1986) Salt balance of leaves of the mangrove *Avicennia marina*. *Physiol Plant* 67:67–72

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