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Summary

1. Photosynthesis, transpiration and carbon isotope ratios of 11 mistletoes and their hosts were measured in central and eastern Australia to test hypotheses regarding (i) similarity of photosynthetic rate between host and parasite and (ii) significance of host xylem carbon as a contributor to parasite carbon gain.
2. Differences in photosynthetic rates of mistletoes and their hosts were not statistically significant, although most mistletoes had slightly lower photosynthetic rates and much higher transpiration rates than their hosts.
3. Uptake of carbon dissolved in the xylem sap of the host was estimated from the discrepancy between observed and predicted carbon isotope ratios. Dividing xylem carbon gain by measured transpiration yielded a mean ± SE xylem carbon concentration of 10 ± 2·0 mM. Addition of xylem carbon gain to photosynthesis for the mistletoes further reduced differences between mistletoe and host carbon gain.
4. Heterotrophic carbon gain, derived from the host xylem sap, represented approximately 15% of the total carbon gain on average. Patterns are discussed in terms of possible selection for equivalent shoot growth rates between parasite and host.

Key-words: Hemiparasite, photosynthesis, transpiration, xylem sap
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Introduction

Mistletoes are obligate epiphytic parasites of higher plants, which, upon germination, form a haustorium that penetrates to the host cambium (Calvin 1967; Kuijt 1969). The haustorium connects the mistletoe with the host, allowing the parasite to acquire host resources via the xylem and/or phloem. All mistletoes are photosynthetic, but vary in the extent to which they obtain reduced carbon from their hosts (Hull & Leonard 1964b). At one extreme are the 'xylem-tapping' mistletoes (the most common pattern), which parasitize only the xylem of their hosts. Such mistletoes have no access to the phloem—either for import or for export. They therefore accumulate high concentrations of xylem-transported cations in their tissues (Lamont 1983) and are thought to obtain reduced carbon primarily by their own photosynthetic activity. At the other extreme are the 'phloem-tapping' mistletoes capable of parasitizing both xylem and phloem of their hosts (Hull & Leonard 1964a).

This study focuses on xylem-tapping mistletoes in Australia, which differ from their hosts in many aspects of their carbon and water relations. Xylem-tapping mistletoes generally transpire at much higher rates than their hosts, as much as ninefold greater in some species (Ullmann *et al.* 1985). This is surprising given that the haustorium is a hydraulic bottleneck (Glatzel 1983; Davidson, True & Pate 1989; Goldstein *et al.* 1989), which should instead result in a reduced transpiration rate. Differences in water-use efficiency [*A/E*, the molar ratio of photosynthesis (*A*) to transpiration (*E*)] have been noted between Australian mistletoes and their hosts (Ehleringer *et al.* 1985), and high *E* values appear to be the basis for the decreased *A/E* pattern. While high *A/E* values might be anticipated for plants in arid lands (Cohen 1970), mistletoes appear to be clear exceptions to this rule.

What might be the advantage of low *A/E* to mistletoes? At least two hypotheses have been proposed. Schulze, Turner & Glatzel (1984) suggested that low *A/E* (due to high *E* values) may improve the mineral nutrition of the mistletoe by providing sufficient nitrogen from the xylem sap to meet growth and reproductive requirements, as these mistletoes have no access to nitrogen within the host's phloem. The Schulze *et al.* hypothesis suggests that without high

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transpiration rates insufficient amounts of nitrogen would be taken up to meet the needs of the mistletoe. As support for this hypothesis, Schulze & Ehleringer (1984) showed that growth rates of *Phoradendron* species were correlated with transpiration rate and that they were higher on hosts with greater nitrogen concentrations in their xylem sap. A second advantage of low *A/E* (due to high *E* values) may be the acquisition of large amounts of host carbon obtained from the solutes in xylem sap (Raven 1983; Marshall & Ehleringer 1990; Stewart & Press 1990; Schulze *et al.* 1991). This mode of carbon acquisition may significantly contribute to a mistletoe's carbon budget. In the mistletoe *P. juniperinum*, xylem sap carbon is thought to have contributed as much as 60% of the total carbon in the parasite (Marshall & Ehleringer 1990). Similarly, C_3 mistletoes growing in the Namib Desert on C_3 and CAM (Crassulacean and metabolism) hosts were observed to have carbon isotope ratios intermediate between those of the host and their own photosynthate, indicating that 50–70% of their tissue carbon was obtained from their hosts, presumably due to uptake of host xylem solutes (Schulze *et al.* 1991).

This paper examines two hypotheses. First, it is hypothesized that the carbon isotope ratios of Australian xylem-tapping mistletoes will be significantly less negative than one would predict based on their gas exchange due to acquisition of significant amounts of carbon via xylem sap. If host xylem sap is a significant source of mistletoe carbon, then mistletoe photosynthetic rates need not be as high as those of their host in order for parasite and host tissues to have equivalent rates of carbon gain. The second hypothesis is that mistletoe assimilation rates, including xylem carbon from the host, should be equal to host photosynthetic rates.

Materials and methods

Diurnal photosynthetic gas-exchange rates were measured and leaf samples for $\delta^{13}C$ analyses were collected from mistletoes and their hosts in central and eastern Australia during the spring of 1981. Details of the sample locations and of the gas-exchange sampling design were presented in Schulze *et al.* (1982) and Ullmann *et al.* (1985). A summary of maximum photosynthetic rate and leaf conductance values of the species appeared in Ehleringer *et al.* (1985). Complete diurnal gas-exchange data were available for eight mistletoe–host pairs. These were: (1) *Lysiana exocarpi* on *Acacia victoriae*, 8 September, Tolarno, New South Wales; (2) *L. spathulata* on *Acacia coriaceae,* 18 September, Davenport Range, Northern Territory; (3) *L. spathulata* on *Acacia cowleana,* 18 September, Davenport Range, Northern Territory; (4) *Amyema maidenii* on *Acacia monticola,* 18 September, Davenport Range, Northern Territory; (5) and (6) *Diplatia grandibracteata* on *Eucalyptus leucophloia*, 20 September, Camooweal, Queensland; (7) *L. subfalcata* on *Atalaya hemiglauca,* 22 September, Mt. Isa, Queensland; (8) *L. subfalcata* on *Ceriops tagal,* 26 September, Townsville, Queensland. Gas-exchange data were available at the time of daily maximum for three additional mistletoe–host pairs: (9) *Amyema quangdang* on *Acacia brachystachya,* 11 September, between Mt. Gunson Mines and Pimba, South Australia; (10) *Amyema maidenii* on *Acacia kempeana,* 14 September, Curtin Springs, Northern Territory; (11) *Amyema gibberulum* on *Hakea eyreana*, 14 September, Curtin Springs, Northern Territory. Scientific names follow Jessop (1981). Maximum photosynthetic rate data were extracted from the full diurnal observations and compared, by regression analysis, to time-weighted daily averages. The regression equations were used to estimate average gas-exchange values from daily maxima available in the literature.

Leaf samples were collected and tissue nitrogen concentrations analysed by Kjeldahl analysis on an autoanalyser (Technicon, Terrytown, New York, USA) (Lillivek 1970). Carbon isotope ratios ($\delta^{13}C$) of the leaf samples were measured on an isotope ratio mass spectrometer, relative to the PeeDee belemite (PDB) standard (Farquhar *et al.* 1982a).

One of our objectives was to compare $\delta^{13}C$ values predicted from gas-exchange data to measured values. Farquhar, O'Leary & Berry (1982b) proposed that $\delta^{13}C$ should be related to photosynthetic gas exchange as:

$$\delta^{13}C_{plant} = \delta^{13}C_{air} - a - (b-a)\left(\frac{c_i}{c_a}\right) \qquad \text{eqn 1}$$

where $\delta^{13}C_{plant}$ is the carbon isotope ratio of plant tissue, $\delta^{13}C_{air}$ is the value of ambient CO_2 (assumed to be –8‰), c_i is intercellular CO_2 concentration within the leaves and c_a is the ambient CO_2 concentration. Equation 1 was insufficient to explain $\delta^{13}C$ in tissues of a xylem-tapping mistletoe from the south-western USA (*P. juniperinum* growing on *Juniperus osteosperma*) (Marshall & Ehleringer 1990). Instead they suggested that carbon flux from the xylem sap modified the expected carbon isotope composition of the parasite. This influx of host carbon, fixed at a lower internal CO_2 concentration in the leaves of the host, changed the $\delta^{13}C$ of the mistletoe tissues to a value intermediate between those of host and mistletoe photosynthate. The parasite $\delta^{13}C$ composition should then be described as:

$$\delta^{13}C_{parasite} = \frac{A[\delta^{13}C_{air} - a - (b-a)\,(c_i/c_a)] + Ec_x\delta^{13}C}{A + Ec_x} \qquad \text{eqn 2}$$

where A is photosynthetic rate, E is transpiration rate, c_x is the concentration of carbon in the xylem sap, and $\delta^{13}C_x$ is the carbon isotope ratio of host xylem carbon (assumed to be the same isotopic composition as that of host leaf).

In the analyses that follow, total carbon gain by mistletoes was estimated by summing measured A values and an estimate of xylem carbon gain. Xylem carbon gain was calculated by multiplying average measured E by the mean xylem carbon concentration (c_x). Xylem carbon concentrations were estimated as:

$$c_x = \frac{AH}{E(1-H)} \qquad \text{eqn 3}$$

where H is proportional heterotrophy, as estimated by Press *et al.* (1987) from all data for which measured mistletoe $\delta^{13}C$ lay between the values predicted for host and mistletoe from gas exchange. Xylem carbon was not added to host photosynthetic rates because: (1) unlike the mistletoe, the host has access to the phloem and can therefore export xylem-derived carbon, and (2) xylem carbon gain by hosts is negligible (5–10% of the photosynthetic rate). Throughout the paper, data are presented as means ± SE and analysed by either paired Student's t-tests or by linear regression.

Results and discussion

Time-weighted daily averages of E and A were analysed for Australian mistletoe–host pairs from which complete diurnal cycles were available. Average E values were significantly higher in the mistletoes than in the hosts (Table 1). However, photosynthetic rates were not significantly different between mistletoe and host. Mean instantaneous water-use efficiency (A/E) of mistletoes was approximately half that of their hosts (1·11 ± 0·13 *vs* 2·42 ± 0·17 mmol mol^{-1}). Large differences in A/E should be associated with large differences in c_i/c_a and, therefore, based on equation 1, carbon isotope ratios should also differ between mistletoes and hosts. In fact, comparison of mistletoes to hosts resulted in significant differences ($t = 5{\cdot}30$, df = 10, $P < 0{\cdot}001$) with mistletoes averaging –28·67 ± 0·23‰ and hosts –26·81 ± 0·25‰. No consistent pattern was observed in nitrogen concentrations, although Ehleringer *et al.* (1986b) found that nitrogen concentrations were related to mimicry patterns between mistletoe and host.

Estimates of xylem carbon concentration derived from equation 3 ranged from 3 to 16 mM. The mean estimate was 10 ± 2 mM, half the value of 22 mM measured by Marshall & Ehleringer (1990). Estimates of total carbon gain by mistletoes and their hosts were not significantly different (paired $t = 0{\cdot}38$, df = 7, $P = 0{\cdot}72$), averaging 4·0 ± 0·5 μmol m^{-2} s^{-1} for mistletoes and 4·8 ± 0·7 μmol m^{-2} s^{-1} for hosts. The improvement in the fit is presented by the arrows in Fig. 1, which show a general convergence on the 1:1 line. As further evaluation of hypothesis 1, gas-exchange data were extracted from other studies in the literature involving mistletoe–host combinations. From these paired mistletoe–host photosynthetic and transpiration rates (similarly assuming host xylem sap carbon concentrations of 10 mM), total rates of carbon gain were calculated. The paired rates of total carbon gain were again similar between mistletoe and parasite; a

Table 1. Daily average photosynthetic rates of mistletoes and their hosts

Mistletoe Host	A (μmol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	A/E (μmol mmol^{-1})	Nitrogen (mmol N g^{-1})
Lysiana exocarpi	4·84	5·37	0·90	1·97
Acacia victoriae	8·14	2·91	2·80	1·97
Lysiana spathulata	2·00	2·19	0·91	ND
Acacia coriaceae	6·17	3·19	1·93	1·16
Lysiana spathulata	2·90	4·36	0·67	0·58
Acacia cowleana	2·91	1·68	1·73	1·32
Amyema maidenii	2·21	1·80	1·23	ND
Acacia monticola	1·31	0·58	2·26	1·21
Diplatia grandibracteata	4·46	5·61	0·81	0·61
Eucalyptus leucophloia	5·30	2·11	2·51	0·85
Diplatia grandibracteata	5·38	4·86	1·11	0·32
Eucalyptus leucophloia	5·09	2·24	2·27	0·46
Lysiana subfalcata	5·27	2·88	1·83	1·68
Atalaya hemiglauca	4·31	1·70	2·54	1·23
Lysiana subfalcata	4·56	3·23	1·41	0·99
Ceriops tagal	5·35	1·63	3·28	0·67
Mistletoe mean ± SE	4·0 ± 0·5	3·8 ± 0·5**	1·11 ± 0·13***	1·02 ± 0·23
Host mean ± SE	4·8 ± 0·7	2·0 ± 0·3	2·42 ± 0·17	1·11 ± 0·20

Paired t-tests comparing mistletoes to hosts were significant at: ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.
ND, not determined.

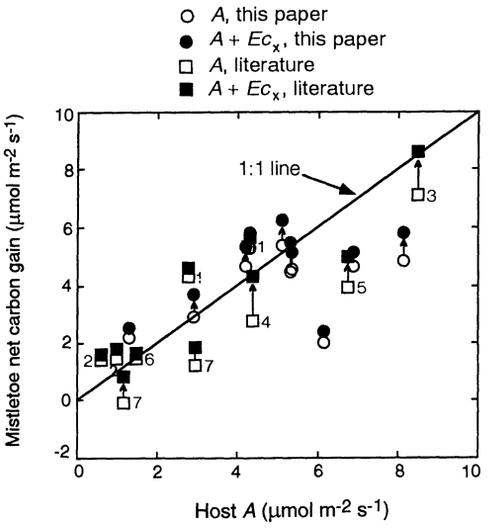

Fig. 1. Relationship between host photosynthetic rate, mistletoe photosynthetic rate and mistletoe photosynthetic rate plus xylem carbon uptake by transpiration. Open symbols show photosynthetic rates, closed symbols include xylem carbon gain estimated by assuming xylem carbon concentrations were 10 mM. Circles are data from this paper. Numbered squares are from the following sources: (1) Schulze *et al.* 1984; (2) Hellmuth 1971; (3) Hollinger 1983; (4) Ehleringer, Cook & Tieszen 1986a; (5) El-Sharkawy, Cock & Hernandez 1986; (6) Davidson *et al.* 1989; (7) Goldstein *et al.* 1989.

linear regression through the origin yielded a slope of 0·92±0·07 ($F=192$, $n=20$, $P<0·0001$). The Australian data may be typical of a general pattern of similar rates of carbon gain between parasites and hosts (Fig. 1).

The relationship between predicted $\delta^{13}C$ (equation 1) and measured $\delta^{13}C$ values is presented in Fig. 2. Host data are offset from the 1:1 line by just over 1‰, but they lie parallel to the line as if the $\delta^{13}C_{air}$ value were offset by a constant amount. In contrast, the mistletoe data are considerably above the 1:1 line and show no clear tendency. Accounting for the host carbon assimilated through 10 mM xylem sap (equation 2) brings the expected and measured carbon isotope ratios for mistletoes towards the 1:1 line for 10 of the 11 parasites, implying that mistletoe carbon isotope composition was being significantly influenced by carbon imported from the host xylem.

Accounting for xylem carbon in the mistletoe carbon budget drew the data towards the theoretically expected values in all cases (Fig. 2), and would do so over a broad range of xylem carbon concentrations. However, *L. exocarpi* remained a considerable distance from the line. There was surprisingly little effect from adding xylem carbon in two cases, perhaps because host xylem carbon concentrations may have been significantly greater than 10 mM, a relatively low xylem sap value (Raven 1983). In contrast to the low *A/E* values in *P. juniperinum* (Marshall & Ehleringer 1990), the Australian mistletoes had relatively high *A/E* values so that the impact of xylem sap carbon on mistletoe carbon isotope ratio was relatively smaller. Averaging over all species, it was estimated that xylem carbon contributed approximately 15% of total carbon gain; values for individual species ranged from 5 to 21%. These values are considerably less than the 60% previously reported for other xylem-tapping mistletoes (Marshall & Ehleringer 1990; Schulze *et al.* 1991).

Selection for carbon gain equivalent to that of its host can be interpreted in terms of selection for similar shoot growth between mistletoe and host, if it is first assumed that carbon gain is a primary determinant of growth rate, that leaf area ratios are similar between the two species and that the gas exchange measured on these dates was representative of seasonal gas exchange as a whole. The advantages of correlated growth between parasite and host are clearest at the extremes. If the mistletoe grew much more slowly than its host, it was probably shaded out by host leaves or the haustorium possibly engulfed in the host tissues [as observed by Calvin (1967)]. At the other extreme, if the mistletoe grew much more rapidly than its host branch, hydraulic connections between the host and parasite, which influence water transport rates, probably created a severe bottleneck (particularly during periods of water stress) and could possibly lead to xylem cavitation and mistletoe death. Schulze & Ehleringer (1984) noted a significant correlation between mistletoe size and host sapwood cross-sectional area, further indicating a coordination of host and parasite growth rates. The disadvantages of the two extremes should lead to convergence in shoot growth rates between host and parasite.

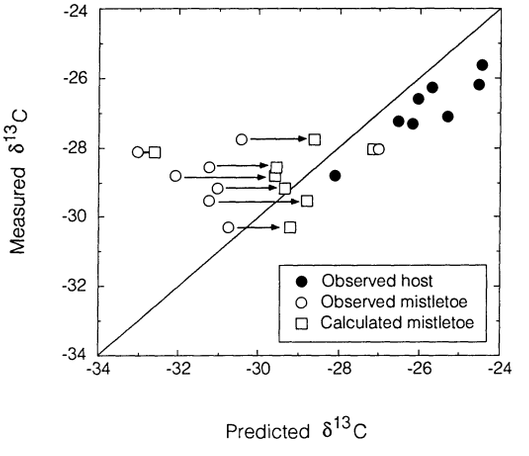

Fig. 2. Relationship between observed leaf carbon isotope ratio values for mistletoes and their hosts in Australia and values predicted from measured intercellular CO_2 concentrations (equation 1). Hosts are represented by open triangles and mistletoes by open circles. Closed circles represent mistletoes, assuming that leaf carbon isotope ratio reflects some heterotrophic contribution by the host (equation 2). Closed circle values assume that host xylem carbon concentrations were 10 mM.

Selection for convergence in parasite and host growth rates provides a basis for the nitrogen–parasitism hypothesis. While the Schulze *et al.* (1984) nitrogen–parasitism hypothesis states that an advantage of low *A/E* to mistletoes is that it allows mistletoes to obtain sufficient nitrogen for reproduction and growth, it does not specify how the nitrogen requirement is determined. The annual mistletoe nitrogen requirement could be reduced if the mistletoe simply reduced its growth rate. However, if the mistletoe must maintain a growth rate similar to that of its host to prevent being overgrown or shaded out, then the mistletoe nitrogen requirement may be determined by the need to maintain a growth rate sufficient to prevent displacement from the cambium or shading by the host. Clearly any hypothesis suggesting similarity in parasite–host growth rate is only conjecture at this point, but the expected patterns are consistent with observed carbon gain data (as presented above) and xylem growth patterns (Schulze & Ehleringer 1984) and provide a rationale to explain the Schulze *et al.* (1984) nitrogen–parasitism hypothesis.

References

Calvin, C.J. (1967) Anatomy of the endophytic system of the mistletoe, *Phoradendron flavescens*. *Botanical Gazette* **128,** 117–137.

Cohen, F. (1970) The expected efficiency of water utilization in plants under different competition and selection regimes. *Israel Journal of Botany* **19,** 50–54.

Davidson, N.J., True, K.C. & Pate, J.S. (1989) Water relations of the parasite:host relationship between the mistletoe *Amyema linophyllum* (Fenzl) Tieghem and *Casuarina obesa* Miq. *Oecologia* **80,** 321–330.

Ehleringer, J.R., Schulze, E.-D., Ziegler, H., Lange, O.L., Farquhar, G.D. & Cowan, I.R. (1985) Xylem-tapping mistletoes: water or nutrient parasites? *Science* **227,** 1479–1481.

Ehleringer, J.R., Cook, C.S. & Tieszen, L.L. (1986a) Comparative water use and nitrogen relationships in a mistletoe and its host. *Oecologia* **68,** 279–284.

Ehleringer, J.R., Ullmann, I., Lange, O.L., Farquhar, G.D., Cowan I. R., Schulze E.-D. & Ziegler H. (1986b) Mistletoes: a hypothesis concerning morphological and chemical avoidance of herbivory. *Oecologia* **70,** 234–237.

El-Sharkawy, M.A., Cock, J.H. & Hernandez, A.D.P. (1986) Differential response of stomata to air humidity in the parasitic mistletoe (*Phthirusa pyrifolia*) and its host, mandarin orange (*Citrus reticulata*). *Photosynthetic Research* **9,** 333–343.

Farquhar, G.D., Ball, M.C., von Caemmerer, S. & Roksandic, Z. (1982a) Effect of salinity and humidity on $\delta^{13}C$ value of halophytes—evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. *Oecologia* **52,** 121–124.

Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982b) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* **9,** 121–137.

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* **56,** 193–201.

Goldstein, G., Rada, F., Sternberg, L., Burguera, J.L., Burguera, M., Orozco, A., Montilla, M., Zabala, O., Azocar, A., Canales, M.F. & Celis, A. (1989) Gas exchange and water balance of a mistletoe species and its mangrove hosts. *Oecologia* **78,** 176–183.

Hellmuth, E.O. (1971) 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. *Journal of Ecology* **59,** 351–363.

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

Hull, R.J. & Leonard, O.A. (1964a) Physiological aspects of parasitism in mistletoes (*Arceuthobium* and *Phoradendron*). I. The carbohydrate nutrition of mistletoe. *Plant Physiology* **39,** 996–1007.

Hull, R.J. & Leonard, O.A. (1964b) Physiological aspects of parasitism in mistletoes (*Arceuthobium* and *Phoradendron*). II. The photosynthetic capacity of mistletoe. *Plant Physiology* **39,** 1008–1017

Jessop, J. (1981) *Flora of Central Australia*. A.H. and A.N. Reed PTY Ltd, Sydney.

Kuijt, J. (1969) *The Biology of Flowering Parasitic Plants*. University of California Press, Berkeley.

Lamont, B. (1983) Mineral nutrition of mistletoes. In: *The Biology of Mistletoes* (eds D. M. Calder & P. Bernhardt), pp. 185–204. Academic Press, New York.

Lillivek, H.A. (1970) The determination of total organic nitrogen. In: *Methods in Food Analysis* (ed. M. A. Joslyn,) pp. 601–616. Academic Press, New York.

Marshall, J.D. & Ehleringer, J.R. (1990) Are xylem-tapping mistletoes partially heterotrophic? *Oecologia* **84,** 244–248.

Press, M.C., Shah, N., Tuohy, J.M. & Stewart, G.R. (1987) Carbon isotope ratios demonstrate carbon flux from C_4 host to C_3 parasite. *Plant Physiology* **85,** 1143–1145.

Raven, J.A. (1983) Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Advances in Ecological Research* **13,** 136–239.

Schulze E.-D., Hall, A.E., Lange, O.L. & Walz, H. (1982) A portable steady-state porometer for measuring the carbon dioxide and water vapour exchange of leaves under natural conditions. *Oecologia* **53,** 141–145.

Schulze, E.-D. & Ehleringer, J.R. (1984) The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. *Planta* **162,** 268–275.

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

Schulze, E.-D., Lange, O.L., Ziegler, H. & Gebauer, G. (1991) Carbon and nitrogen isotope ratios of mistletoes growing on nitrogen and non-nitrogen fixing hosts and on CAM plants in the Namib Desert confirm partial heterotrophy. *Oecologia* **88,** 457–462.

Stewart, G.R. & Press, M.C. (1990) The physiology and biochemistry of parasitic angiosperms. *Annual Review of Plant Physiology Plant Molecular Biology* **41,** 127–151.

Ullmann, I., Lange, O.L., Ziegler, H., Ehleringer, J., Schulze, E.-D. & Cowan, I.R. (1985) Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia. *Oecologia* **67,** 577–587.

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