

# How does a mistletoe affect the water, nitrogen and carbon balance of two mangrove ecosystem species?

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Received 30 April 1990; received in revised form 15 June 1990; accepted for publication 5 July 1990

**Abstract.** The effect of a mistletoe, *Phthirusa maritima*, on the water, nitrogen and carbon balance of two mangrove host species, *Conocarpus erectus* and *Coccoloba uvifera*, was studied. Several daily cycles of water potential and its components (pressure-volume curves); leaf nitrogen and its components (Kjeldahl method); leaf conductance, transpiration rates and carbon assimilation (portable gas exchange system) were measured on mistletoe, infested and uninfested plants in the Caribbean coast of Venezuela. The mistletoe on both host species showed higher transpiration rates and lower CO<sub>2</sub> assimilation rates, and therefore lower water use efficiencies. With respect to infested and uninfested plants, *C. erectus* did not show large differences in the parameters measured with the exception of assimilation rates which were significantly lower in the infested plants. On the other hand, *C. uvifera* did show differences in all parameters and, therefore, was affected to a greater degree by the mistletoe. The behaviour of mistletoe-infested and uninfested plants, with respect to habitats with different degrees of water stress and with respect to the salinity gradient in which these mangroves grow, is discussed.

**Key-words:** *Phthirusa maritima*; *Conocarpus erectus*; *Coccoloba uvifera*; mistletoe; mangroves; water relations; carbon balance.

## Introduction

Hemiparasite-host relationships in plants have received much attention with respect to their anatomy and systematics although less is known about some of their physiological features (Ehleringer *et al.*, 1985). Mistletoe and its host can be used as a model system for the study of some aspects of water, nutrient and carbon relations, since they have very particular characteristics: a common source of water and inorganic nutrients, and

although each species in this relation has independent mechanisms for the regulation of transpiration rates and carbon assimilation, each individual response affects the functioning of the whole system (Glatzel, 1983). In this study, we have selected a hemiparasite-host system where the two host species, *Conocarpus erectus* and *Coccoloba uvifera*, grow in an environment characterized by saline substrates. In these tropical environments, a combination of high irradiance and high air temperatures leads to high rates of water loss and salt loading that result in lower photosynthetic rates (Clough, Andrews & Cowan, 1982).

Since these mangrove species grow on highly saline substrates, mechanisms to withstand low soil water potentials are required for the maintenance of a gradient for water transport from the soil to the leaves (Rada *et al.*, 1989). On the other hand, the mistletoes are faced with the problem of maintaining even lower water potentials than their hosts in order to keep a positive water balance in the soil-host-mistletoe continuum (Goldstein *et al.*, 1989). These authors have shown how the mistletoe, *Phthirusa maritima*, is able to mimic some of the host's physiological characteristics, therefore coexisting with mangrove plants growing along a salinity gradient.

One of the common physiological features of mistletoes is that they have higher transpiration rates than those of their hosts (Schulze, Turner & Glatzel, 1984; Ullmann *et al.*, 1985; Ehleringer *et al.*, 1985; El-Sharkawy, Cock & Hernandez, 1986; Goldstein *et al.*, 1989). In a study conducted in the system *Phoradendrum juniperinum*/*Juniperum oosteyperma*, Ehleringer, Cook & Tieszen (1986) found that, because of higher rates of water loss induced by mistletoe parasitism, infested juniper trees experienced lower leaf water potentials than uninfested trees. These authors also showed how several aspects of juniper water and nutrient relations (leaf conductance, leaf water potential, water use efficiency and leaf nitrogen content) were worsened by the presence of these parasites. The degree of infestation by the mistletoes would be of great importance not only for the long-term survival of the host, where a decreased growth rate has been observed (Schulze & Ehleringer, 1984), but also for the mistletoe, because it may

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deplete soil water resources to the point that it endangers the host's existence which, in turn, may result in parasite mortality (Ullmann *et al.*, 1985).

The main objective of this research was to study some physiological effects of a mistletoe species on the water, nitrogen and carbon economy of two different hosts, that grow under different saline conditions, comparing infested versus uninfested (control) plants. The main question addressed in this work was: How do infested plants behave in terms of photosynthesis, stomatal response, water potentials and leaf nitrogen content compared to control plants? The problem becomes even more interesting since the hosts not only have to cope with the use of resources by the mistletoes but also have to face the problem of high substrate salinity which results in lower leaf water potentials and a reduction of CO<sub>2</sub> assimilation rates as a consequence of salt loading (Goldstein *et al.*, 1989; Ball & Farquhar, 1984a,b). Our field observations in the study area indicate the existence of an infestation gradient which correlates with the salinity gradient from seashore inland (Goldstein *et al.*, 1989). *Rhizophora mangle* at the more saline extreme, with lower soil water potentials shows very few if any infested trees. In *C. erectus* growing at intermediate soil water potentials, we found a greater number of infested trees; and finally, *C. uvifera*, at the less saline extreme with the highest soil water potentials, shows almost all trees infested by the mistletoe. A second objective of this research was to explain how the mistletoe-host relationship is affected by changes in substrate salinity.

## Materials and methods

The study site was located in the Morrocoy National Park, on the Caribbean coast of Venezuela (10°N, 68°14'W). The mean annual precipitation is 1053 mm, with a bimodal distribution showing maximums in October and April. The mean annual temperature is 26.5°C with a 2.0°C variation between the warmest and coolest month.

The species chosen for this study were: *C. erectus* L. (Combretaceae), a mangrove species which grows on sandy substrates that are not permanently flooded nearest to the seashore, and *C. uvifera* Jacq. (Polygonaceae), a conspicuous constituent of the intertidal communities in the study area. *Rhizophora mangle*, a dominant mangrove species in this area was not chosen due to the small degree of mistletoe infestation it showed. The mistletoe *Phthirusa maritima* Rizz. (Loranthaceae) infests several mangrove species and it is particularly abundant in the area (Goldstein *et al.*, 1989). Measurements were done on several ( $n = 4-6$ ) infested (leaves distal to the infection) and non-infested (control) plants of both host species. Measurements were carried out four times during 1985-1986 for both wet and dry seasons.

Leaf water potentials were measured with a pressure chamber approximately every 2 h through-

out 48-h cycles in adult leaves ( $n = 4-6$ ) of each species. Air and leaf temperatures were measured with copper-constantan thermocouples (36 gauge) and relative humidity with an Assman aspirated wet-dry bulb psychrometer. These environmental variables were used to determine leaf-air vapour pressure differences. Quantum flux density was measured with a filtered selenium photocell incorporated to the gas exchange system. Leaf water potential components were determined from pressure-volume curves for mistletoes, infested and non-infested control host plants. Values of osmotic potential at full turgor ( $\Psi_{\pi}^{100}$ ) and at turgor loss ( $\Psi_{\pi}^0$ ) were calculated from these curves (Tyree & Hammel, 1972; Tyree & Richter, 1981; Tyree & Jarvis, 1982).

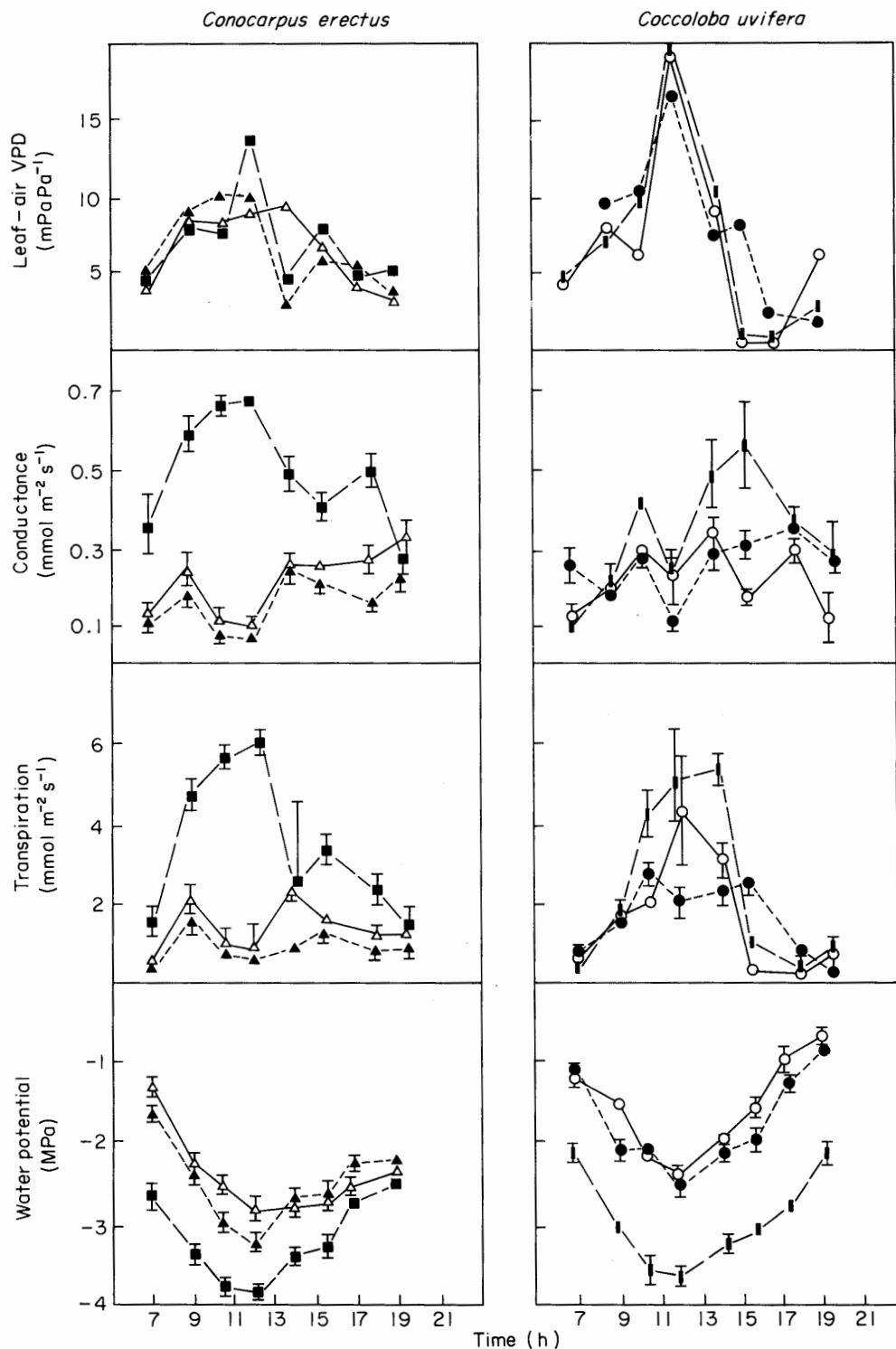
A fully portable system was used to measure gas exchange in the field (LCA-2 system, ADC Ltd, U.K.) The system consisted of leaf chamber, air supply unit and infrared gas analyser. Gas exchange rates were determined from flow rates, projected leaf surface area, and water vapor and CO<sub>2</sub> concentration differences between a reference and analysis air. Gas exchange calculations were conducted according to von Caemmerer & Farquhar (1981). Total leaf nitrogen content was determined with the Kjeldahl method described by Muller (1961).

## Results

Representative daily cycles of leaf water potential ( $\Psi_L$ ), leaf conductance ( $K_s$ ), transpiration ( $E$ ) and leaf-air vapor pressure difference (VPD) are shown in Fig. 1, for mistletoes, non-infested and infested hosts. The mistletoes on *C. erectus* and *C. uvifera* exhibited more negative values of  $\Psi_L$  than their hosts. Leaf water potentials of *C. erectus* infested plants were more negative than the control plants, from 0700 to 1300 h (Fig. 1). This difference was particularly higher at midday when vapor pressure difference was higher.

Transpiration rates and conductances were significantly higher in the mistletoe as compared to its host *C. erectus*. Maximum transpiration rates of  $6 \text{ mol m}^{-2} \text{ s}^{-1}$  and conductances of approximately  $0.7 \text{ mol m}^{-2} \text{ s}^{-1}$  were observed in the mistletoes as compared to  $2 \text{ mol m}^{-2} \text{ s}^{-1}$  and  $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$ , respectively, for the control plants. Transpiration rates and conductances were not statistically significant for control and infested *C. erectus* plants. Similarly to *C. erectus*, infested *C. uvifera* plants tended to have lower  $\Psi_L$  than non-infested plants (Fig. 1). Transpiration rates and conductances were also higher in the mistletoe than in the host plants.

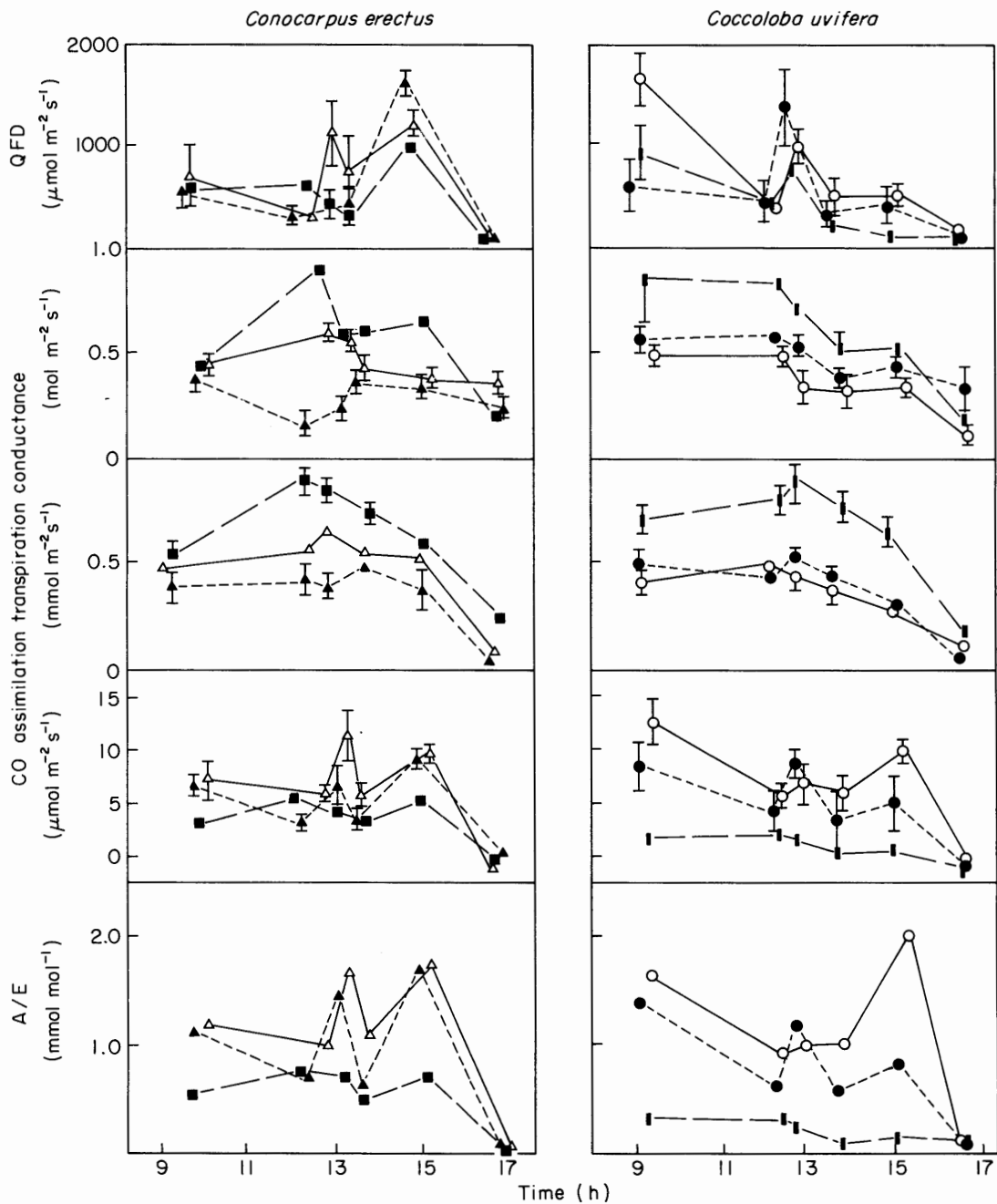
The differences in gas exchange between infested, control and mistletoe plants are depicted in Fig. 2. Transpiration rates and leaf conductances were consistently higher in control *C. erectus* plants. In contrast to these results, infested *C. uvifera* plants showed higher leaf conductances throughout the day. Carbon dioxide assimilation rates tended to be higher



**Figure 1.** Diurnal courses of leaf-air VPD, leaf conductance, transpiration rate and leaf water potential for *C. erectus*: control plants ( $\Delta$ ), infected plants ( $\blacktriangle$ ) and mistletoe ( $\blacksquare$ ); and *C. uvifera*: control plants ( $\circ$ ), infected plants ( $\bullet$ ) and mistletoe ( $\blacksquare$ ). Vertical bars are standard errors ( $n = 5$ ).

in control plants than in infested ones in both species. Water use efficiency was not significantly different between infested and control *C. erectus* plants. On the other hand, water use efficiency for *C. uvifera* was markedly higher throughout the day except at

1300 h. The mistletoe shows higher leaf conductance values on both hosts. Carbon dioxide assimilation rates in mistletoe are lower than their hosts; maximum values are 5.2 and 2.3 for mistletoe on *C. erectus* and *C. uvifera*, respectively.



**Figure 2.** Diurnal courses of quantum flux density (QFD), leaf transpiration, leaf conductance, CO<sub>2</sub> assimilation and water use efficiency (A/E) for *C. erectus*: control plants ( $\Delta$ ), infected plants ( $\blacktriangle$ ) and mistletoe ( $\blacksquare$ ); and *C. uvifera*: control plants ( $\circ$ ), infected plants ( $\bullet$ ) and mistletoe ( $\blacksquare$ ). Vertical bars are standard errors ( $n = 5$ ).

The effects of mistletoe on CO<sub>2</sub> assimilation can be better observed in the light response curves in Fig. 3. These curves were obtained from pooled data of photosynthesis and photosynthetically active radiation in the field. The control plants had higher CO<sub>2</sub> assimilation rates at light saturation values than do the infested plants in both species. However, mistletoe on *C. uvifera* showed lower assimilation rates than the mistletoe on *C. erectus*.

Leaf osmotic potentials at full saturation and at

turgor loss, as well as leaf nitrogen content, are presented in Table 1. There were no significant differences between infested and control plants of *C. erectus* in either leaf osmotic potentials or leaf nitrogen content. On the other hand, there were significant differences in all parameters between infested and control *C. uvifera* plants. Osmotic potential at full turgor and turgor loss were lower in infested plants, showing differences of 0.4 and 0.7 MPa, respectively. Nitrogen content was almost

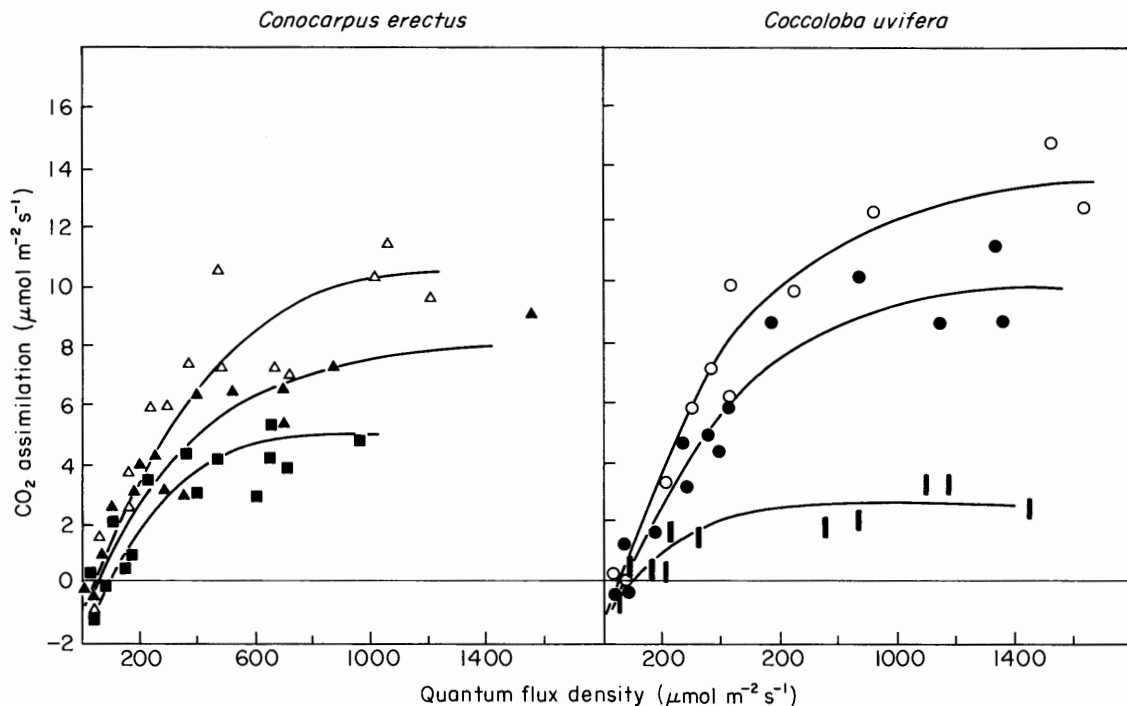


Figure 3. Relationships between  $\text{CO}_2$  assimilation and quantum flux density for *C. erectus*: control plants ( $\Delta$ ), infested plants ( $\blacktriangle$ ) and mistletoe ( $\blacksquare$ ); and *C. uvifera*: control plants ( $\circ$ ), infested plants ( $\bullet$ ) and mistletoe ( $\blacksquare$ ).

two-fold higher in the control plants. Mistletoe on both hosts showed significantly lower leaf osmotic potentials at full turgor and turgor loss. Leaf nitrogen content in mistletoe was lower than in both control species. These nitrogen values were significantly lower in mistletoe as compared to its host *C. erectus*. However, mistletoe and its host *C. uvifera* showed similar leaf nitrogen contents.

## Discussion

There are few studies regarding the effects of mistletoes on the physiological performance of their hosts. Ehleringer *et al.* (1986) investigated the impact of mistletoe *Phoradendrum juniperinum* on the nitrogen and water relations of its host *Juniperus ostiosperma*

by comparing infested and uninfested (control) plants. Contrasting with the lack of literature on physiological and ecological effects of mistletoes on their hosts, there is an abundant literature on the physiological and ecological interactions between mistletoes and their hosts. Mistletoes have higher conductances and transpiration rates than their hosts (Vareschi & Pannier, 1953; Hellmuth, 1971; Glatzel, 1983; Schulze & Ehleringer, 1984; Ullman *et al.*, 1985; Ehleringer *et al.*, 1986; Goldstein *et al.*, 1989; Montilla, Azocar & Goldstein, 1989). Schulze *et al.* (1984) have proposed that higher transpiration rates represent a mechanism to obtain sufficient nitrogen from the host xylem stream.

Our results support the general pattern suggesting that mistletoes have higher transpiration rates and conductances than their hosts. On the other hand, our results and those of Goldstein *et al.* (1989) show that mistletoe  $\text{CO}_2$  assimilation rates are lower than those of the host. This contrasts with the results reported by Schulze *et al.* (1984), where mistletoes and hosts exhibit similar photosynthetic rates. Due to these high transpiration rates and the lower  $\text{CO}_2$  assimilation values, the water use efficiency for *P. maritima* is also much lower. Further evaluation of the water use efficiencies by carbon isotope ratios (Ehleringer *et al.*, 1986; Goldstein *et al.*, 1989) show that indeed water use efficiency is lower for the mistletoes than for their hosts.\*

The focus of the present study was to investigate the effect of mistletoe on gas exchange and water relations by comparing infested and non-infested

Table 1. Leaf nitrogen content (N), Osmotic potential at saturation ( $\Psi_{\pi}^{100}$ ), Osmotic potential at turgor loss ( $\Psi_{\pi}^0$ ) for mistletoe, control and infested host plants ( $n = 5 \pm$  standard error)

	N ( $\text{mg g}^{-1}$ )	$\Psi_{\pi}^{100}$ (MPa)	$\Psi_{\pi}^0$ (MPa)
<i>C. uvifera</i> control plants	$9.60 \pm 1.42$	$-1.26 \pm 0.06$	$-1.64 \pm 0.11$
<i>C. uvifera</i> infested plants	$5.48 \pm 0.66$	$-1.67 \pm 0.15$	$-2.66 \pm 0.25$
<i>P. maritima</i>	$4.70 \pm 0.38$	$-1.94 \pm 0.09$	$-2.89 \pm 0.10$
<i>C. erectus</i> control plants	$8.55 \pm 0.79$	$-1.84 \pm 0.15$	$-2.62 \pm 0.19$
<i>C. erectus</i> infested plants	$9.32 \pm 1.25$	$-1.89 \pm 0.08$	$-2.63 \pm 0.06$
<i>P. maritima</i>	$5.87 \pm 0.31$	$-2.42 \pm 0.13$	$-3.20 \pm 0.18$

plants. Leaf water potential of infested plants of both species was lower than for control plants, although this trend was more consistent throughout the day in *C. uvifera* plants. Osmotic potentials at full turgor and at turgor loss were significantly different between infested and control *C. uvifera*, whereas small differences were observed in *C. erectus*. These results suggest that the mistletoe strongly affects the water relations of *C. uvifera* plants and to a lesser degree the water relations of *C. erectus*. This lowered leaf water potential may be explained by a higher leaf conductance and transpiration rates of infested *C. uvifera* plants. Ehleringer *et al.* (1986) also found that leaf conductances and transpiration rates were higher in infested as compared to uninfested host stems. They explain this difference as a method whereby infested tissues can obtain sufficient mineral nutrition to reproduce. If phloem translocation to infested areas is reduced and/or the nitrogen content of host xylem fluid distal to the parasite is reduced, there may be few other options for acquiring sufficient amounts of the minerals necessary for reproduction available for infested tissues (Ehleringer *et al.*, 1986).

*Phthirusa maritima* also affects CO<sub>2</sub> assimilation in *C. uvifera* to a greater degree than in *C. erectus*. This is observed in Fig. 3, where maximum rates of photosynthesis are reduced from 14.5  $\mu\text{mol m}^{-2}\text{s}^{-1}$  in control plants to 10.5  $\mu\text{mol m}^{-2}\text{s}^{-1}$  for infested *C. uvifera*, representing approximately a 30% reduction. In *C. erectus*, photosynthesis decreases from 9.5  $\mu\text{mol m}^{-2}\text{s}^{-1}$  to 7.5  $\mu\text{mol m}^{-2}\text{s}^{-1}$ , which represents a 20% reduction in infested plants. The reduction in CO<sub>2</sub> assimilation rates in infested *C. uvifera* plants as compared to control plants may be partially explained by the decrease in leaf nitrogen content observed in infested plants as has been proposed by Field & Mooney (1986). The reduction in leaf nitrogen in infested hosts may be the result of the high transpiration rates of the mistletoes that efficiently compete with the host in the use of nitrogen (Schulze *et al.*, 1984; Schulze & Ehleringer, 1984). Although leaf nitrogen content in *C. erectus* control and infested plants was similar, the infested plants also show a reduction in photosynthetic capacity. This may be due to lower stomatal conductances observed in infested hosts.

Ball & Farquhar (1984a,b) have reported that seedlings of *Avicennia marina* and *Aegiceras corniculatum*, grown under experimental conditions of increasing salinity, show a reduction in photosynthesis. Our data, obtained under field conditions, also support these findings. *Conocarpus erectus* grows in more saline conditions than *C. uvifera* and shows lower CO<sub>2</sub> assimilation rates (Figure 3). This may be a consequence of internal ionic concentrations (Ball & Farquhar, 1984a,b); greater external sodium concentrations interfere with potassium uptake (Munns, Greenway & Kirst, 1983; Ball, Chow & Anderson, 1987). Comparing Na/K ratios for mangroves under

different substrate salinities, we found that *C. uvifera*, on the less saline substrate of the gradient, shows the lowest ratio (1.14); *C. erectus*, on intermediate substrate, has a ratio of 5.96; and *R. mangle*, on the more saline substrate, shows the highest ratio (8.39) (unpublished data). On the other hand, Flanagan & Jefferie (1988) found no change in the Na<sup>+</sup>/K<sup>+</sup> ratio of *Plantago maritima* leaves and roots grown with different salinity levels. They also found that, despite the large growth reduction and high accumulation of Na<sup>+</sup> ions, leaf photosynthetic rate was only slightly reduced by salinity stress.

The differences observed in leaf water potential and CO<sub>2</sub> assimilation rates between control and infested plants for both species may explain the differences in the degree of infestation in the study area. Our results strongly suggest that the greater physiological effect of mistletoes on *C. uvifera* may be due to more favourable soil water conditions and, therefore, the mistletoe exploits a less critical habitat, as compared to more extreme saline conditions. Comparing our results to those of different host-mistletoe systems growing along a gradient from favourable soil water conditions to saline substrates, it can be suggested that the physiological effect of mistletoes on their host is less marked when water is readily available, as described for tropical montane seasonal forest with the system *Inga edulis*/*Phthirusa pyriformis* (Montilla *et al.*, 1989). Under hot and dry semi-arid conditions using different host-mistletoe systems, it has been pointed out that mistletoes show a conservative water use efficiency that seems to be a prerequisite for their survival (Ullmann *et al.*, 1985). In tropical mangroves exposed to high substrate salinities, we found that, at the more saline extreme (seashore), infestation is either low or absent, probably due to the critical leaf water potentials that have to be developed by the mistletoe in order to cope with the host's water availability. In the same environment, but with less extreme salinities the mistletoe can easily overcome the physiological responses of the host leading to an excessive water consumption of the parasite that may deplete host water resources, to the point that it endangers the host's existence and mistletoe survival. This appears to be the case for the *C. uvifera*/*P. maritima* system.

### Acknowledgments

We thank INPARQUES for allowing us to conduct research at the Parque Nacional Morrocoy and the directors and personnel of this park for their cooperation. Technical assistance in the field was provided by Luis Nieto and Helisaul Rangel. This research was supported by the CDCHT-ULA (grant C-290-86).

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