Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia

I. Ullmann[1], O.L. Lange[1], H. Ziegler[2], J. Ehleringer[3], E.-D. Schulze[4], and I.R. Cowan[5]

[1] Lehrstuhl für Botanik II der Universität, Mittlerer Dallenbergweg 64, D-8700 Würzburg, Federal Republic of Germany
[2] Botanisches Institut der Technischen Universität, D-8000 München, Federal Republic of Germany
[3] Department of Biology, University of Utah, Salt Lake City, UT 84112, USA
[4] Lehrstuhl für Pflanzenökologie der Universität, D-8560 Bayreuth, Federal Republic of Germany
[5] Research School of Biological Sciences, Australian National University, Canberra, ACT 2601, Australia

Summary. In Australia, diurnal courses of leaf conductance and transpiration of hemiparasitic mistletoes (Loranthaceae) and their hosts were measured using steady-state porometers under conditions of partial drought and high evaporative demand. The sites spanned a diversity of climatic regions ranging from the subtropical arid zone with winter rainfall, through the subtropical arid zone with summer rainfall to the tropical summer rainfall zone. With one exception (*Acacia farnesiana* with deciduous leaves), the hosts were trees or shrubs with evergreen, sclerophyllous leaves or phyllodes.

The measurements confirm previous observations that mistletoes transpire at higher rates than their hosts. For adult leaves from all of the 18 different host/mistletoe pairs investigated, the daily average leaf conductances were higher in the parasites than in their hosts. The ratios ranged from 1.5 to 7.9. In the most extreme case, *Amyema maidenii* had a daily rate of water loss 8.9 times higher than its host *Acacia cowleana*. However, the parasites did not exhibit unlimited transpiration. Despite high water loss rates, leaf conductance showed large and consistent changes during the course of the day, indicating definite stomatal regulation. The typical diurnal pattern of conductance in both mistletoes and hosts consisted of an early morning peak followed by a continuous decrease throughout the remainder of the day. There was no abrupt decrease in leaf conductance of the parasites that might be interpreted as a threshold response with respect to internal water potential. In most cases, the continuous stomatal closure occurred without substantial changes in leaf water potential over a time span of several hours. The decrease in leaf conductance was correlated with an increase in leaf-to-air water vapor difference, which was associated with increasing leaf temperatures. It seems probable that external humidity plays a major role in the stomatal response. Diurnal courses of leaf conductance of the host/parasite pairs usually showed similar general patterns, even when the absolute rates were quite different. Thus, mistletoes not only control their water loss by stomatal action but this regulation seems to occur in coordination with the stomatal response of their hosts.

The integrated mistletoe/host system must also endure severe drought conditions. Controlled water use is necessary for long-term survival of the host. Assuming stomatal behavior in the host is well adapted to ensure its existence, then similar performance in the mistletoe would promote survival of both host and parasite.

Hemiparasitic mistletoes of the Loranthaceae tap the xylem vessels of their hosts to obtain water and minerals. A number of mineral elements accumulate in the parasite (Wolff 1880; Glatzel 1983; Lamont 1983), because there is no retranslocation of mineral nutrients from the parasite back to the host. Early measurements by Kamerling (1910) and Wood (1924) demonstrated that mistletoes usually exhibited higher transpiration rates than their hosts. Given that host xylem water is the only source of minerals for the mistletoe, Schulze et al. (1984, see Ehleringer and Schulze 1985) hypothesized that such high transpiration rates by the parasite were necessary in order to acquire sufficient nitrogen for biomass production. Increased water use thus would confer an advantage to the parasite with respect to its nutritional status. This is in agreement with Härtel (1956, see also Calder and Bernhardt 1984), who concluded from earlier experimental findings (e.g., Kamerling 1910; Härtel 1937; Vareschi and Pannier 1953; Walter and Steiner 1936) that mistletoes exerted relatively little stomatal control over water loss. Others have suggested that stomatal closure occurred, but mainly when water demand of the host-parasite system exceeded host supply rate and leaf water content of the mistletoe decreased below the hydropassive threshold (Glatzel 1983).

A rich and diverse mistletoe vegetation occurs in the semi-arid and arid regions of Australia, where the evergreen parasites grow on the branches of xerophytic trees and shrubs (Beadle 1981). The host trees are characterized by sclerophyllous assimilatory organs (leaves or phyllodes), a feature thought to be adaptive to the drought conditions in their habitats. These plants must survive extended periods with low soil moisture availability, and the combination of a sensitive control over water loss and a conservative soil water depletion rate should be performance characteristics which facilitate their survival (Hellmuth 1971 a; Körner and Cochrane 1985). The question arises as to how mistletoes behave under such circumstances. If mistletoes exhibited unrestricted rates of water loss under hot, arid conditions, they may soon critically deplete the water sources common with their host and thereby jeopardize their own existence. Under such conditions, stomatal control of water

loss by the parasite might be necessary for long-term survival of both the mistletoe and host in the host-parasite system.

Actually, several recent studies on mistletoes provide evidence for diurnal stomatal control over rates of water loss (Schulze et al. 1984; Glatzel 1983; Ehleringer et al. 1985a). Additionally, Hollinger (1983) found that leaf conductance of the Californian mistletoe *Phoradendron villosum* responded to changes in leaf-to-air water vapor concentration gradients (ΔW). Recently, Ehleringer et al. (1985b) and Schulze and Ehleringer (1984) provided evidence from numerous host-mistletoe pairs in arid and semi-arid regions in North America, South Africa, and Central Australia, which indicated that the water use efficiency of the parasites differed from their hosts depending on host nitrogen supply in the transpiration stream. This effect could also be due to variable mistletoe transpiration rates, which could arise from changes in stomatal conductance.

Few data are available to describe stomatal behavior of mistletoes and their hosts under arid-climate conditions. Gas exchange data on Australian mistletoes have been reported for only three species thus far, and it is difficult to generalize from these. As early as 1924, Wood measured transpiration rates in *Loranthus quandang* growing upon *Acacia aneura* and observed that water loss rates from the parasite were "greatly in excess of that of its host". Hellmuth (1971b) found that under optimal water conditions daily transpiration rates were higher in the host *Acacia grasbyi* than in its parasite *Amyema nestor*, but that under water stress the parasite transpired about 2.5 times greater than the host. In a study involving different species, Chapman and Jacobs (1979) found no obvious differences between leaf resistances in *Heterodendrum oleifolium*, *Eucalyptus socialis*, *Rhagodia gaudichiana* and the mistletoe *Lysiana exocarpi*.

We present here diurnal courses of leaf conductance and transpiration in several pairs of parasites and hosts investigated in southern and central Australia under conditions of partial drought and high evaporative demand. In this study, the focus was on understanding diurnal trends in stomatal response and to the differences in leaf conductance and concomitant water loss rates between parasites and hosts.

Plant material and habitat description

The measurements were made in September 1981 at different sites along the route from Mildura (New South Wales), via Broken Hill, Port Augusta (South Australia), Kingoonya, Kulgera (Northern Territory), Ayers Rock, Alice Springs, Tennant Creek, Mount Isa (Queensland) to Townsville. This expedition was organized by the Research School of Biological Sciences, Australian National University, Canberra, and involved 14 scientists who provided help and assistance during the cooperative investigations. Additional measurements were collected in the Uluru National Park in November 1981. The geographical locations of the measurements are shown in Fig. 1. Short descriptions of the general landscape (G), specific situation at the measuring site (S), vegetation (V) and the experimental plants (H/P) at each site are given below. These sites spanned a diversity of climatic regions ranging from the subtropical arid zone with winter rainfall (site 1, see Fig. 1), through subtropical arid zone with summer rainfall (sites 5 and 6), to the tropical summer rainfall zone (site 7).
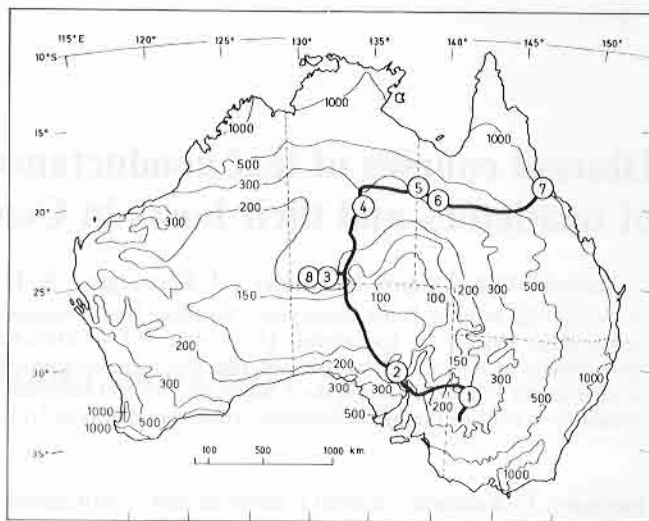

Fig. 1. Itinerary of the field tour during which measurements were conducted, with average annual precipitation indicated (50 percentile, after Climatic Atlas of Australia, Map Set 5: Rainfall; Austral. Government Publishing Service, Canberra 1977). The numbers refer to the single measuring sites; see Section Plant material and habitat description

1. Tolarno, south of Menindee, NSW (Sept. 8)

G: Sand dunes associated with the flood plains of the Darling River. S: Marginal dune slope near crest. V: *Acacia victoriae* dominated low shrubland (1–2.5 m, occasionally to 5 m); ground stratum of (in part introduced) annual species. H/P: *Acacia victoriae/Lysiana exocarpi*.

2. Between Mt. Gunson Mines and Pimba, SA (Sept. 11)

G: Reticulate sand dunes associated with saltpans. S: Upper dune slope in disturbed area near a road. V: *Acacia brachystachya* dominated open shrubland (1.5–4 m) with sparse ground stratum of short grasses and annuals. H/P: *Acacia brachystachya/Amyema preissii*.

3. Curtin Springs (120 km east of Uluru Nation. Park), NT (Sept. 14)

G: Sand dunes associated with clay pans. S: Flat area of rocky outcrops adjacent to dunes. V: Mixed open shrubland of *Hakea eyreana* (5–6 m), *Acacia tetragonophylla* and *Acacia kempeana* (2–4 m); sparse ground stratum of short grasses, subshrubs and forbs. H/P: *Hakea eyreana/Amyema gibberulum*; *Acacia kempeana/Amyema maidenii*, *Amyema preissii*, *Lysiana murrayi*; *Acacia tetragonophylla/Lysiana murrayi*.

4. Davenport Range, north of Devils Marbles, NT (Sept. 18)

G: Undulating foothills of the Davenport Range. S: Flat area adjacent to low dunes. V: Mixed open shrubland (2–5 m) dominated by *Acacia cowleana*, *Acacia coriacea*, *Acacia monticola*, with occasionally *Grevillea wickhamii*, *Heterodendrum* spp. and *Eucalyptus* spp. and a diverse ground stratum of grasses and subshrubs. H/P: *Acacia cowleana/Amyema maidenii*, *Lysiana spathulata*; *Acacia coriacea/Amyema maidenii*, *Lysiana spathulata*; *Acacia monticola/Lysiana spathulata*.

5. Camooweal, QLD (Sept. 20)

G: Flat plain east of Camooweal. S: Area with surface gravel on lateritic red soil. V: Eucalyptus leucophloia – Triodia low open woodland (5–8 m) with low shrub stratum dominated by Acacia spp. (Acacia lysiphloia, Acacia cowleana, Acacia tenuissima). H/P: Eucalyptus leucophloia/Diplatia grandibractea.

6. Near Mt. Isa, QLD

G: Dissected hills of the Mt. Isa complex.

6.a (Sept. 22). S: Lower slopes of hillside. V: Eucalyptus leucophloia – Triodia low open woodland (5–8 m) with Acacia dominated low shrub stratum and very sparse ground layer of short grasses between Triodia tussocks. H/P: Eucalyptus leucophloia/Diplatia grandibractea; Atalaya hemiglauca/Lysiana subfalcata.

6.b (Sept. 23). S: Flood plain (drainage channel adjacent to 6.a). V: Eucalyptus argillacea low open woodland (5–7 m), low shrub stratum with Cassia oligophylla and Acacia spp., sparse ground stratum of short grasses. H/P: Acacia farnesiana/Lysiana spathulata; Cassia oligophylla/Lysiana subfalcata.

7. Near Townsville, QLD (Sept. 26)

G: Coastline southeast of Townsville (near AIMBS). S: Inner, dry fringe of Mangrove belt. V: Ceriops tagal dominated shrub community (1.5–4 m) with scattered Avicennia marina. H/P: Ceriops tagal/Lysiana subfalcata.

8. Uluru National Park, NT (Nov. 21)

G: Alluvial southern hill frontage of Mt. Olga complex. S: Gently sloping area between creeks, adjacent to sandy area. V: Mixed open shrubland (up to 4 m) of Hakea suberea, Acacia victoriae, Gossypium sturtianum, Eremophila spp., Cassia spp.; ground stratum of short grasses. H/P: Acacia victoriae/Lysiana exocarpi.

Methods

Transpiration rate (Tr) of the assimilatory organs (leaves or phyllodes, both subsequently referred to as "leaves"), leaf temperature (T_L), incident photosynthetically active photon flux density (PAR, horizontal, quantum sensor), air temperature (T_A) and relative air humidity (r.h.) were obtained with a LI-1600 steady-state porometer (Li-Cor, Inc.; Lincoln, Nebraska). The leaf-to-air water vapor pressure gradient (ΔW) was calculated from measurements of T_A, T_L, and r.h., leaf diffusive conductance to water vapor (G) from ΔW and Tr. The LI-1600 cuvette was modified to include the leaves in a small chamber in which the hinged top was covered with a thin polyethylene film (Schulze et al. 1982). Depending on leaf size, one single leaf, only a segment of a large leaf, or a small twig with several leaves were enclosed in the cuvette in their natural orientation (Fig. 2). With broad assimilatory organs, the porometer thermocouple for tissue temperature measurement, which is suspended beneath the lid at the level of the cuvette opening, was pressed against the under surface of the leaf. Clear contact was difficult to achieve with irregularly-shaped and small leaves. However, we think the errors which resulted
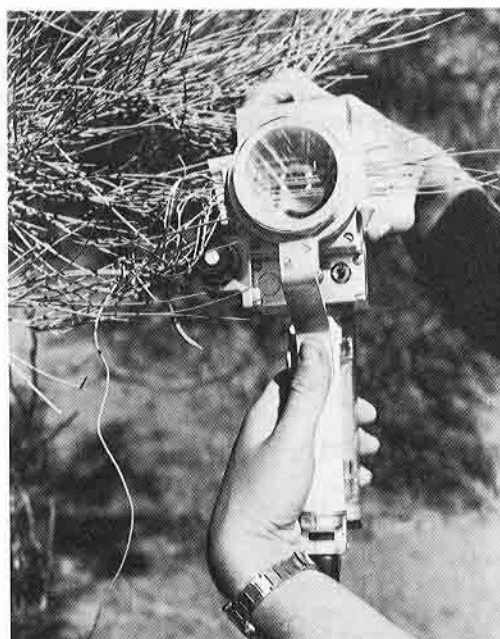

Fig. 2. Porometer measurement with Acacia brachystachya. Central sections of the needle-like phyllodes are enclosed in the porometer cuvette

were small, because rapid ventilation of the leaves in the cuvette insured that differences in temperature between air and leaf were small. Readings were taken under steady-state conditions, which occurred 30 to 120 s after enclosure of the leaf material. High turbulence in the porometer cuvette was provided by a fan which resulted in a boundary layer conductance of the exposed leaf surface of approximately $2 \text{ mol m}^{-2} \text{ s}^{-1}$. Such wind speeds were typically higher for the enclosed leaf material than would occur under natural conditions. Therefore, the estimated transpiration rates might be slightly overestimated with respect to natural situations. On the other hand, leaf boundary resistances in the cuvette were so small that possible variations from measurement to measurement could be neglected in comparison with the total leaf resistance. Changes therefore, were reliable estimates of changes in leaf conductance and thus natural stomatal responses. Rates of Tr and G of the amphistomous assimilatory organs were related to total surface area rather than projected leaf area.

Transpiration measurements usually began at about sunrise and were continued until sunset. One to six leaf samples in each species (see Table 1) were monitored every 30 to 60 min always in the same sequence; average values are presented in Table 1 and in Figs. 4 to 9. We attempted to sample the assimilatory organs of the host on the same branch occupied by the parasite and as close to the parasite as possible. Water potentials (ψ) of cut leaves, phyllodes or small twigs were determined by means of a pressure chamber at approximately the same times as the transpiration measurements (see Slavik 1974).

Results

Diplatia grandibractea, a parasite growing to a large size on Eucalyptus leucophloia, and its host were studied at the Camooweal site when under high water stress (Fig. 3). Five leaves of the same mistletoe plant and five leaves of the

Table 1. Leaf conductances and rates of transpiration in the cuvette for 19 host/mistletoe pairs (18 different combinations). The numbers of leaf specimens continually sampled during the course of the day is given in parentheses with the species names. For site of investigation see numbers in Section Plant material and habitat description. $\bar{G}$ and G_{max}: daily average and daily maximum of leaf conductance for 'host' and 'parasite'; $\sum Tr$ and Tr_{max}: daily sum and daily maximum of transpiration for host and parasite. Average leaf conductance and sum of transpiration are estimated from the plotted diurnal response curve usually for the period between 8:00 a.m. and 5:30 p.m., but in five cases from 8:00 a.m. to 3:00 p.m. (indicated by a), and in one case from 8:00 a.m. to 1:30 p.m. (indicated by b)

Host/Parasite Pair	Site	$\dfrac{\bar{G}_{parasite}}{\bar{G}_{host}}$	$\bar{G}$ [mmol m^{-2} s^{-1}]	G_{max} [mmol m^{-2} s^{-1}]	$\dfrac{\sum Tr_{parasite}}{\sum Tr_{host}}$	$\sum Tr$ [mol m^{-2} d^{-1}]	Tr_{max} [mmol m^{-2} s^{-1}]
Hakea eyreana (1)[a]	3	1.3	27.6	91.3	1.8	16.9	1.6
Amyema gibberulum (1)			36.2	76.5		30.4	1.6
Acacia farnesiana (1)	6b	1.4	56.3	105.0	1.4	90.4	3.7
Lysiana spathulata (1)			76.2	151.3		123.6	4.6
Acacia coriacea (1)	4	1.8	18.8	38.9	1.9	24.6	0.9
Amyema maidenii (1)			32.8	47.5		46.8	1.9
Acacia kempeana (1)[a]	3	1.8	30.9	55.1	1.4	18.3	1.0
Amyema maidenii (1)			54.0	65.1		25.9	1.7
Acacia kempeana (1)[a]	3	1.8	30.9	55.1	2.0	18.3	1.0
Amyema preissii (1)			56.3	96.3		36.7	2.1
Acacia victoriae (2)	8	1.8	75.8	152.0	1.7	96.3	5.0
Lysiana exocarpi (2)			137.9	257.0		158.9	9.6
Ceriops tagal (4)[b]	7	1.9	38.6	64.5	–	–	1.3
Lysiana subfalcata (6)			71.3	112.4		–	2.2
Eucalyptus leucophloia (2)	6a	2.0	24.1	61.6	2.3	28.7	1.5
Diplatia grandibractea (2)			48.8	95.5		64.9	2.8
Acacia coriacea (1)	4	2.2	18.8	38.9	2.6	24.5	0.9
Lysiana spathulata (1)			40.6	65.7		64.7	3.2
Eucalyptus leucophloia (5)	5	2.4	17.0	45.1	2.4	22.3	1.5
Diplatia grandibractea (5)			40.4	100.2		53.0	3.5
Cassia oligophylla (1)	6b	2.9	9.7	24.4	4.0	14.1	0.9
Lysiana subfalcata (1)			28.2	50.9		55.7	2.6
Atalaya hemiglauca (1)	6a	3.1	16.9	42.2	3.5	21.1	0.9
Lysiana subfalcata (2)			52.4	77.9		73.8	3.5
Acacia brachystachya (3)	2	3.9	38.8	78.6	4.1	19.6	1.2
Amyema preissii (1)			150.0	207.6		79.6	3.4
Acacia tetragonophylla (2)[a]	3	3.9	41.2	67.7	4.3	30.6	1.5
Lysiana murrayi (1)			160.1	244.8		131.8	7.9
Acacia cowleana (1)	4	4.6	5.0	12.8	5.4	6.3	0.3
Lysiana spathulata (1)			23.1	37.0		34.1	1.3
Acacia kempeana (1)[a]	3	5.0	30.9	55.1	5.8	18.3	1.0
Lysiana murrayi (1)			154.6	244.1		105.5	5.9
Acacia monticola (1)	4	6.6	3.8	12.9	8.1	4.9	0.3
Lysiana spathulata (1)			25.0	39.9		40.0	2.1
Acacia victoriae (1)	1	7.2	15.8	53.1	8.3	10.6	0.2
Lysiana exocarpi (1)			113.3	170.4		88.3	3.5
Acacia cowleana (1)	4	7.9	5.0	12.8	8.9	6.3	0.3
Amyema maidenii (1)			39.7	58.5		56.1	2.1

host near to the parasite were simultaneously sampled. Individual leaves differed in their exposure and consequently in their leaf temperatures. Average air temperature and air vapor pressure deficit in the measuring cuvette are given for each sampling period. Maximum air temperature was 35° C and the minimum relative air humidity was 13%, resulting in a maximum mistletoe ΔW of about 53 mbar bar^{-1}. The parasite and host had similar predawn water potentials, -34 and -32 bar, respectively. Then ψ decreased more in the mistletoe, soon reaching a minimum

of about -50 bar. There were no further large ψ changes during the next 8 h, until a slight late afternoon recovery. Water potential of the host always remained less negative by 3 to 8 bar. Variability in absolute rates of leaf conductance was high amongst the individual mistletoe leaves, with rates differing by as much as three-fold. However, the general response patterns were similar in all cases. Stomates of the parasite opened quickly in the morning, and subsequently there was a gradual decrease in leaf conductance. Closure began between 0800 and 1100 and was associated
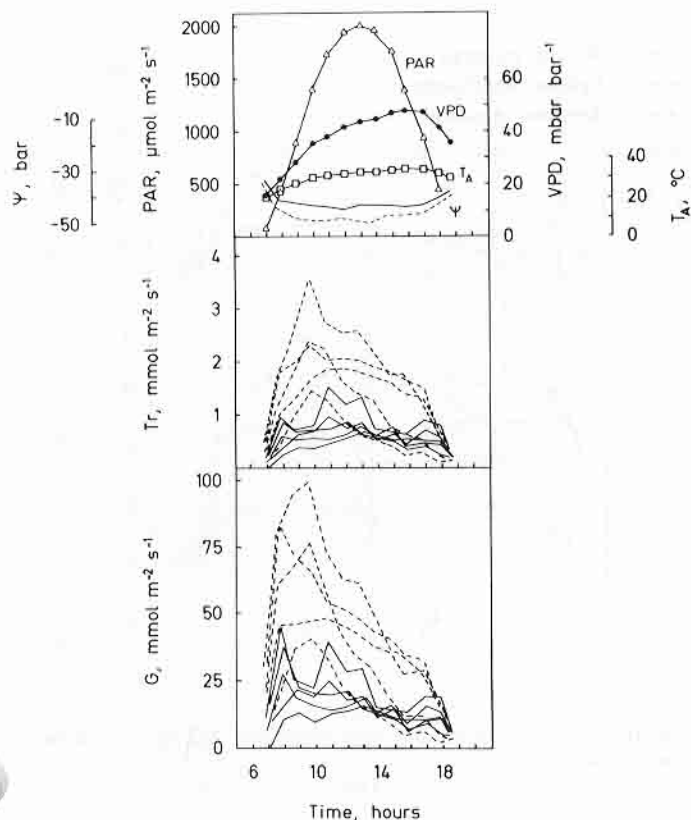
Camooweal   20.09.81

Eucalyptus leucophloia —
Diplatia grandibractea ---

Fig. 3. *Eucalyptus leucophloia* and *Diplatia grandibractea*. Diurnal time courses of leaf conductance (G), rates of transpiration in the porometer cuvette (Tr) and leaf water potential (ψ) in host (drawn lines) and mistletoe (dashed lines). Also shown are the air vapor pressure deficit (VPD) and air temperature (T_A) in the cuvette during measurement, and incident photon flux density (photosynthetic active radiation, PAR) on a horizontal surface
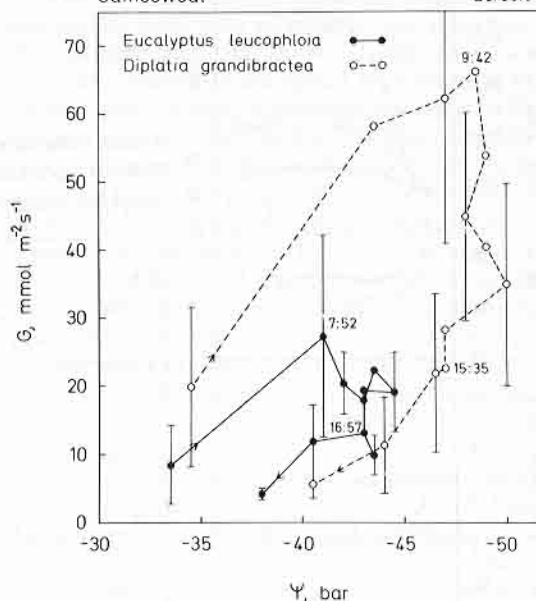

Fig. 4. *Eucalyptus leucophloia* and *Diplatia grandibractea* (same day as Fig. 3). Relationship between leaf conductance and leaf water potential, data points being connected in chronological order (time of day indicated at characteristic phases of the hysteresis loop). Vertical bars indicate 1 SD

with increasing ΔW. Host leaf conductances were significantly lower than those of the mistletoe. The ratio of the daily average G in the parasite was twice that in the host (Table 1). The eucalypt leaves showed a tendency for reduced stomatal conductance after opening in the morning. There was a limited late afternoon increase in host leaf conductance that was not observed in the mistletoes.

The average hourly leaf conductances in *Eucalyptus leucophloia* and its parasite *Diplatia grandibractea* plotted as functions of leaf water potential showed similar patterns (Fig. 4). They exhibited hysteresis loops like the tri-phasic pattern described for *Eucalyptus pauciflora* by Körner and Cochrane (1985). The morning stomatal opening was associated with a relatively quick and large decrease in water potential (phase 1). Then ψ remained more or less constant for many hours while G decreased (phase 2), until ψ recovered slightly during the late afternoon and evening hours (phase 3). During phase 2, mistletoe leaf conductance decreased about 50% with no significant change in ψ, which ranged between -47 and -50 bar.

Figure 5 illustrates performance of five different combinations of mistletoes with similar exposures growing on *Acacia* species at the Davenport Range site. Predawn water

potentials were approximately -30 bar in both hosts and parasites. Again, in all cases, leaf conductances and transpiration rates were higher in the parasites than in the hosts. In the extreme case, *Amyema maidenii* had an average daily leaf conductance 7.9 times, and an average transpiration rate 8.9 times higher than its host, *Acacia cowleana*. In the acacias, the highest conductance occurred early in the morning. However, the absolute leaf conductance values differed greatly with *Acacia monticola* and *Acacia cowleana* leaves having much lower conductances than *Acacia coriacea* leaves. Two sets of the *Acacia*-mistletoes showed a partial stomatal closure between 0800 and 1000 when atmospheric stress increased. Only in *Lysiana spathulata* on *Acacia coriacea* did the maximum of leaf conductance occur at about noon. However, in this case stomates closed rapidly thereafter. It should be mentioned that, due to the increase of ΔW during the course of the day, the maximum rates of transpiration did not coincide with maximum leaf conductance, but occurred later.

Data for mistletoes on non-acacia hosts near Mt. Isa and Curtin Springs are depicted in Fig. 6. Transpiration rates in the parasites were again always higher than in the hosts. The diurnal pattern of conductance in *Amyema gibberulum* on *Hakea eyreana* was similar to those we have so far described. The trends in the other species, *Lysiana subfalcata* growing on *Cassia oligophylla* and on *Atalaya hemiglauca*, were different. In the first case, there was only limited stomatal closure, and in the second case, leaf conductance was more or less constant during most of the daylight hours. The similarity of host and parasite leaf conductance patterns in each of these three pairs is rather striking.

All examples discussed so far concerned hosts with evergreen, sclerophyllous leaves or phyllodes. We also investigated a host with deciduous leaves, the bipinnate *Acacia*
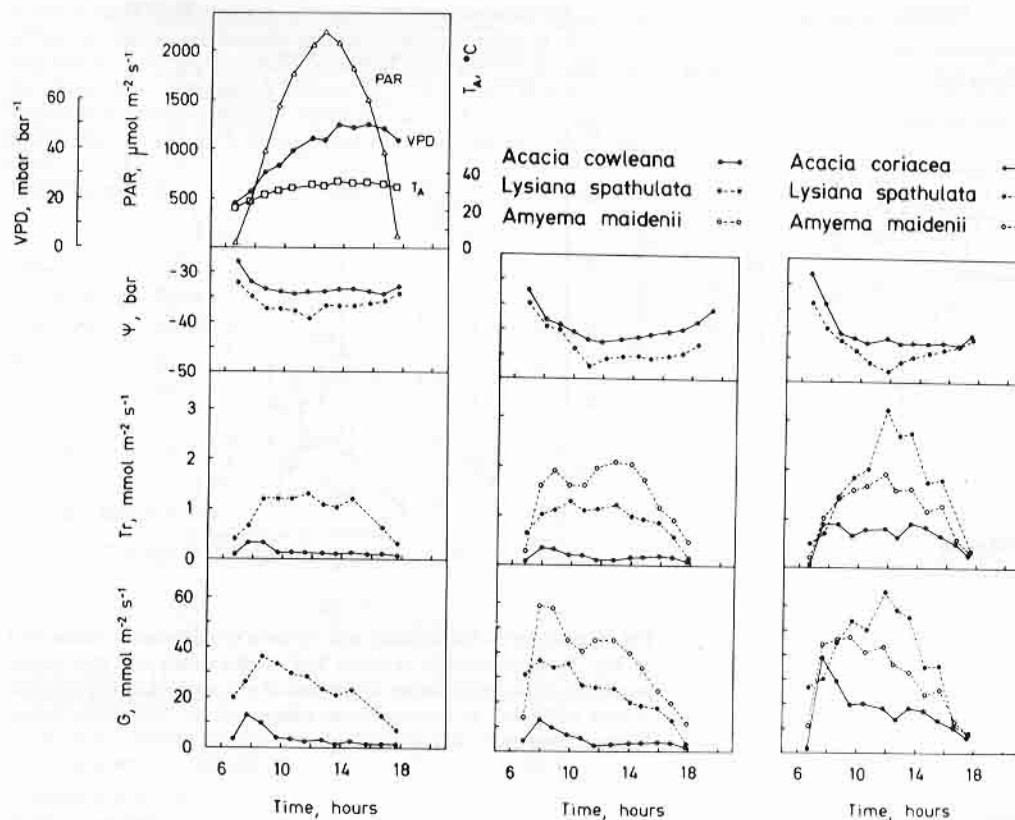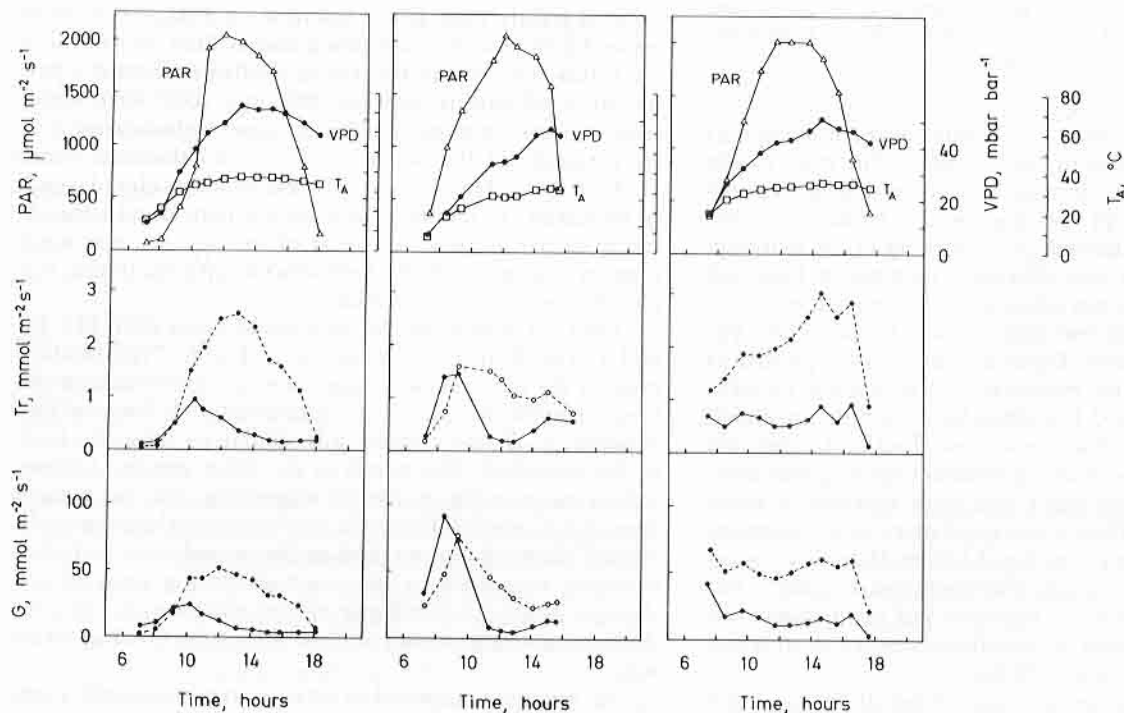
Fig. 5. Diurnal courses of leaf conductance and rate of transpiration of three *Acacia* species and their parasites, and representative meteorological data for one of the host/mistletoe pairs. For further explanation see Fig. 3

Fig. 6. Diurnal courses of leaf conductance, rate of transpiration, and meteorological data for three non-acacias and their parasites. For further explanation see Fig. 3
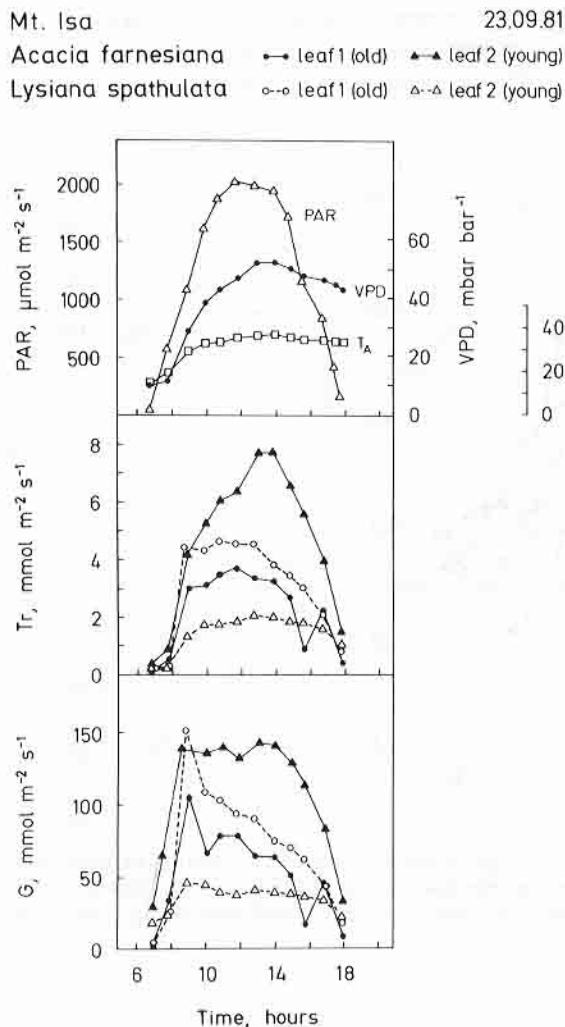
Mt. Isa   23.09.81

Acacia farnesiana   •—• leaf 1 (old)   ▲—▲ leaf 2 (young)

Lysiana spathulata   ○--○ leaf 1 (old)   △--△ leaf 2 (young)

Fig. 7. *Acacia farnesiana* and *Lysiana spathulata* (young and adult leaves). Diurnal courses of leaf conductance, rate of transpiration, and meteorological data. For further explanation see Fig. 3

farnesiana infested by *Lysiana spathulata*. This species was examined at the Mt. Isa site, where it was growing together with several phyllode-bearing acacias and sclerophyllous-leaved *Eucalyptus* and *Cassia* species. The leaves of *Acacia farnesiana* exhibited the highest leaf conductance of all of the investigated hosts. The daily transpiration rates in adult leaves were 3.2, 4.3 and 6.4 times higher than that of *Eucalyptus leucophloia*, *Atalaya hemiglauca* and *Cassia oligophylla*, respectively, in the same habitat. This may reflect the differences in water use performance between the deciduous and evergreen life forms. Even though transpiration rates in *Acacia farnesiana* were high, the rates in adult leaves were nevertheless exceeded by those of its parasite by about 30% (Fig. 7). Leaf conductance of both mistletoe and host followed the already described daily patterns with a high morning peak and subsequent continual decline. Young leaves of both species behaved differently. As with the observations of Ullmann (1985) with deciduous-leaved acacias in Africa, incompletely expanded leaves of *Acacia farnesiana* did not close stomates during the second part of the day. An adjacent young mistletoe leaf reached much lower conductances, but exhibited a similar diurnal response pattern.

The typical closure of stomates, beginning before noon and lasting until later afternoon, was apparently independent of light intensity. However, the decrease in conductance was obviously correlated with increase in leaf-to-air water vapor gradient, which was associated with increasing leaf temperatures. In Fig. 8 this is demonstrated for several hosts and several mistletoes. Leaf conductances are plotted against ΔW for the period of the day between the morning peak for G and the beginning of decrease of ΔW with decreasing temperatures in the late afternoon. This period of time usually lasted 5 to 8 h and corresponded to phase 2 of the time-dependent hysteresis loop of the conductance versus water potential plot as described in Fig. 4 (see also Körner and Cochrane 1985). Generally mistletoe leaf conductances were higher than those of the hosts. However, in all cases conductance decreased with increasing ΔW (and increasing temperature).

Stomatal performance was apparently different under better soil moisture conditions. In the Uluru National Park, *Lysiana exocarpi* growing on *Acacia victoriae* was investigated on an almost clear day immediately after a two week rain period (which resulted in a total of about 30 mm precipitation). The same host/parasite pair had been investigated 10 weeks earlier at the Tolarno site under soil moisture stress. Differences in mistletoe/host behavior under water stressed and non-stressed conditions were striking (Fig. 9). Host performance under water stress resulted in a reduced average daily conductance of 75.8 to 15.8 mmol m^{-2} s^{-1}, that is to only about 20% of maximum, whereas the mistletoe daily average G was reduced only to about 80% of maximum. Thus, ratios in daily mean conductance between mistletoe and its host amounted to 1.8 under good moisture conditions, but 7.2 under water stress. Also the shape of the diurnal courses in leaf conductance differed when comparing the two different situations. Stomatal closure in the stressed plants began two hours earlier in the day than in the unstressed plants. In water stressed plants there was a sharp decline in conductance that was not so pronounced in the nonstressed plants. However, it is clear that in each of these situations, *Acacia* and mistletoe exhibited similar diurnal patterns. Maximal conductance was reached by both the host and parasite almost exactly at the same time.

For all adult leaves from host/mistletoe pairs investigated, the daily average leaf conductances were higher in the parasites than in their hosts (Table 1). The ratios ranged from 1.3 up to 7.9. Concomitantly, daily maximal leaf conductance was usually higher in the mistletoe leaves. Only in the case of *Amyema gibberulum* growing on *Hakea eyreana* was there a slightly lower maximum G in the parasite. Differences in G were reflected by differences in transpiration rates. In the most extreme case, *Amyema maidenii* exhibited a daily rate of water loss 8.9 times higher than that of its host *Acacia cowleana*.

Discussion

The reported measurements confirm previous observations that hemiparasitic mistletoes transpire at higher rates than their hosts and that this is due to their greater leaf conductances. The ratios of parasite/host leaf conductance and the ratios of water loss turned out to be quite different for different plant pairs investigated (see Table 1). In one pair it seems clear that the water relations of the host in-
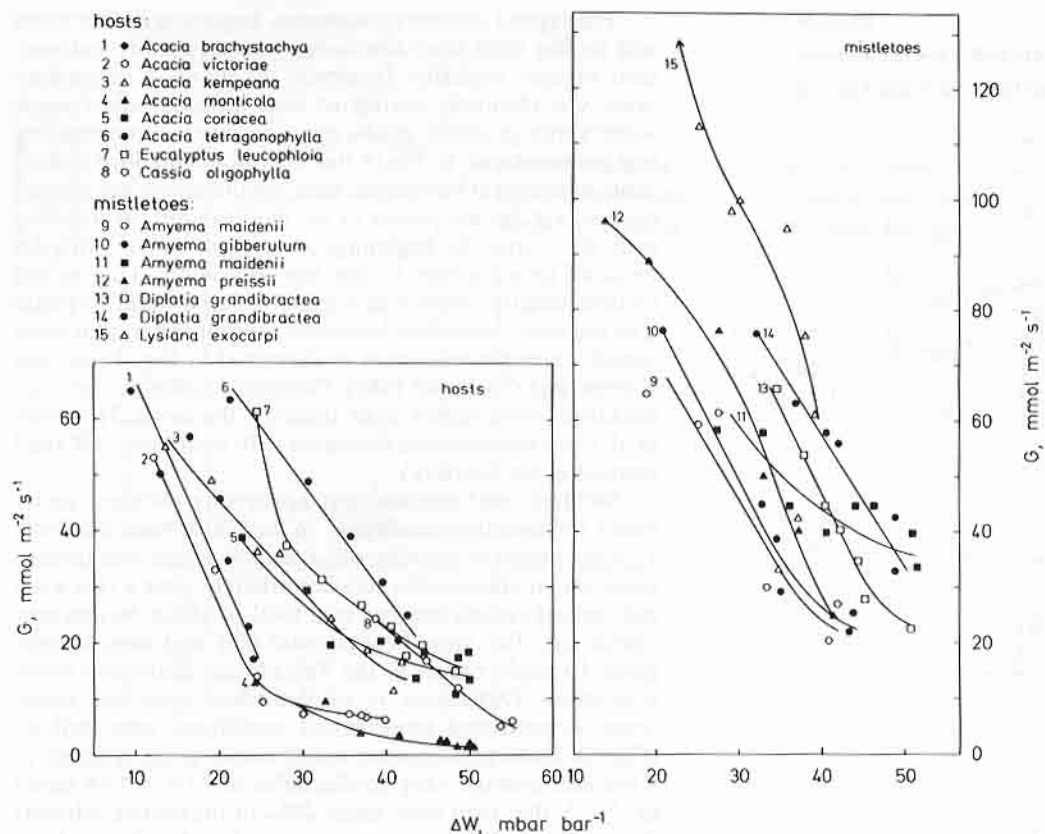
Fig. 8. Relationship between leaf conductance (G) and leaf-to-air water vapor pressure difference (ΔW) in a selection of hosts and mistletoes. Data encompass the period between the time at which conductance was maximum in the morning and the time at which ΔW began to decrease during the late afternoon. Note, that during the course of the day, temperature and light changes occur, in addition to the changes in ΔW

fluenced the ratios. *Lysiana exocarpi* had a daily average of leaf conductance only 1.8 times higher than its host *Acacia victoriae* when soil moisture was plentiful, but 7.2 times higher when under water stress. The greater stomatal sensitivity to stress in the host was probably responsible for this change (see Hellmuth 1971 b). However, many of the other species were investigated when under water stress, and there was not a general correlation between host leaf conductance and the ratio of conductances in parasite and host.

Based on carbon isotope discrimination values, Ehleringer et al. (1985b) showed that water use efficiency of parasites was closer to that of their hosts if they were growing on a nitrogen-fixing than on a non-nitrogen-fixing plant. Table 1 shows no correlation between this characteristic and ratios of absolute water consumption of plant pairs. However, possible differences in photosynthetic capacity must be taken into account when measuring water use efficiency and this parameter was not measured in this study.

Several of the earlier investigations of mistletoe water relations led to the conclusion that the parasite exhibited unlimited transpiration and closed stomates only when a threshold internal water potential was reached (associated with a loss of turgor, see Härtel 1956). Glatzel (1983) determined this water status threshold for the deciduous oak mistletoe *Loranthus europaeus* by a freezing-cuff technique; the critical water potential for stomatal closure of the parasite was well below that of the host and changed seasonally.

He concluded that water "is fully utilized in day-to-day transpiration behavior" by the parasite provided the water potential exceeded the threshold for hydropassive stomatal closure. Parasitic epiphytes commonly lose turgor and have a flaccid appearance under some natural conditions during the warm hours of the day. For tropical *Loranthaceae* in Venezuela, Vareschi and Pannier (1953) concluded that "even during the highest evaporation in the dry season they (mistletoes) do not restrict their transpiration"; they did not find any stomatal control of water loss in the mistletoes. In contrast, all of the investigated Australian mistletoes have behaved differently. Despite high water loss rates, leaf conductance showed large and consistent changes during the course of the day, indicating decisive stomatal regulation of transpiration.

The typical diurnal pattern of conductance in both mistletoes and hosts comprised an early morning peak followed by a continuous decrease throughout the remainder of the day. With extreme water stress conditions, stomates of the hosts seemed to be almost fully closed after the initial peak. Such performance has often been observed in evergreen sclerophylls during soil moisture shortage and when plants were subjected to high atmospheric stress (see Schulze et al. 1982; Körner and Cochrane 1985; Tenhunen et al. 1985). In some cases, the Australian hosts (e.g., *Eucalyptus leucophloia*) showed a slight tendency to reopen stomates again during the later afternoon hours, however, no pronounced two-peaked courses of conductance occurred. In contrast,
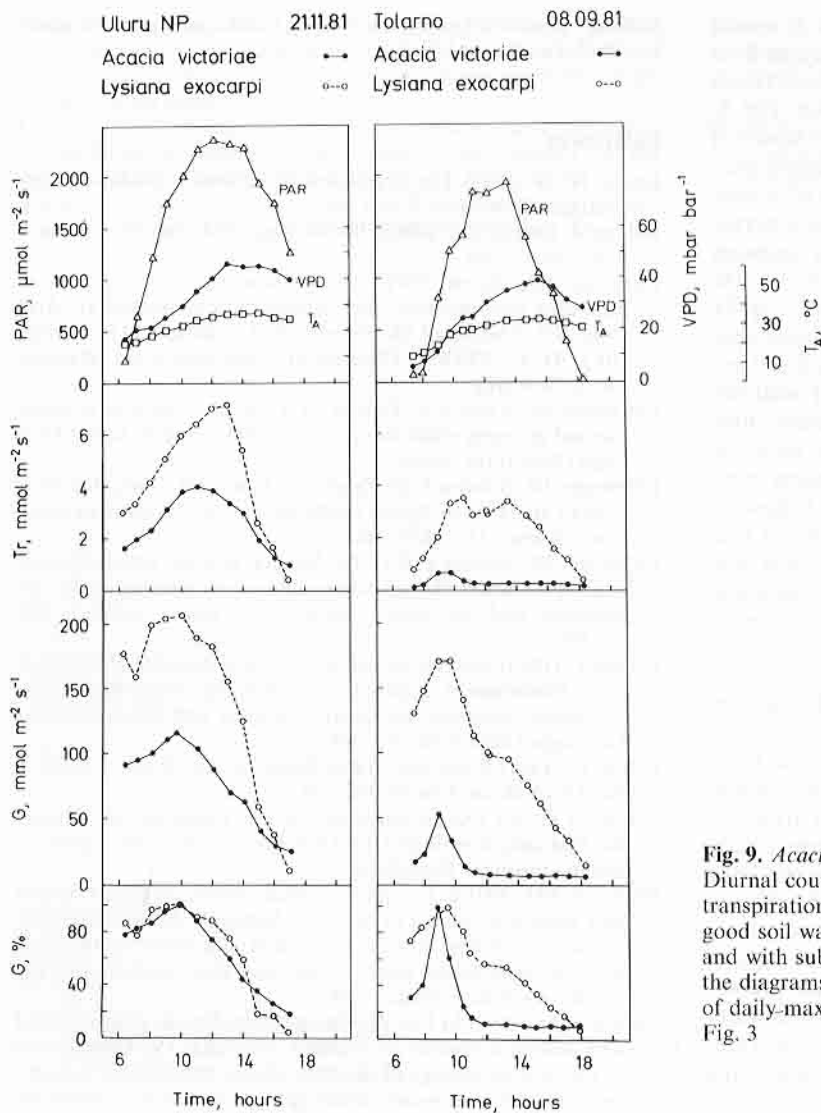
Fig. 9. *Acacia victoriae* and *Lysiana exocarpi.* Diurnal courses of leaf conductance, rate of transpiration, and meteorological data under good soil water conditions after a rain fall (left) and with substantial soil water stress (right). In the diagrams below, G is expressed in percent of daily-maximum. For further explanation see Fig. 3

Australian eucalypts and acacias cultivated under Mediterranean climatic conditions in Portugal, can exhibit a strong and reversible depression of stomatal conductance during midday time (Pereira et al. 1985, and unpublished data). The absence of such a response in the present investigations may be due to the fact, that under the dry weather conditions experienced during the measurement period in Central Australia, the water vapor deficit of the air did not substantially decrease in the late afternoon. Thus, humidity-controlled stomatal reopening appeared not to be possible.

A steady decline in stomatal aperture in the mistletoe following the morning peak of leaf conductance usually continued for most of the daylight period, including the period of high solar radiation and increasing temperatures. There was no abrupt decrease in conductance, which could be interpreted as a threshold response with respect to internal water potential. As depicted in Fig. 4, the continuous decline in conductance occurred without substantial change in leaf water potential. Körner and Cochrane (1985) discussed different possible explanations for such a response. Our data do not allow a definite decision about responsible controlling mechanisms. However, it seems probable that

external humidity plays a role. Figure 8 shows a clear relationship between the complex of leaf-to-air water vapor deficit in combination with temperature and stomatal conductance. A causal dependence becomes conceivable since Hollinger (1983) showed direct stomatal responses of a mistletoe of the Loranthaceae-family to air humidity. Even if the controlling mechanism cannot yet be exactly defined, it is clear that strong decreases in leaf conductances took place during the course of the day, which restricted transpirational water loss of the Australian mistletoes to such an extent that transpiration was only a small proportion of that rate which would have occurred with maximally open stomates.

A surprising result of the present investigations is that the mistletoes not only control their water loss by stomatal action but that this regulation seems to occur in coordination with the stomatal responses of their hosts. Diurnal courses of leaf conductance of the parasite/host pairs often showed similar general patterns, even when the absolute levels of conductance were quite different. This was especially obvious with *Lysiana exocarpi* on *Acacia victoriae* at two different soil moisture levels (Fig. 9). In many of

the other investigated plant pairs, the onset of stomatal closure occurred almost at the same time of day in host and parasite (see for instance *Lysiana spathulata/Acacia monticola* and *Amyema maidenii/Acacia cowleana*, Fig. 5; *Amyema gibberulum/Hakea eyreana*, Fig. 6; adult leaves of *Lysiana spathulata/Acacia farnesiana*, Fig. 7; *Lysiana exocarpi/Acacia victoriae*, Fig. 9). Such a correlation in stomatal behavior may be due to similar responses to external controlling factors, possibly to leaf-to-air vapor pressure deficit. On average at the same humidity conditions, the mistletoes have higher conductance than the hosts (Fig. 8). On the other hand, the slopes of decrease in conductance with increase in ΔW tend to be steeper with the mistletoes. The data are not sufficient for a more detailed analysis. However, if it is assumed that such responses reflect functional dependencies, coordinated trends in diurnal stomatal conductance are conceivable. Nevertheless it remains questionable, if such regulation can be responsible for triggering of the point at which the closure reaction begins, so that peak conductances occur at the same time for host and for parasite. More probably the concordance in stomatal behavior in parasite and host might be induced by an internal signal common to both. Hormonal control is one possible explanation for the synchronized responses.

Epiphytic, hemiparasitic mistletoes and their hosts form integrated systems which are stable for many years or even decades (Schulze and Ehleringer 1985). In the arid and semi-arid zones of Australia these systems have to exist under severe drought conditions with infrequent and irregular rain. Controlled water use is necessary for long-term survival of the host. Unrestricted transpiration by the mistletoe would certainly improve its nitrogen and mineral nutrition status as well as potentially allow for more photosynthetic carbon gain. However, under extreme dry and hot habitat conditions, a conservative water use seems to be the prerequisite also for survival of the parasite; an excessive water consumption of the parasite might deplete the soil water resources of the host to the point that it endangers the host's existence. This, in turn, would result in parasite mortality, too. Perhaps the parasite has developed a control system which restricts water consumption and growth to such an extent that long-term survival is guaranteed. Assuming stomatal behavior in the host is well adapted to promote the survival of the host, then a similar behavior in the parasite is a requirement to promote the survival of both host and parasite.

References

Beadle NCW (1982) The Vegetation of Australia. Fischer-Verlag, Stuttgart New York

Calder M, Bernhardt P (1983) The Biology of Mistletoes. Academic Press, New York

Chapman EA, Jacobs SWL (1979) Photosynthetic responses in semi-arid environments. In: Studies of the Australian Arid Zone. IV. Chenopod Shrublands (RD Graetz, KMW Howes, eds.), 41–53. CSIRO, Division of Land Resources Management, Canberra

Ehleringer JR, Cook CS, Tieszen LL (1985a) Comparative water use and nitrogen relationships in a mistletoe and its host. Oecologia (Berlin) (in review)

Ehleringer JR, Schulze E-D, Ziegler H, Lange OL, Farquhar GD, Cowan IR (1985b) Xylem mistletoes: Water or nutrient parasites? Science 227:1479–1481

Ehleringer JR, Schulze E-D (1985) Mineral nutrient concentrations in an epiparasitic *Phoradendron californicum* growing on *P. californicum* and its host, *Cercidium floridum*. Amer J Bot 72:568–571

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 (Berlin) 58:193–201

Härtel O (1937) Über den Wasserhaushalt von *Viscum album* L Ber Dtsch Botan Ges 55:310–321

Härtel O (1956) Der Wasserhaushalt der Parasiten. In: Handb der Pflanzenphysiologie III (O Stocker, ed.), 951–960. Springer, Berlin Göttingen Heidelberg

Hellmuth EO (1971a) Eco-physiological studies on plants in arid and semi-arid regions in Western Australia. III. Comparative studies on photosynthesis, respiration and water relations of ten arid zone plants under winter and later summer climatic conditions. J Ecol 59:225–259

Hellmuth EO (1971b) Eco-physiological studies on plants in arid and semi-arid regions in Western Australia. IV. Comparison of the field physiology of the host, *Acacia grasbyi* and its hemiparasite, *Amyema nestor* under optimal and stress conditions. J Ecol 59:351–363

Hollinger DY (1983) Photosynthesis and water relations of the mistletoe, *Phoradendron villosum*, and its host, the California valley oak, *Quercus lobata*. Oecologia (Berlin) 60:396–400

Kamerling Z (1910) Verdunstungsversuche mit tropischen Loranthaceen. Ber Dtsch Bot Ges 32:17–24

Körner Ch, Cochrane PM (1985) Stomatal responses and water relations of *Eucalyptus pauciflora* in summer along an elevation gradient. Oecologia (Berlin) (in press)

Lamont BB (1983) Mineral nutrition of mistletoes, p. 185–204. In: The Biology of Mistletoes, Calder M, Bernhardt P (eds), Academic Press, New York

Pereira JS, Tenhunen JD, Lange OL, Beyschlag W, Meyer A (1985) Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees growing in Portugal. Can J Forestry (submitted)

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, Hall EA, Lange OL, Walz H (1982) A portable steady-state porometer for measuring the carbon dioxide and water vapor exchange of leaves under natural conditions. Oecologia (Berlin) 53:141–145

Schulze E-D, Turner NC, Glatzel G (1984) Carbon, water and nutrient relations of two mistletoes and their hosts: a hypothesis. Plant, Cell and Environment 7:293–299

Slavik B (1974) Methods of studying plant water relations. Ecological Studies 9, Springer, Berlin Heidelberg New York

Tenhunen JD, Lange OL, Harley P, Beyschlag W, Meyer A (1985) Limitation due to water stress on leaf net photosynthesis of *Quercus coccifera* in the Portuguese evergreen scrub. Oecologia (Berlin) (in press)

Ullmann I (1985) Tagesgänge von Transpiration und stomatärer Leitfähigkeit Sahelischer und Saharischer Akazien in der Trockenzeit. Flora 176:383–409

Vareschi V, Pannier F (1953) Über den Wasserhaushalt tropischer Loranthaceen am natürlichen Standort. Phyton (Austria) 5:140–152

Walter H, Steiner M (1936) Die Ökologie der ostafrikanischen Mangrove. Z F Bot 30:65–193

Wolff EV (1880) Aschenanalysen von landwirtschaftlichen Produkten, II. Teil Weigant, Hempel, Parey, Berlin

Wood JG (1924) The relations between distribution, structure, and transpiration of arid south Australian plants. Trans Roy Soc S Austr 48:226–235