

Gas exchange and water relations of two mistletoes, *Tapinanthus oleifolius* and *Viscum rotundifolium*, on the same host, *Acacia nebrownii*, in south-eastern Namibia

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Received 5 December 1994; revised 26 June 1995

Gas exchange patterns and water relations of two mistletoes, *Tapinanthus oleifolius* and *Viscum rotundifolium* on the same deciduous host tree, *Acacia nebrownii*, have been studied intensively in the dry and wet seasons in semi-arid south-eastern Namibia, where rain falls only in the summer. Comparative measurements of *Tapinanthus oleifolius* on the stem-succulent CAM plant, *Euphorbia virosa*, and on *Ziziphus mucronata* in the same area were also made. All measurements of CO₂ exchange and transpiration were performed in fully acclimatized cuvettes of a gas exchange system which allowed continuous measurements of the host and the parasite simultaneously. The water potential results confirm previous observations that mistletoes have a lower water potential throughout the day than their hosts. In the dry season, pre-dawn and minimum water potential was about 1 MPa lower than in the wet season, for both the leafless and fully foliated host and the evergreen mistletoes. There was an effective stomatal control in all mistletoe plants investigated. The results obtained for transpiration, leaf conductance, internal CO₂ concentration and water-use efficiency (WUE) contradicted commonly accepted generalizations. Transpiration and leaf conductance were found to be higher for the host than for any of its common mistletoes as long as the leaf-to-air water vapour pressure difference (Δw) did not exceed 30 mPa Pa⁻¹. At higher values of Δw , *Tapinanthus oleifolius*, but not *Viscum rotundifolium*, transpired at higher rates than the host. CO₂ balance over 24 hours and photosynthetic CO₂ uptake were significantly higher for the host than for any of its parasites. Although the WUE over 24 h was slightly better for *Acacia nebrownii* compared with *Tapinanthus oleifolius*, apparent WUE during photosynthetic CO₂ uptake was always better for both mistletoes. Measurements of CO₂ and water balance over 24 h, photosynthetic CO₂ uptake, night respiration, internal CO₂ concentration, leaf conductance and WUE indicate that *Tapinanthus oleifolius* and *Viscum rotundifolium* behaved in opposite ways in the dry and wet seasons, indicating that different phenological cycles of both species might be involved in determining mistletoe performance on the same host. The results presented contribute to a better understanding of the host/parasite relationship and indicate that commonly accepted generalizations may not always be applicable.

Gaswisselingspatrone en waterverhoudings van twee voënte *Tapinanthus oleifolius* en *Viscum rotundifolium* op dieselfde bladwisselende gasheerplant *Acacia nebrownii* is bestudeer in die droë en nat seisoene in Suid-Oos-Namibië. Vergelykende studies van *Tapinanthus oleifolius* op *Ziziphus mucronata* en die stamsukkulente CAM plant *Euphorbia virosa* is ook uitgevoer. Alle bepalinge is in ten volle ge-akklimatiseerde kuvette uitgevoer wat deurlopende bepalinge op die gasheer en parasiet moontlik gemaak het. Die resultaat van die waterpotensiaalbevestiging vorige waarnemings dat voënte 'n laer waterpotensiaal gedurende die dag het as hulle gasheer. Die minimum waterpotensiaal voor dagbreek in die droë seisoen was ongeveer 1 MPa laer as in die nat seisoen vir beide die blaarloos en blaarbevattende gasheerplant en die immergroen voënte wat ondersoek is. In al die voënte was daar effektiewe stomatêre beheer teenwoordig. Die resultate wat behaal is vir transpirasie, blaargeleiding, interne koolsuurgaskonsentrasie en waterbenuttingsdoeltreffendheid het nie ooreengestem met aanvaarde veralgemenings nie. Transpirasie en blaargeleiding was hoër vir die gasheer as vir enige van die voënte solank as die blaar-tot-lug waterdampdruk verskil nie 30 mPa Pa⁻¹ oorskry het nie. By hoër waardes het *Tapinanthus oleifolius*, maar nie *Viscum rotundifolium* nie, teen 'n hoër tempo as die gasheerplant getranspireer. Die koolsuurgasbalans oor 24 uur en die fotosintetiese koolsuurgasopname was betekenisvol hoër vir die gasheer as vir enige van die parasiete. Alhoewel die waterbenuttingsdoeltreffendheid oor 24 uur effens beter vir *Acacia nebrownii* as vir *Tapinanthus oleifolius* was, was die skynbare waterbenuttingsdoeltreffendheid gedurende fotosintetiese koolsuurgasopname altyd beter. Bepaling van die koolsuurgas en waterbalans oor 24 uur, fotosintetiese koolsuurgasopname, nagrespirasie, interne koolsuurgaskonsentrasie, blaargeleiding en waterbenuttingsdoeltreffendheid het aangedui dat die twee parasiete teenoorgestel gereageer het in die nat en droë seisoene. Dit mag beteken dat verskillende fenologiese siklusse van albei spesies betrokke mag wees in die bepaling van voëntprestasie op dieselfde gasheer. Die resultate lei tot 'n beter begrip van gasheer/parasietverwantskappe en dui daarop dat die aanvaarde veralgemenings nie altyd korrek is nie.

Keywords: *Acacia nebrownii*, gas exchange, host/parasite relationship, mistletoe, Namibia, *Tapinanthus oleifolius*, *Viscum rotundifolium*, water relations.

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Introduction

The semi-arid to arid areas receiving summer rainfall in the south-east of Namibia show a rich mistletoe vegetation growing on seasonal and drought deciduous shrubs and trees. Very few

trees are not parasitized, and most carry a heavy load of parasites, among which *Tapinanthus oleifolius* (Loranthaceae) is by far the dominant species. The last summer rains fall in April and rain falls again in January, hence the dry season is rather

extended and mistletoes might be expected to suffer significantly from water shortages towards the end of the dry season. Many trees in this area, especially acacias, carry two mistletoe species, namely, *Tapinanthus oleifolius* and *Viscum rotundifolium* (Viscaceae).

It is well established that these two mistletoes belong to different phenotypes with regard to how they handle calcium (Horak 1974). Species in the Viscaceae are calcifuge; they precipitate calcium with oxalic acid. Members of the Loranthaceae, on the other hand, accumulate free calcium in the cell sap and are regarded as calcitrophous. With respect to their vegetative and reproductive phases the two mistletoes also differ from each other. *V. rotundifolium* flowers in midwinter, June and July, while *T. oleifolius* has a flowering peak in late spring but continues to flower throughout the whole summer (Visser 1981). The end of the dry season is therefore a dormant period for *V. rotundifolium* but a highly active time for *T. oleifolius*. Consequently, one might expect a higher photosynthetic activity in *T. oleifolius* compared with *V. rotundifolium*. This stage of higher activity in *T. oleifolius* coincides with the leafless stage of the host tree.

The initial aim was to determine the nutrient and carbon flow from the host to the mistletoe. In order to quantify such flows, gas exchange and water potentials of host and parasites were measured. Most previous work on parasites has shown that hosts transpire less than their parasites, have lower leaf conductance and internal CO₂ concentrations, and a better water-use efficiency than their parasites (i.e. Hellmuth 1971; Schulze *et al.* 1984; Ehleringer *et al.* 1986; Goldstein *et al.* 1989; Küppers *et al.* 1993; Midgley *et al.* 1994). On the other hand, Küppers *et al.* (1992) continuously measured gas exchange of the host/mistletoe pair *Eucalyptus behriana*/*Amyema miquelii* and reported that host transpiration greatly exceeded that of the mistletoe. Unfortunately, however, the data presented were not obtained simultaneously for host and parasite. We therefore sought to obtain ecophysiological data for host and parasite simultaneously, and ours is the first report of continuous and simultaneous measurements of the gas exchange of host and mistletoe *in situ*.

Our results with the two mistletoes, *T. oleifolius* and *V. rotundifolium*, parasitizing the same host tree, *Acacia nebrownii*, indicate that our understanding of the host/parasite relationship is far from complete, and that some generalizations require modification.

Materials and Methods

The study site

The study was carried out on the farm Geitsanes situated in the northern part of the Karas Mountains in south-eastern Namibia (Figure 1). The study site is about 1 200 m in altitude on a flat plain next to a dry river bed. The area receives about 250 mm of rain annually, which falls predominantly in the summer, between December and April. The rest of the year is dry. In winter, temperatures can drop well below freezing at night, but daytime temperatures still reach about 20°C (pers. commun. from the farmer). The vegetation at the study site is a summer-green dwarf shrub savanna with scattered trees especially along the rivers (Giess 1971). The study site itself was a former river bed, filled with rocks, sand and other sediments.

Hosts and mistletoes

The study area was characterized by an overwhelming abundance of mistletoes, with *T. oleifolius* (Wendl.) Danser being by far the dominant species, but *V. rotundifolium* L.f. and *V. capense* L.f. were also present. *T. oleifolius* is not restricted to a particular host (Visser 1981) and was found on *Acacia nebrownii* Burt Davy, *A. hebeclada* DC, *Catophractes alexandri* D. Don, *Ziziphus mucronata* Willd, *Grewia flava* DC, *Rhigozum trichotomum* Burch, *Euphorbia virosa* Willd. and others. Mostly, host trees and shrubs were infected by a

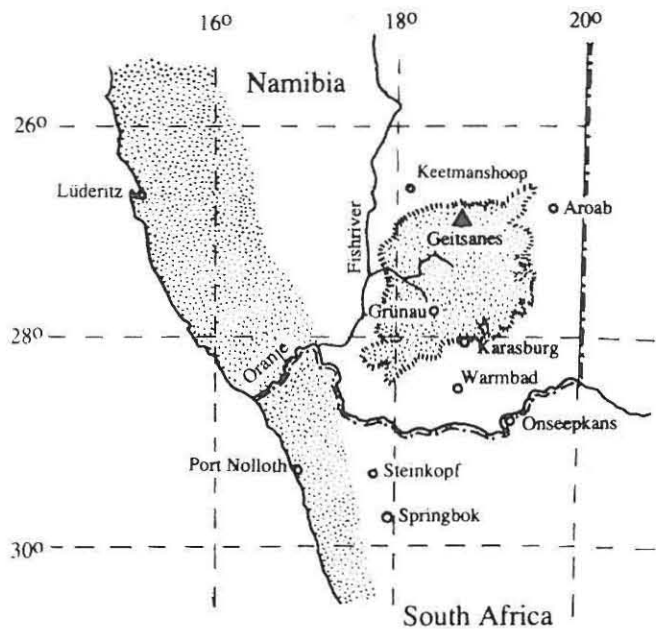


Figure 1 Map of the southern part of Namibia in which the Karas Mountains are situated. The dotted area along the Atlantic coast marks the Namib Desert. The dotted area east of the Fish River marks the Karas Mountains. The filled triangle gives the location of the farm Geitsanes where the study was done. The dashed and dotted line marks the border between Namibia and South Africa.

great number of mistletoes. For this study we selected an *Acacia nebrownii* tree about 5 m high which was parasitized by 122 *T. oleifolius* and 46 *V. rotundifolium* individuals. For comparison, *T. oleifolius* parasitizing the CAM succulent, *Euphorbia virosa*, and another C₃ shrub, *Ziziphus mucronata*, was also investigated.

Measurements were taken in December 1990 prior to rainfall when *Acacia* was still without leaves and in February and March 1991 during and after heavy summer rains, when the leaves of *Acacia* were fully expanded.

Measurement of gas exchange and water-potential

Gas exchange of attached shoots of the host (except for *E. virosa*) and mistletoe was measured with a Walz minicuvette system (Walz, Effeltrich, Germany) as described earlier (von Willert & Wagner-Douglas 1994). This system consists of two identical assimilating chambers, allowing a continuous and simultaneous measurement of two plant samples. The design of the assimilating chambers allowed a whole shoot of the target plant to be sampled in its natural position. Either host and parasite or two parasites were fixed into the chambers and measured simultaneously and continuously over a period of several days. The gas exchange system was controlled by a data-logging unit which also stored the data collected. Data were transferred from the data-logging unit to a PC for further computation. All gas exchange parameters were calculated using the equations of von Caemmerer & Farquhar (1981). Fluxes are generally expressed on a total leaf area. CO₂ balances over 24 h, daily sums of transpiration, mean Δw , and mean transpiration per hour for a given period of time were determined using a commercial computer program (InPlot, GraphPad software, San Diego, USA) by measuring the area under the curve.

Water potential of either leaves or branches of hosts and mistletoes was measured with a Scholander pressure bomb. Samples were wrapped in aluminium foil before they were cut from the plant. Measurements were made either pre-dawn with at least three replications or during the course of the day. As an accurate determination of the equilibrium pressure was time consuming (at least two consecutive readings between depressurizing had to be equal) and intervals

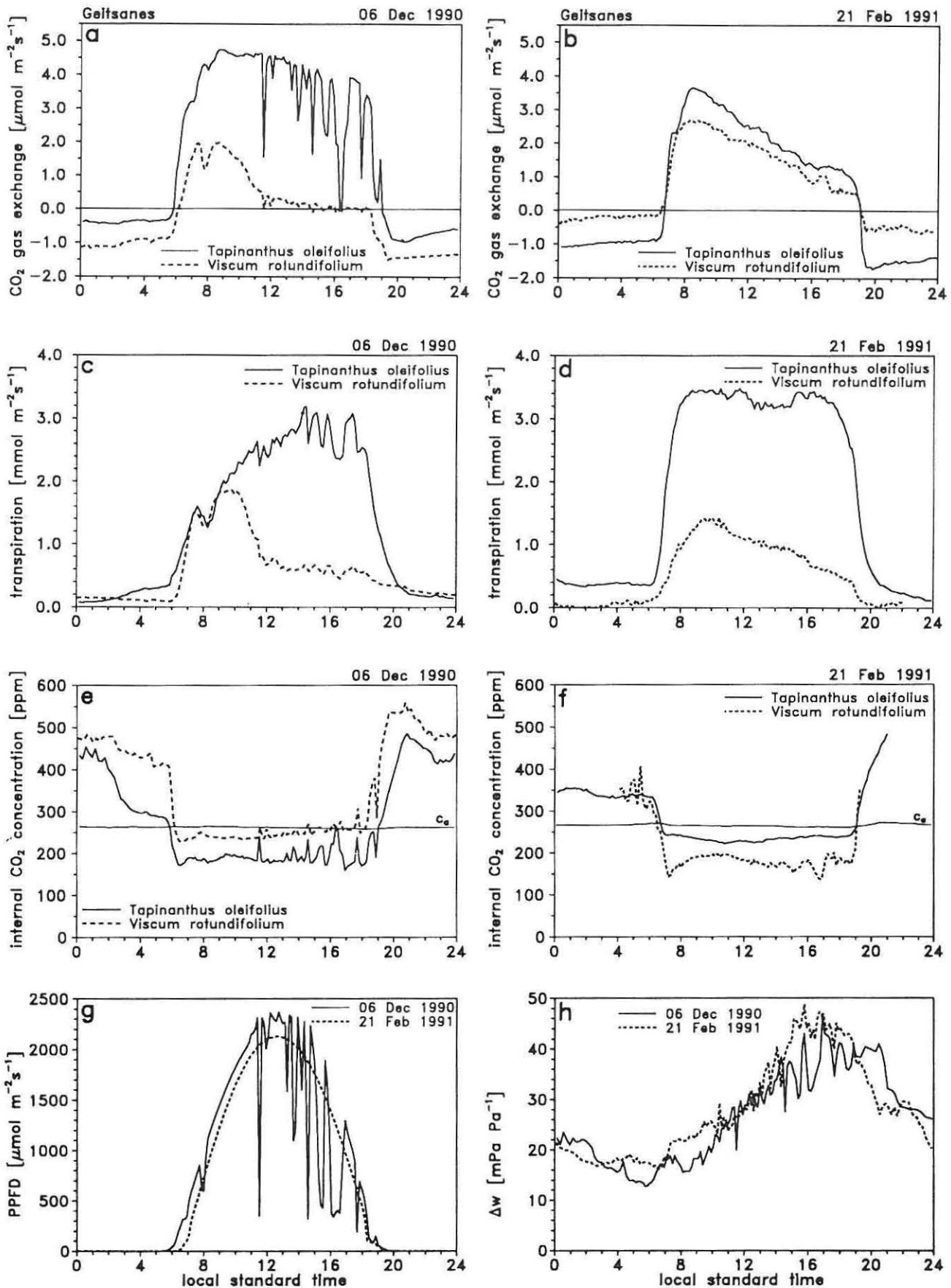


Figure 2 Diurnal courses of CO₂ exchange, transpiration, internal CO₂ concentration, photosynthetic active photon flux density (PPFD) and leaf-to-air water vapour pressure difference (Δw) for the two mistletoes *Tapinanthus oleifolius* and *Viscum rotundifolium* parasitizing the same host tree, *Acacia nebrownii*. Measurements were made at the end of the dry season (December 1990) when *Acacia nebrownii* had no leaves, and during the wet season (February 1991) when *Acacia nebrownii* was fully foliated. Representative days with fairly similar courses of radiation (g), temperature (not shown) and Δw (h) were selected for this comparison.

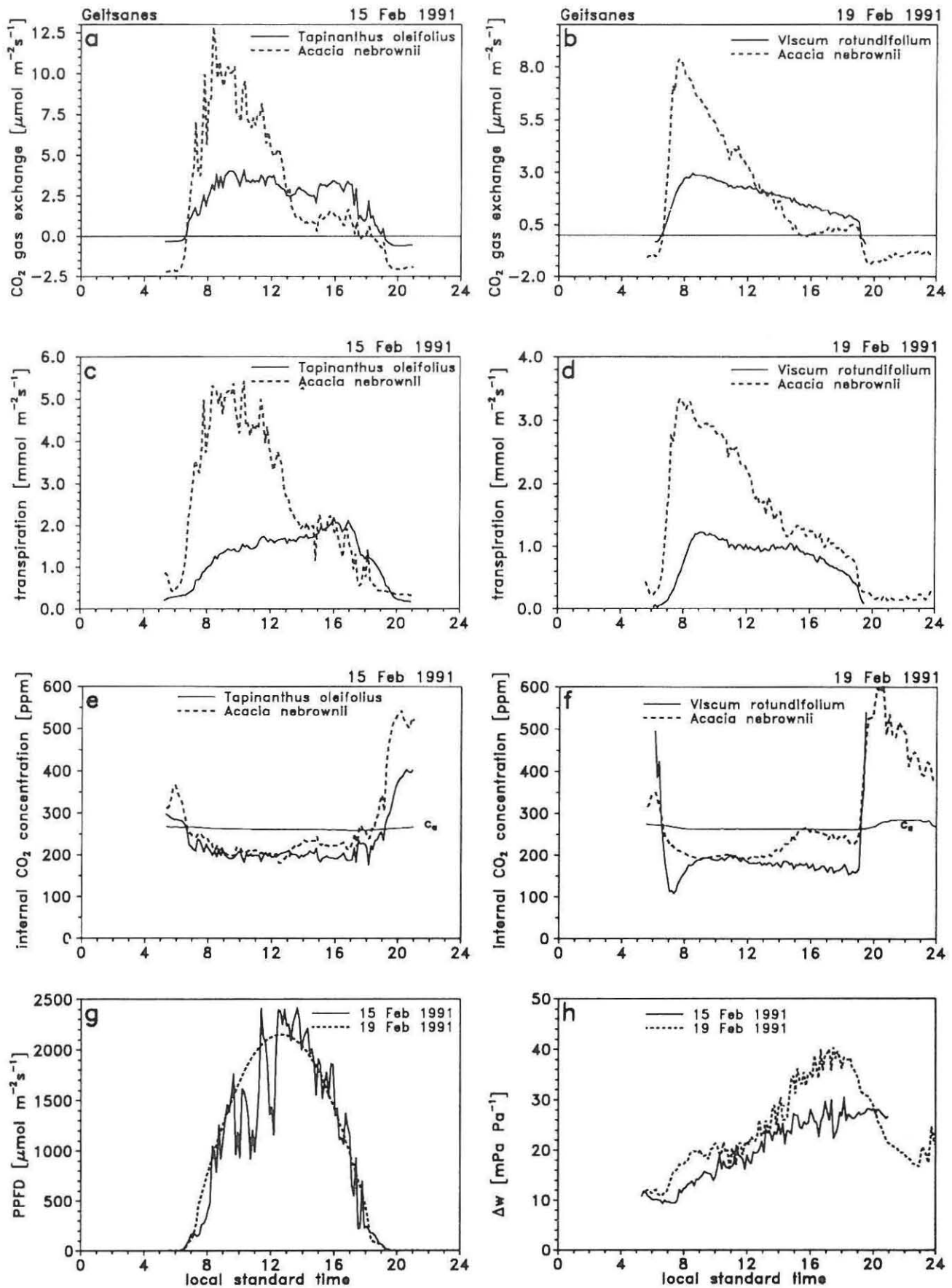


Figure 3 Diurnal courses of CO₂ exchange, transpiration, internal CO₂ concentration, photosynthetic active photon flux density (PPFD) and leaf-to-air water vapour pressure difference (Δw) for the two mistletoe/host systems *Tapinanthus oleifolius*/Acacia nebrownii and *Viscum rotundifolium*/Acacia nebrownii. Both mistletoes parasitized the same tree. Measurements were made during the wet summer season in February and March 1991. Representative days have been chosen for this comparison. The diurnal courses of radiation (g) and Δw (h) for the two days are given in the bottom graphs.

between the determinations in the course of the experiment had to be as short as possible, no replications were made.

Results

Diurnal courses of CO₂ uptake, transpiration, leaf conductance, WUE and internal CO₂ concentration

Diurnal courses of CO₂ exchange, transpiration and internal CO₂ concentration of the two mistletoes *V. rotundifolium* and *T. oleifolius* on the same *Acacia nebrownii* tree are given in Figure 2 for a representative day of both measuring periods, the dry and the wet season. PPFD, Δw and air temperature (not shown) were fairly similar on those two days (Figure 2). The measuring period in December was at the end of the dry season and *A. nebrownii* had no leaves. Consequently, a comparison with the host plant in terms of gas exchange characteristics was not possible at this time.

The measuring period in February was preceded by the first summer rains. *A. nebrownii* had fully expanded leaves which allowed simultaneous measurements of the gas exchange of both host and mistletoe. This comparison is presented in Figure 3 for both *T. oleifolius* and *V. rotundifolium* on the same host tree, *A. nebrownii*. Unfortunately, Δw was not identical on the two days but there were no two days with more similar Δw than these.

In the early morning, leaf conductance of the two mistletoes characteristically lagged behind leaf conductance of the host. Later, the host stomata closed while mistletoe stomata were still open. As can be seen from Figure 3 this results in a slower increase of both photosynthetic CO₂ uptake and transpiration after sunrise. Furthermore, quantum yields for the mistletoes are significantly lower than for the host, as is shown in Figure 4, in which CO₂ exchange is given as a function of photosynthetic active photon flux density.

In the dry season, *T. oleifolius* exhibited a high positive CO₂ balance over 24 h, whereas that of *V. rotundifolium* was negative (Figure 5). The concomitant water loss of *V. rotundifolium* in the dry season was about 63% of that of *T. oleifolius*. In the wet season both mistletoes had the same CO₂ balance over 24 h. These seasonal changes were accompanied by a decrease in water loss for *V. rotundifolium*, whereas the water loss for *T. oleifolius* was in the same range as in the dry season. Compared with their host, both mistletoes had a significantly lower CO₂ balance over 24 h in the wet season. Transpiration of *T. oleifolius* was

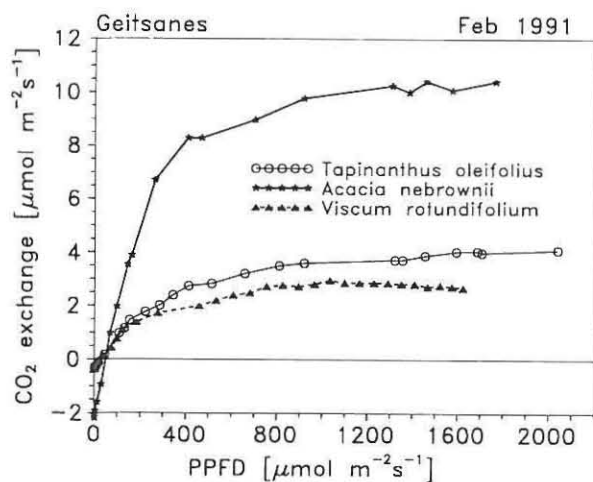


Figure 4 CO₂ exchange of the two mistletoes, *Tapinanthus oleifolius* and *Viscum rotundifolium*, and their host, *Acacia nebrownii* as a function of photosynthetic active photon flux density (PPFD). Δw was set to 20 mPa Pa⁻¹ and leaf temperature to 25°C.

similar to that of the host but was only 40% of the host's water loss for *V. rotundifolium*.

From the data presented in Figure 5 it follows that the 24-h WUE for *T. oleifolius* decreased from 1.1 [mmol mol⁻¹] in the dry to 0.6 in the wet season. For *V. rotundifolium*, on the other hand, WUE increased from a non-existent while negative value to 1.4 in the wet season. At the same time, WUE of *A. nebrownii* was 0.8, slightly higher than that of *T. oleifolius*, but significantly lower than that of *V. rotundifolium*.

A comparison of the daytime CO₂ uptake and nocturnal CO₂ release of both parasites shows that the increase in CO₂ balance of *V. rotundifolium* is due to both a more than twofold increase in photosynthetic CO₂ uptake and a substantial reduction in respiratory CO₂ release. The significant decrease in the CO₂ balance of *T. oleifolius* results from an almost 50% reduction of photosynthetic CO₂ uptake and a threefold increase in dark respiration (Figure 5c). The ratio of internal to external CO₂ reflects the changes in the photosynthetic CO₂ uptake. It increases for *T. oleifolius* and decreases for *V. rotundifolium* from the dry to the wet season (Figure 5d).

The different performance of the two mistletoes *T. oleifolius* and *V. rotundifolium* in the dry and wet seasons becomes obvious when CO₂ exchange is plotted as a function of leaf conductance. In the dry season, *V. rotundifolium* opens its stomata wider than *T. oleifolius* but exhibits only low rates of photosynthetic CO₂ uptake. In contrast, *T. oleifolius* has a threefold higher CO₂ uptake rate with much lower leaf conductances (Figure 6a). In the wet season, with sufficient water supply in the soil, but also with a fully foliated host, CO₂ uptake of both mistletoes is about equal. *V. rotundifolium* achieves this CO₂ uptake at a very low leaf conductance compared with both that of *T. oleifolius* and its own leaf conductance in the dry season (Figure 6b).

T. oleifolius parasitizing *Euphorbia virosa* doubles its CO₂ balance over 24 h from the dry to the wet season, whereas transpiration increases by only 70%. This leads to a shift of the 24-h WUE from 1.3 to 1.5 (data not shown). Leaf conductance of the parasite on the succulent CAM-exhibiting host is much lower than that for the same parasite growing on *A. nebrownii*. A comparison of the relationship between CO₂ exchange and leaf conductance of *T. oleifolius* on the two different hosts is given in Figure 7.

Water relations

Generally, pre-dawn water potentials (Ψ) of *T. oleifolius* and *V. rotundifolium* were more negative than those of *A. nebrownii* (Figure 8). At the end of the dry season (December 1990), pre-dawn water potentials were around -2.5 MPa but were about 1 MPa higher after the first rains in January and February. An abundant rainfall event in March raised Ψ by another 1 MPa.

At the end of the dry season, the two mistletoes on *A. nebrownii* exhibited a pronounced diurnal change in water potential (Figure 9); $\Delta\Psi$, the difference between pre-dawn and minimum water potential, was about 2.5 MPa for *V. rotundifolium* and about 2 MPa for *T. oleifolius*. Increases in water potential started early in the afternoon and were nearly completed at sunset. $\Delta\Psi$ for the leafless *A. nebrownii* was less than 1 MPa.

In the wet season, pre-dawn water potential for the mistletoes was about 0.2 MPa lower than that of the host. Decline of the water potential in the morning was much faster in the wet season, and recovery started later in the afternoon. Due to high rates of transpiration in the early morning, the water potential of *A. nebrownii* also decreased rapidly in the morning, but $\Delta\Psi$ was still only 20% greater than that of the leafless tree.

The water potential of *T. oleifolius* on *E. virosa* did not show a marked diurnal change in either of the two seasons. In accord-

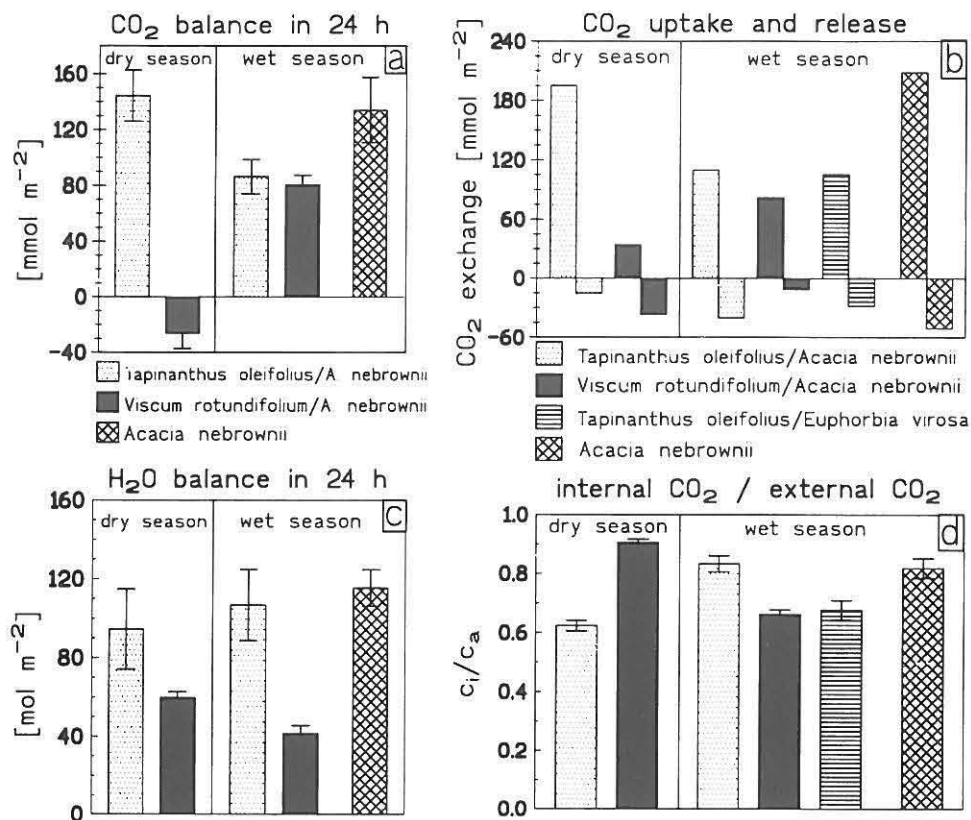


Figure 5 Twenty four-hour balances of CO₂ uptake (a) and water loss (c) for the mistletoes *Tapinanthus oleifolius* and *Viscum rotundifolium* as well as for their common host, *Acacia nebrownii*. Balances of all days were pooled regardless of the climatic conditions, and mean values with standard deviation are presented. As *Acacia nebrownii* did not have leaves in the dry season, balances for the host are only available for the wet season. (b) Photosynthetic CO₂ uptake and nocturnal CO₂ release for *Tapinanthus oleifolius*, *Viscum rotundifolium*, their common host, *Acacia nebrownii*, and for *Tapinanthus oleifolius* on the stem-succulent CAM plant, *Euphorbia virosa*. Days with most similar day and night temperatures were selected for this comparison. (d) Ratio of internal to external CO₂ concentrations given as a mean over all days for the time from sunrise to sunset for the same species as in (b). Measurements in the dry season were done in December 1990 and those for the wet season in February and March 1991. Number of days per bar is at least five in the dry season and eight in the wet season.

ance with the higher transpiration rates measured in the wet season, the water potential dropped faster and lower but recovered quickly after sunset (Figure 9). The pre-dawn water potential of *T. oleifolius* on *E. virosa* was 0.2 MPa higher in the wet season compared with that measured in the dry season.

A comparison of the relationship between leaf conductance and leaf water potential between host and parasite reveals that leaf conductance of *A. nebrownii* increased only until 8:00 and then sharply declined, while that of *T. oleifolius* continued to increase until 10:00. From 12:00 to 16:00, leaf conductances of both the mistletoe and the host were similar, as were their rates of transpiration, but water potential of the mistletoe was more than 1 MPa lower (Figure 10).

Mean transpiration rates of all three species increased with increasing mean Δw . However, if the mean vapour pressure deficit of the air was too high, *A. nebrownii* reduced transpiration by gradually closing stomata, whereas *T. oleifolius* markedly increased transpiration. Consequently, only at very high Δw did *T. oleifolius* transpire more than its host. The transpiration rates of *V. rotundifolium* never approached that of its host even at high Δw . Unfortunately, very high pressure deficits occurred only in the dry season so corresponding measurements for *A. nebrownii* are not available at the high range (Figure 11).

Leaf areas of sampled branches were carefully determined and extrapolated for the number of branches per mistletoe and for the number of mistletoes. This calculation resulted in a transpiring

leaf surface area of 2.28 m² for *T. oleifolius* and 1.34 m² for *V. rotundifolium* in one tree. Based on the mean daily transpiration for both species in the dry season, all 122 *T. oleifolius* specimens accounted for a daily water consumption of 3.88 l while the 46 *V. rotundifolium* specimens consumed 1.50 l. This means that at the end of the dry season, the leafless host *A. nebrownii* must supply 5.38 l of water per day for its mistletoes. Because the mean daily loss of water for *T. oleifolius* increased to 4.35 l and that of *V. rotundifolium* decreased to 1.04 l in the wet season, the amount of water consumed by the 168 mistletoes remained about the same. The transpiring leaf area of *A. nebrownii* was estimated to be 10.8 m² which, when multiplied by the mean daily transpiration, resulted in a water loss of 22.4 l per day for the host. In the wet season, the daily water loss of the *Acacia* and its mistletoes added up to nearly 28 l. Hence, of the water used by the host, about 20% is consumed by its parasites.

Discussion

The data presented here conflict with many of the commonly accepted generalizations which are thought to characterize the relationship between hosts and hemiparasitic mistletoes. These generalizations are (a) transpiration and leaf conductance of mistletoes are always higher than that of their hosts, (b) internal CO₂ concentration is higher in the mistletoe, (c) water-use efficiency (WUE) is lower for mistletoes than for their hosts, (d) $\delta^{13}\text{C}$ values for mistletoes are more negative than those of their hosts, and

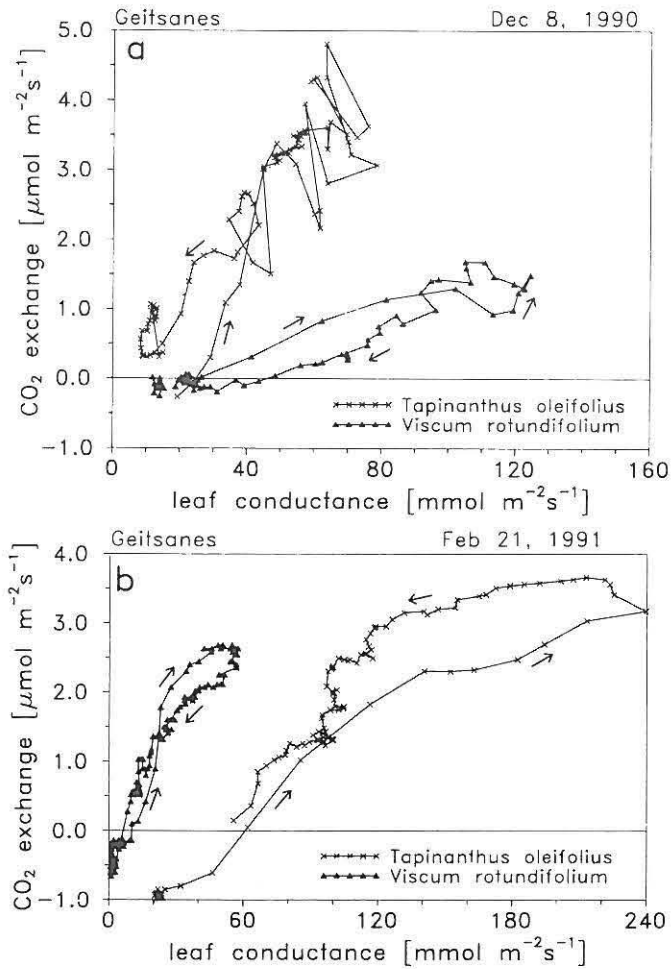


Figure 6 (a) Relationship between CO₂ exchange and leaf conductance for two mistletoes, *Tapinanthus oleifolius* and *Viscum rotundifolium* on the same host, *Acacia nebrownii*, at the end of the dry season when the host tree had not yet grown new leaves. (b) The same relationship about 3 months later during the wet season when the host tree was fully foliated. For the comparison, days with similar climatic conditions were selected. Arrows at the curves indicate the direction of progressing time.

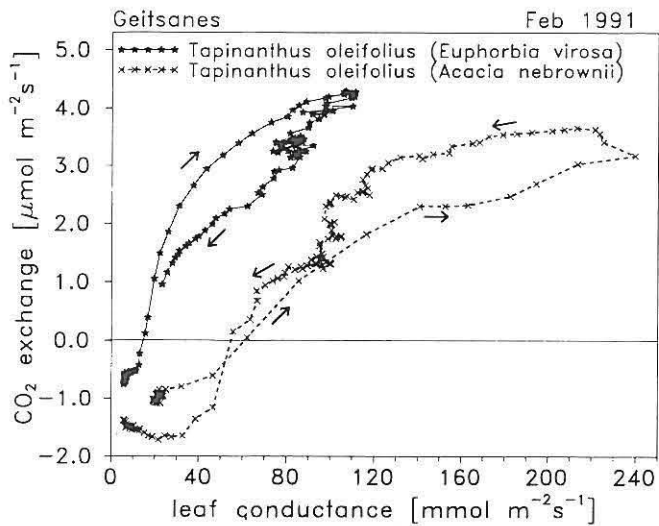


Figure 7 Relationship between CO₂ exchange and leaf conductance for two *Tapinanthus oleifolius* specimens parasitizing different hosts, *Acacia nebrownii*, and the stem-succulent CAM plant, *Euphorbia virosa*. Arrows at the curves indicate the direction of progressing time.

(e) the water potential of mistletoes is always lower compared to their hosts (Davidson *et al.* 1989; Ehleringer *et al.* 1985; Glatzel 1983; Hellmuth 1971; Hollinger 1983; Schulze & Ehleringer 1984; Schulze *et al.* 1984; Stewart & Press 1990; Ullmann *et al.*

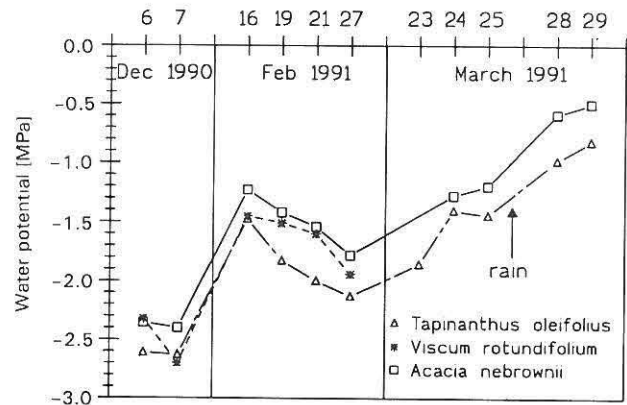


Figure 8 Pre-dawn water potential for the two mistletoes, *Tapinanthus oleifolius* and *Viscum rotundifolium*, and their common host tree, *Acacia nebrownii*, at the end of the dry season and during the wet season. On 26 March, 78 mm of rain fell.

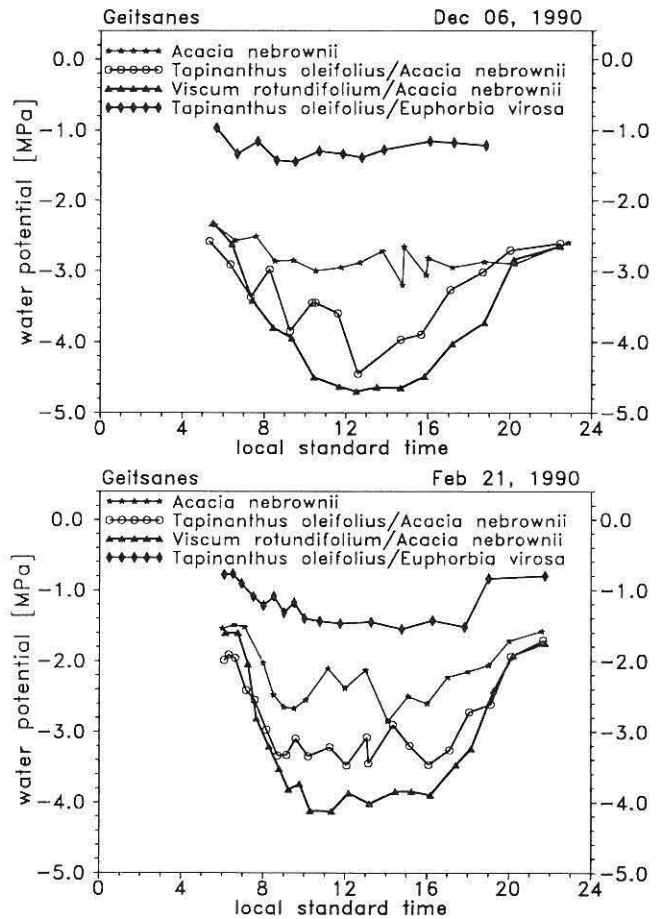


Figure 9 Diurnal course of water potential of the two mistletoes, *Tapinanthus oleifolius* and *Viscum rotundifolium* and their common host tree, *Acacia nebrownii*, at the end of the dry season (December 1990) when the host was still in its leafless stage, and after the first rains in the wet season (February 1991) when the host was fully foliated. For comparison, the water potential of *Tapinanthus oleifolius* parasitizing the stem-succulent CAM plant, *Euphorbia virosa*, is also given.

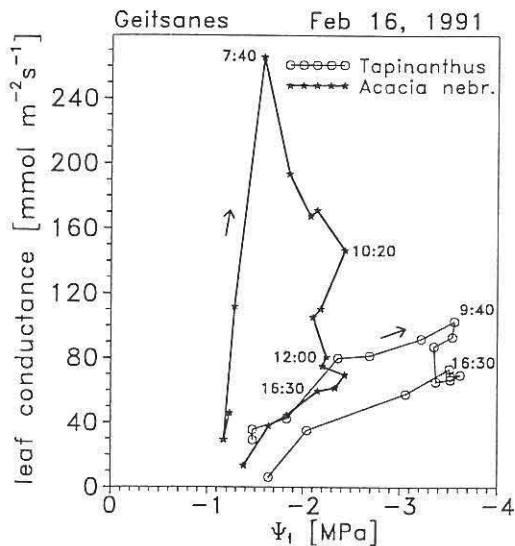


Figure 10 Relationship between leaf conductance and leaf water potential for the mistletoe, *Tapinanthus oleifolius* and its host, *Acacia nebrownii*, in the course of a day in the wet season. Arrows at the curves indicate the direction of progressing time.

1985; Whittington & Sinclair 1988). Results of other studies, however, do not support these generalizations. Fisher (1983) reported that mistletoes may transpire less than the host when water is abundant. A similar result was obtained when transpiration of *Amyema nester* was compared with that of its host *Acacia grasbyi* under conditions of optimal soil moisture (Hellmuth 1971). Under these conditions, the host transpired slightly more than its mistletoe, whereas under severe stress the opposite was found. Among the 19 Australian mistletoe/host pairs investigated, the host, *Acacia farnesiana*, exhibited a higher transpiration than its mistletoes *Lysiana spathulata* (Ullmann *et al.* 1985). Continuous measurement of CO₂ exchange and transpiration of *Eucalyptus behriana* and its mistletoe *Amyema miquelii* at low plant water status in the field indicated a much higher transpiration rate in the host (Küppers *et al.* 1992). There are two reports concerning South African mistletoe/host systems, including three *Viscum* species, where the $\delta^{13}\text{C}$ value of the host was more negative than that of the mistletoe (De la Harpe *et al.* 1980, 1981).

The results of our study indicate the following:

(a) Water potentials of the mistletoes were always lower than that of their hosts in both the dry and the wet season. The water potential gradient between the mistletoes, *T. oleifolius* and *V. rotundifolium* and their common host, *A. nebrownii*, steepened with increasing drought but only by 0.2 MPa, which is at least qualitatively in accordance with earlier reports (Fisher 1983; Hollinger 1983; Schulze *et al.* 1984). However, the pre-dawn gradient for *T. oleifolius* in the wet season was significantly greater than in the dry season, indicating either that stomata were open (compare with the night transpiration in Figure 2) or rehydration problems occurred overnight (Whittington & Sinclair 1988). Regarding water potentials, our results are in full accordance with all earlier reports on host/parasite relationships.

(b) Photosynthetic CO₂ uptake rates of the host were always higher than for the two mistletoes (Figure 5). The same holds true for the CO₂ balance over 24 hours. However, the photosynthetic CO₂ uptake rate of *T. oleifolius* in the dry season was as high as that of its host when it was foliated in the wet season.

Our most surprising finding is that the ecophysiology of *T. oleifolius* and of *V. rotundifolium* contrasted with each other in

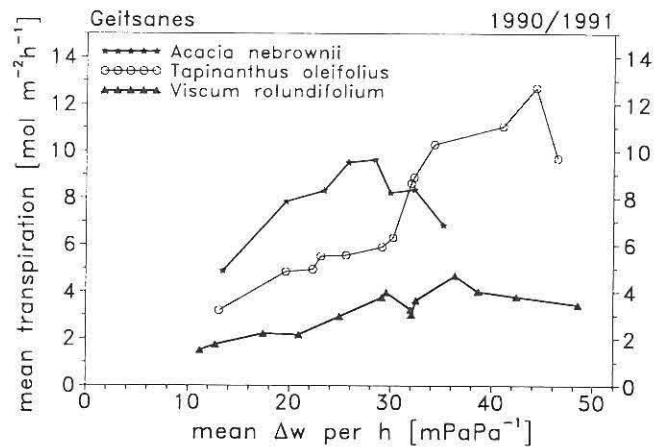


Figure 11 Relationship between mean transpiration and mean leaf-to-air water vapour pressure difference (Δw) for the two mistletoes, *Tapinanthus oleifolius* and *Viscum rotundifolium*, parasitizing the same host tree, *Acacia nebrownii*. The data are taken from all available continuous measurements of transpiration regardless of the season and other climatic conditions. Transpiration and Δw are given as hourly means for the time between one hour after sunrise and one hour before sunset.

the dry and wet seasons. Whereas CO₂ uptake rates, as well as the 24-h CO₂ balance, declined significantly for *T. oleifolius* with a better water supply, both features increased for *V. rotundifolium*. The overnight respiration data, however, (CO₂ release) were just the opposite (Figure 5). For *V. rotundifolium* the ratio of CO₂ release to CO₂ uptake changed from 1:0.9 in the dry season to 1:7.2 in the wet season, while the ratios for *T. oleifolius* changed in the opposite direction from 1:12.7 to 1:2.7. For *T. oleifolius* on *E. virosa*, this ratio was 1:3.7 in the wet season and for *A. nebrownii*, the common host of *V. rotundifolium* and *T. oleifolius*, it was 1:4.1. Night respiration of the mistletoes is high but it is still lower than that of the host.

We do not have an explanation for the finding that *T. oleifolius* and *V. rotundifolium* behave opposite to each other in nearly all respects. Perhaps in the wet season *T. oleifolius* but not *V. rotundifolium* relies more on the host for organic solutes in the xylem stream tapped by the mistletoe. Perhaps the opposite effects shown by the two mistletoes reflect seasonal differences in their respective haustorial features, as has been suggested to occur with the haustorial hydraulic conductivity in the course of a day (Whittington & Sinclair 1988; Davidson *et al.* 1989). It is also possible that the apparently different phenological cycle of the two mistletoes is responsible for the opposite reactions. Besides a recent article (Küppers *et al.* 1992) suggesting seasonal differences in mistletoe performance, the phenological cycle of host and mistletoe as a possible factor influencing the host/parasite relationship has not been investigated.

(c) According to our results, the answer to the question whether transpiration of the mistletoes is higher than that of the hosts, is complex. When transpiration was measured continuously with the minicuvette system, water loss of *V. rotundifolium* was always lower than that of its host, *A. nebrownii*. For *T. oleifolius*, transpiration was always higher than that of its parasitizing competitor on the same host. However, compared with its host, transpiration of *T. oleifolius* was lower at low Δw but exceeded that of its host at higher Δw (Figure 11). This is due to the fact that *A. nebrownii* closes its stomata earlier and to a greater extent than does *T. oleifolius*. That *T. oleifolius* exhibits stomatal control, as was shown for other mistletoes by Glatzel (1983) and Schulze *et al.* (1984), is well-documented by the fact that *T. oleifolius* keeps

its water potential at a constant value for most of the daylight period despite increasing Δw . This is achieved by partial stomatal closure (see Figures 2, 3, 10). Our results strongly indicate good stomatal control in mistletoes regardless of the season.

We also continuously measured transpiration of the host/mistletoe system *Ziziphus mucronata*/*Tapinanthus oleifolius*. The data confirmed the findings for *A. nebrownii*/*T. oleifolius*. As transpiration of *E. virosa* was not measurable with our equipment, we have no data for the *E. virosa*/*T. oleifolius* system. Judged from the transpiration of CAM succulents in the Namib Desert (von Willert *et al.* 1992), it is, however, most likely that the transpiration of *E. virosa* is much lower than that of *T. oleifolius*. This assumption is additionally evidenced by a recent report of Midgley *et al.* (1994). In their study, the rate of transpiration of *Viscum crassulae* was about four times higher than that of its host, *Euphorbia grandidens*.

Why do our results for transpiration and leaf conductance contrast with those in the literature? In this context we want to focus on three aspects: First, can the number of mistletoes parasitizing one host influence the relative rates of transpiration between mistletoe and host? Our *Acacia* tree was heavily infested by 168 mistletoes, which, in the wet season consumed about 20% of the water taken up by the host, and which at the end of the dry season, when water should be scarce, required the host to supply more than 5 l of water per day for transpiration by the parasites. Although there are no similar estimations in other studies for comparison, we believe the answer to the above question is no. We also made measurements on less infected *A. nebrownii* and *Ziziphus mucronata* and always obtained lower transpiration rates for the mistletoe than for the host.

Second, can the contrasting results be a matter of the technique used to measure transpiration? Most past measurements have been conducted with porometers and clamp-on cuvettes without temperature control and rather short measurement times. There are only two reports using other systems (Hollinger 1983; Küppers *et al.* 1992). Although Küppers *et al.* (1992) measured continuously, they did not measure host and parasite simultaneously. In spite of this technique Küppers *et al.* (1992) consistently obtained the same findings as we reported. Also, Hollinger (1983) did not mention whether or not host and mistletoe were measured continuously and simultaneously, as we have done.

The great disadvantage of the older porometer clamp-on cuvettes is that they lacked temperature control and the ventilation inside the porometer head was not as efficient as in a minicuvette. This leads to a rapid increase in both cuvette and leaf temperature and hence to a steep increase of Δw . As stomata of mistletoes were found to be less sensitive to increasing Δw than those of the hosts (Figure 11), a higher Δw would result in a closure of the host's stomata and hence in an effective reduction of rate of host transpiration measured.

Third, comparing results obtained from a minicuvette system and a clamp-on cuvette is further impeded by the fact that the latter normally use only one leaf for the measurement, whereas we enclosed a branch in its natural position, with up to 15 leaves, within the minicuvette. Consequently, a clamp-on cuvette includes one, or little more than one, class of leaf ages whereas the minicuvette sums up over nearly all available leaf age classes from young to mature leaves. For *T. oleifolius* on *E. virosa*, we measured transpiration and CO₂ exchange for young and old leaves separately but simultaneously, and found that transpiration over 24 h was 68 mol m⁻² for young, but 239 mol m⁻² for old leaves, whereas the CO₂ balance over the same time was 96 mmol m⁻² for young and 29 mmol m⁻² for old leaves. Similar substantial differences in leaf conductance and transpiration between young and old leaves have been reported for *Lysiana spathulata* (Ullmann *et al.* 1985). The fraction of old leaves of the total leaf area

sampled in the cuvette will therefore influence rates of transpiration and CO₂ exchange. We regard the greater number of leaves as a more representative sampling technique.

We present, for the first time, to our knowledge, gas exchange measurements for host and mistletoe that were conducted simultaneously and continuously in microclimate, controlled minicuvettes. Measurements in the dry and wet seasons revealed different phenological aspects of the respective mistletoe and host but also of the two different mistletoe species on the same host. The results demonstrate that some of the commonly accepted generalizations regarding the host/parasite relationship require re-examination. Further work is required to fully understand this host/mistletoe relationship.

Acknowledgements

We are indebted to Mr A.J. Foster who allowed us to work on his property (Geitsanes) for so many months and who generously supported us during our stay, especially during and after a disastrous rainfall event in March 1991. We also thank Volkswagen (Uitenhage, RSA) for providing us four-wheel-drive Combis which allowed us to reach the plants with our gas exchange vehicle, even in rough field conditions. Thanks also go to the Deutsche Forschungsgemeinschaft who generously sponsored the whole project in Namibia by subsidizing the necessary transportation and reconstruction of the gas exchange device for measuring two plant samples simultaneously and continuously. The support of the Botany Department in Stellenbosch (RSA) and the helpful advice of Mr Barry Hall are thankfully acknowledged. We thank Frank von Willert for developing the necessary transfer, converting and calculating computer programs. For unremitting help with the field work we thank Ute Wagner-Douglas, Matthias Steinberg and Maik Veste. For critical and helpful comments with the manuscript we thank Prof. C.E. Martin and three reviewers.

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