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Photosynthesis of mistletoes in relation to their hosts at various sites in tropical Brazil*

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Abstract Chlorophyll *a* fluorescence parameters showing the instantaneous performance and carbon-isotope ratios reflecting long-term behaviour of leaves were determined for a large number of mistletoe/host-pairs in the cerrado belt of Brazil. Study sites were a very exposed rupestrian field, a semi-exposed savanna and a highly shaded gallery forest. The major question asked was if photosynthetic capacity of mistletoe leaves differed from that of the leaves of their respective hosts. It is shown that except for the very exposed rupestrian field site, photosynthetic capacity appeared to be similar in mistletoes and host leaves. The superior behaviour of host leaves in the rupestrian field was due to particularly expressed sun-plant characteristics of the host. However, mistletoes always had higher average sto-

matal conductances, lower leaf temperatures at similar or even higher irradiance and higher intercellular CO₂-partial pressures than hosts. Photosynthetic performance of mistletoe leaves was independent of whether a given mistletoe species parasitized aluminium-accumulating or non-accumulating host species in the cerrados with their aluminium-rich soils.

Key words Aluminium · Carbon isotope ratios · Cerrado · Chlorophyll fluorescence · Mistletoes

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* Dedicated to Prof. Dr. Benno Parthier, Halle, on the occasion of his 65th birthday

Introduction

Mistletoes mainly belong to two families of the order Santalales, namely the Loranthaceae (approx. 900 species in 65 genera) and the Viscaceae (approx. 400 species, 11 genera). They occur ubiquitously (Sallé et al. 1993) in the temperate zone and in arid regions, but the large majority of mistletoe taxa is found in the tropics.

Mistletoes are generally considered to be hemiparasites feeding on the transpiration stream of their host trees for water and mineral nutrients. However, it is known that mistletoes may also acquire carbon compounds from their hosts (Ehleringer et al. 1985, Pate et al. 1991a, b; Rey et al. 1991; Marshall and Ehleringer 1990), and a holoparasitic mistletoe taxon has even been discovered, i.e. *Tristerix aphyllus*, which grows on the tissue of cactus stems (Kraus et al. 1995). Mistletoes can drag part of the host's transpiration stream towards their own leaves by having a more negative leaf-water potential and a larger leaf-conductance for water vapour and hence a higher transpiration rate than the host leaves (Schulze et al. 1984). This implies that there must also be complex responses of the mistletoe/host-associations to environmental factors, such as irradiance, temperature and water supply. However, comparative ecophysiological studies at different sites and under varying environmental stress conditions are still scant.

Here we present for the first time comparative measurements of chlorophyll-fluorescence parameters and carbon-isotope analyses of many pairs of different mistletoe species (all of them Loranthaceae) and different hosts. Studies were performed at different sites in the cerrado belt of Brazil, where mistletoes are particularly abundant. The cerrados of the central plains of Brazil comprise a complex of various types of vegetation including seasonal savannas, dry forests and gallery forests with different degrees of sun exposure, so that comparative studies of mistletoes and their hosts can be performed under different light climates. Thus, study sites included a very exposed open site in a rupestrian field, a semi-exposed savanna site and a highly shaded gallery forest site. Chlorophyll fluorescence measurements provide information on the instantaneous photosynthetic performance while carbon-isotope ratios of C_3 plants reflect the average stomatal conductance, intercellular CO_2 partial pressure and water use efficiency during photosynthesis over the lifetime of the leaves sampled (Farquhar et al. 1989a, b).

The major question asked was if photosynthetic capacity of mistletoe leaves differed from that of the leaves of their respective hosts. Clearly, under all circumstances mistletoes must have a higher transpiration than their hosts. However, given a certain supply of carbon compounds by the host to the mistletoes, the latter might afford a lower photosynthetic capacity in comparison to the host. On the other hand this may also depend on the productivity of the host as determined by the light climate and sun/shade adaptations. Cerrado soils have high levels of aluminium. Given mistletoe species may occur on hosts which are Al-accumulators or non-accumulators. Since they must receive different loads of the toxic metal via the transpiration stream of these hosts the present data also provide information on the possible effects of Al on the parasites.

Materials and methods

Sites and plants

Chlorophyll-fluorescence measurements were performed and leaf material for carbon-isotope analysis was collected at the following sites in the cerrado belt of Brazil:

1. Two different localities (sites) with similar vegetation of the rupestrian fields in the Serra do Cipó (State of Minas Gerais) at 1100–1200 m above sea level, 19° 12'S, 43° 28'W.
2. In a cerrado vegetation at the base of the Serra do Cipó (Rio Cipó) at 800 m above sea level.
3. In the cerrado vegetation around Brasília (DF), namely (a) near the Centro Olímpico (15° 46'S, 47° 52'W), (b) in the University of Brasília Experimental Station (15° 45'S, 47° 52'W), and (c) in the Parque Nacional de Brasília (15° 44'S, 47° 56'W).
4. In a gallery forest at the ecological reserve of the Instituto Brasileiro de Geografia e Estatística (IBGE), Brasília (DF) (15° 56'S, 47° 54'W).

Names of the mistletoe and host taxa studied are given in full with authorities where they first appear in the Tables, i.e. most of them in Table 1 and a few in Table 2. More details on the vegetation and the plants are found in Ratter (1980, 1986), Pereira et al. (1993) and Felfili et al. (1994). Some of the hosts growing on the aluminium-rich cerrado soils were Al-accumulators while others were non-accumulators.

Chlorophyll fluorescence measurements

The chlorophyll *a* fluorescence measurements were performed with a pulse-amplitude modulated photosynthesis yield analyzer (Mini-PAM) of H. Walz (Effeltrich, Germany) with the leaf clip holder described by Bilger et al. (1995) which kept the leaf at a constant distance (approx. 1 cm) and angle (60°) to the fibre optics. Measurements of light intensity ($\lambda = 400\text{--}700$ nm) close to the leaf surface were taken by a micro-quantum sensor calibrated against a Li-COR quantum sensor (Neb., USA). For measurements of fluorescence parameters in the light adapted state under conditions of ambient irradiance care was taken to keep the natural leaf exposure on the plant and not to shade the leaves by the fibre optics and the leaf clip. Each measurement took less than 5 s insuring minimum disturbance of the leaf. Readings of potential quantum yield of photosystem II (F_v/F_m ; where F_m is maximum fluorescence of the dark adapted leaf under a light saturating flash and F_v is maximum variable fluorescence, $F_m - F_o$) were taken on leaves predarkened for 30 min. A reduction of F_v/F_m below values of approximately 0.8 indicates photoinhibition which was not reversible after 30 min of darkening. Mostly for each mistletoe/host pair five readings on different mistletoe and host leaves were taken and averaged. The effective quantum yield of PSII ($\Delta F/F'_m$) was calculated as $(F'_m - F)/F'_m$, where F is fluorescence of the light-adapted sample and F'_m is the maximum light-adapted fluorescence when a saturating light pulse of 600 ms duration is superimposed on the prevailing environmental light levels (Schreiber and Bilger 1993). Apparent rates of photosynthetic electron transport (ETR) were obtained as $0.5 \times (\Delta F/F'_m) \times \text{PPFD}$ (PPFD is photosynthetic photon flux density, $\lambda = 400\text{--}700$ nm), where the factor 0.5 accounts for the excitation of both PS II and PS I. No correction was made for reflection as this was not known numerically. The quenching coefficients for photochemical, q_p , and non-photochemical, q_n , quenching of fluorescence could not be calculated since the instrument does not allow determination of the minimal fluorescence of the light adapted sample, F'_o . Instead relative excessive PPFD was obtained as $(F_v/F_m - \Delta F/F'_m)/(F_v/F_m)$ (Bilger et al. 1995). Light dependencies of ETR and $\Delta F/F'_m$ were determined using the light-curve programme of the instrument, where actinic light intensity was increased during 4 min in eight steps following each other within 30 s. Due to this short time, most likely photosynthesis of the leaves was never in steady state at any time during these measurements, and correct absolute values of ETR were not obtained. However, comparative assessments of the performance of leaves of mistletoes and their respective hosts under natural environmental conditions within a short time interval are possible in this way.

All measurements were performed between 12 and 19 October 1995 (beginning of the rainy season) and 0900–1600 hours solar time.

Carbon isotope analysis

The carbon isotope ratios ($\delta^{13}C$ values are relative deviations to Pee Dee belemnite standard in ‰) were determined according to Osmond et al. (1975) using a Heraeus CHN rapid elemental analyser coupled on-line to a trapping-box-gas-isotope-mass spectrometer system (Finnigan MAT Delta S). The error of determinations is ± 0.1 ‰ external precision.

Carbon-isotope ratios ($\delta^{13}C$ values) in the leaves of C_3 plants indicate the relations between intercellular CO_2 partial pressures and CO_2 assimilation rates as determined by the average degree of stomatal opening (stomatal conductance) during photosynthesis over the lifetime of the leaf sampled, with more negative values referring to higher conductances. Often, the carbon isotope discrimination (Δ) is calculated, which is directly proportional to average conductance over time as follows

$$\Delta = \frac{\delta^{13}C_a - \delta^{13}C_p}{1000 + \delta^{13}C_p} \times 10^3 (\text{‰}) \quad (1)$$

where $\delta^{13}C_p$ is the value measured for the plant material and $\delta^{13}C_a$ is the value for the CO_2 of the ambient atmosphere. The latter may vary somewhat for different sites. Frequently it is not measured and is taken as -8.00 ‰ (Farquhar et al. 1989a). In the present study $\delta^{13}C_a$ was not

Table 1 Comparison of chlorophyll fluorescence measurements of mistletoe/host pairs at different sites in Brazil. In the sites and species column the first species name indicates that of the mistletoe parasite the second one that of the host. Absolute values are given for the

average PPFD at the level of the parasite leaves during measurements. Errors are standard deviations. The other values are comparisons, where Δ (differences) indicates mistletoe minus host values and r (ratios) mistletoe: host values

Sites and Species (Parasite – Host)	PPFD at mistletoe $\mu\text{mol m}^{-2}\text{s}^{-1}$	Δ ETR $\mu\text{mol m}^{-2}\text{s}^{-1}$	Δ PPFD $\mu\text{mol m}^{-2}\text{s}^{-1}$	r F_v/F_m	r $\Delta F/F'_m$	r relative excessive PPFD
Rupestrian field (Serra do Cipó, Minas Gerais)						
Site 1: <i>Struthanthus marginatus</i> (Desr.) Bl. <i>Trembleya laniflora</i> (Don.) Cogn.	460 ± 385	–155	–990	0.80	1.03	0.79
Site 2: <i>S. marginatus</i> – <i>T. laniflora</i>	683 ± 655	–180	–612	0.86	0.87	1.00
Site 1: <i>Psittacanthus robustus</i> Mart. – <i>T. laniflora</i>	1301 ± 203	–139	–3	0.86	0.34	1.38
Site 2: <i>P. robustus</i> – <i>T. laniflora</i>	1139 ± 258	–179	–156	0.82	0.21	1.58
Cerrado (Brasília)						
Site 1: Centro Olímpico						
<i>Phthirusa ovata</i> (Pohl) Eichl. – <i>Pouteria ramiflora</i> (Mart.) Radlk.	346 ± 454	–23	–168	1.35	1.59	0.79
<i>P. ovata</i> – new leaves		2	–4	1.00	1.09	0.64
<i>Styrax ferrugineus</i> Nees et Mart. old leaves	129 ± 99	26	78	1.01	0.96	1.65
Site 2: Experimental Station						
<i>P. ovata</i> – <i>Dalbergia violacea</i> (Vog.) Malme	250 ± 70	23	112	1.00	0.86	1.72
<i>P. ovata</i> – <i>Byrsonima coccolobifolia</i> (Spr.) Kunth.	203 ± 198	3	94	1.03	0.82	2.02
<i>P. ovata</i> – <i>Qualea parviflora</i> Mart.	64 ± 8	11	32	1.11	1.01	3.03
Site 3: Parque Nacional						
<i>P. ovata</i> – <i>Kielmeyera coriacea</i> Mart.	452 ± 321	5	–236	1.09	1.54	0.78
<i>P. ovata</i> – <i>Vochysia rufa</i> Mart.	218 ± 47	37	94	1.04	1.00	1.18
Gallery Forest (Brasília, IBGE)						
Site 1: Gallery Forest						
<i>P. ovata</i> – <i>Clusia cruva</i> Camb.	91 ± 71	11	53	0.93	0.92	1.05
<i>P. ovata</i> – <i>Ilex</i> cf. <i>affinis</i> Gardner	112 ± 11	14	49	0.88	0.90	0.86
<i>Phoradendron crassifolium</i> (Pohl) Eichl. – <i>I. cf. affinis</i>	0 ± 0	–9	–24	0.98	0.97	1.15
<i>P. crassifolium</i> – <i>Miconia chamissois</i> Naud.	30 ± 8	–12	–67	1.01	1.26	0.19
<i>P. crassifolium</i> – <i>Tapirira guianensis</i> Aubl.	18 ± 12	3	8	0.96	0.93	1.48
Site 2: Ecotone Gallery Forest-Cerrado						
<i>Phoradendron crulsii</i> Urb. – <i>T. guianensis</i>	252 ± 71	18	75	0.88	0.94	0.76

measured, and therefore we preferred to tabulate the $\delta^{13}\text{C}$ values which were the direct results of analyses of carbon-isotope ratios of the leaf material sampled. However, we used Eq. 1 and an assumed value of -8.00‰ for $\delta^{13}\text{C}_a$ to calculate intercellular CO_2 partial pressure, $p^i\text{CO}_2$ as follows

$$p^i\text{CO}_2 = p^a\text{CO}_2 \cdot \frac{\Delta - a}{b - a} \quad (2)$$

where $p^a\text{CO}_2$ is CO_2 partial pressure of the ambient atmosphere, taken here as 340 Pa/MPa, a gives ^{13}C -discrimination due to CO_2 -diffusion in air ($= 4.4\text{‰}$) and b the net fractionation caused by carboxylation in C_3 -photosynthesis ($= 27\text{‰}$) (Farquhar et al. 1989a, b; Broadmeadow et al. 1992).

Errors given are always standard deviations.

Results and discussion

Chlorophyll-fluorescence measurements of mistletoe/host pairs at ambient irradiation

In the *rupestrian field* (Serra do Cipó, Minas Gerais), with the rather open exposed vegetation F_v/F_m (potential quantum yield of PS II after 30 min dark adaptation) was always lower in the mistletoes than in the host leaves on a sunny day (Table 1). The range of F_v/F_m in the hosts was from 0.677 ± 0.113 to 0.814 ± 0.010 and in the mistletoes

0.542 ± 0.042 to 0.702 ± 0.023 . This shows that both mistletoes and host were often under photoinhibition not reversible during the applied darkening period of 30 min ($F_v/F_m < 0.8$) but the mistletoes more strongly than the host. On an overcast day immediately following the sunny day with only $380 \mu\text{mol m}^{-2} \text{s}^{-1}$ ambient irradiance the relationship was inverse, the mistletoes showed F_v/F_m values of 0.732 ± 0.035 (*Psittacanthus robustus*) and 0.839 ± 0.011 (*Struthanthus marginatus*) while the host (*Trembleya laniflora*, Melastomataceae) had 0.615 ± 0.053 showing that the mistletoes had largely recovered from photoinhibition under the lower irradiance in contrast to the host.

When irradiance received by leaves of parasite and host was of comparable intensity the mistletoe (*P. robustus*) on average had much lower $\Delta F/F'_m$ (effective quantum yield) (~ 0.09) and ETR (apparent relative electron transport rate) ($\sim 50 \mu\text{mol m}^{-2} \text{s}^{-1}$) and higher relative excessive PPFD (~ 0.87) than the host, where the respective values were $\Delta F/F'_m \sim 0.30$, ETR $\sim 210 \mu\text{mol m}^{-2} \text{s}^{-1}$, and relative excessive PPFD ~ 0.60 . For the more shaded mistletoe *S. marginatus*, of course, values of $\Delta F/F'_m$ and relative excessive PPFD were more favourable in comparison to the host than in the more exposed *P. robustus* due to the light dependency of these variables. However, average ETR was rather low in the mistletoes ($\sim 40 \mu\text{mol m}^{-2} \text{s}^{-1}$). Overall, the comparison

of the mistletoes *S. marginatus* and *P. robustus* with their host *T. laniflora* (Table 1) shows that mistletoe photosynthesis was less effective than host photosynthesis at the rupestrian field site.

In the *cerrados* around Brasília the more dense vegetation led to lower overall irradiance on both mistletoe and host leaves, and all the chlorophyll fluorescence parameters for the parasite (exclusively *Phthirusa ovata* at the cerrado sites) and its various hosts were much more similar (Table 1). The range of average values measured on leaves of individual plants was as follows for parasites and hosts, respectively: $\Delta F/F'_m$ 0.384 ± 0.181 to 0.693 ± 0.044 and 0.250 ± 0.146 to 0.720 ± 0.026 , ETR 22 ± 4 to 73 ± 45 and 11 ± 2 to $72 \pm 83 \mu\text{mol m}^{-2} \text{s}^{-1}$, relative excessive PPFD 0.117 to 0.499 and 0.040 to 0.644. Photoinhibition also was limited and only occasionally apparent in hosts (e.g., in *Pouteria ramiflora*, Sapotaceae, with an F_v/F_m of 0.576 ± 0.034) with ranges of F_v/F_m values of the mistletoe (*P. ovata*) and hosts (excepting *P. ramiflora*) of 0.757 ± 0.075 to 0.838 ± 0.006 and 0.702 ± 0.084 to 0.805 ± 0.007 , respectively.

In the *gallery forest* (IBGE, Brasília) irradiance was very low during the measurements at midday (1200–1430 hours solar time). The highest PPFD received by mistletoe leaves measured was $112 \pm 11 \mu\text{mol m}^{-2} \text{s}^{-1}$ and it was $97 \pm 92 \mu\text{mol m}^{-2} \text{s}^{-1}$ on host leaves. At the site in the ecotone *gallery forest/cerrado* the irradiance was 252 ± 71 (mistletoe) and 177 ± 132 (host) $\mu\text{mol m}^{-2} \text{s}^{-1}$. At the shaded gallery forest site chlorophyll fluorescence parameters were rather similar for parasites and hosts (Table 1) with ranges of average values as follows: $\Delta F/F'_m$ 0.619 ± 0.156 to 0.790 ± 0.035 and 0.626 ± 0.207 to 0.783 ± 0.012 , ETR 0 ± 0 to 37 ± 3 and 4 ± 1 to $23 \pm 5 \mu\text{mol m}^{-2} \text{s}^{-1}$, relative excessive PPFD 0.045 to 0.207 and 0.062 to 0.233, respectively. There was no or only in a few cases a weak indication of photoinhibition with F_v/F_m values of 0.734 ± 0.049 to 0.827 ± 0.006 and 0.816 ± 0.010 to 0.838 ± 0.012 for mistletoes and host, respectively. By contrast, in the ecotone with its higher irradiance F_v/F_m values of 0.652 ± 0.110 for the mistletoe *Phoradendron crulsii* and of 0.741 ± 0.025 for its host *Tapirira guianensis* (Anacardiaceae) did indicate some photoinhibitory reduction of photosynthetic efficiency. ETRs were higher than in the gallery forest with 66 ± 14 and $48 \pm 30 \mu\text{mol m}^{-2} \text{s}^{-1}$ for mistletoe and host respectively, and the other parameters changed accordingly. However, performance of host and mistletoe was still rather similar (Table 1).

An overall comparison of all mistletoe and host measurements is given in Fig. 1. As expected, effective quantum yield of PSII ($\Delta F/F'_m$) declined with increasing PPFD, both ETR and relative excessive PPFD increased with PPFD with an indication of the typical light-saturation behaviour at higher PPFDs. These relations do not show differences between the general behaviour of mistletoes and their host plants, except for the three points of host measurements at the highest PPFDs in Fig. 1A–C which suggest that in these cases at high PPFD there was better effective quantum yield, higher ETR and lower relative

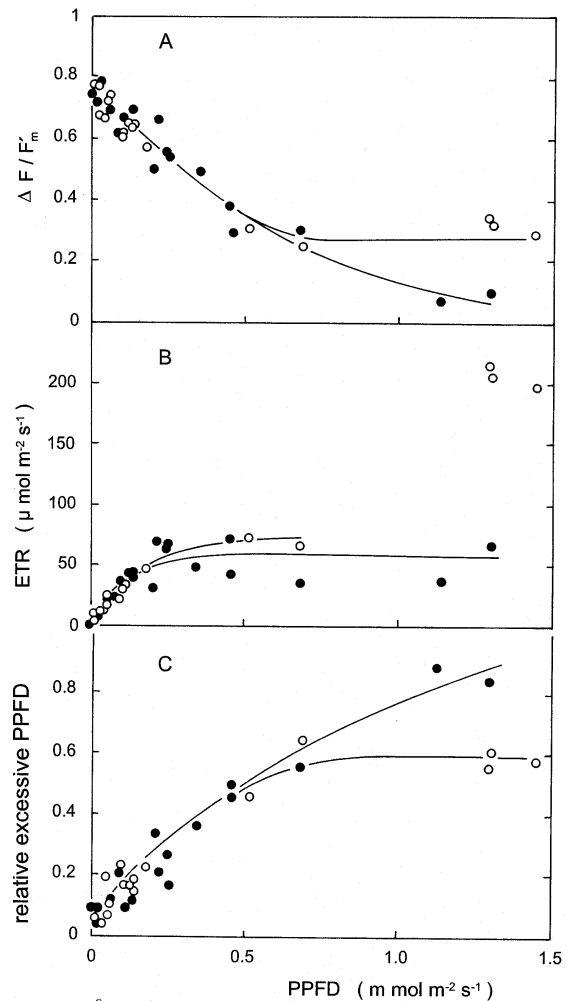


Fig. 1 Comparisons of chlorophyll-fluorescence measurements of all of the various species of mistletoes (closed symbols) and hosts (open symbols) studied at the different sites in Brazil. Relation of effective quantum yield of PSII ($\Delta F/F'_m$) (A), apparent rates of photosynthetic electron transport (ETR) (B) and relative excessive PPFD (C) to PPFD. Note that the data of mistletoes and hosts are well comparable for the different species as well as for parasites and hosts except for the three points of hosts at the highest PPFDs, which are the values of *T. laniflora* on the sunny day in the very exposed rupestrian field site

excessive PPFD in the hosts. These points are all from the measurements of the *T. laniflora* host plants in the rupestrian field site.

Therefore, it appears, on the basis of the actual performance in the field, that the relative behaviour of parasites and hosts in comparison with each other depends on the site and environment and that the strong disadvantage of mistletoes vs hosts was restricted to the rather open and exposed rupestrian field site. On the other hand, it may be argued that this pronounced parasite-host difference in the rupestrian field was mostly due to the particular behaviour of the dominating or almost exclusive host *T. laniflora*. This may be evaluated comparing the respective light-dependence curves (Table 2) which give more insight into the potential capacities of the plant species involved.

Table 2 Comparison of cardinal points of light dependence curves of chlorophyll-fluorescence measurements of mistletoe and host plants at different sites in Brazil. In the sites and species column the first species name indicates that of the mistletoe parasite the second one that of the host. (ETR_{max} , maximum apparent relative electron transport rate; PAR_{50} , PPFD at half ETR_{max} ; $yield_{50}$, yield ($\Delta F/F'_m$) at PAR_{50} ; Δ ,

mistletoe minus host values; r , mistletoe divided by host values. Values are averages of two light-dependence curves except for the bright day on Campo rupestre (Cerra do Cipó) where averages were obtained from 3–4 curves. > refers to curves which did not saturate below a PPFD of 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$

Sites and Species (Parasite – Host)	Parasite			Host			Parasite vs Host			
	PAR_{50} $\mu\text{mol m}^{-2}\text{s}^{-1}$	$Yield_{50}$ $\mu\text{mol m}^{-2}\text{s}^{-1}$	ETR_{max} $\mu\text{mol m}^{-2}\text{s}^{-1}$	PAR_{50} $\mu\text{mol m}^{-2}\text{s}^{-1}$	$Yield_{50}$ $\mu\text{mol m}^{-2}\text{s}^{-1}$	ETR_{max} $\mu\text{mol m}^{-2}\text{s}^{-1}$	Δ PAR_{max} $\mu\text{mol m}^{-2}\text{s}^{-1}$	r $Yield_{50}$	Δ ETR_{max} $\mu\text{mol m}^{-2}\text{s}^{-1}$	
Rupestrian field (Serra do Cipó, Minas Gerais)										
bright day: <i>S. marginatus</i> – <i>T. laniflora</i>	285	0.39	105	515	0.62	>250	–230	0.62	–150	
<i>P. robustus</i> – <i>T. laniflora</i>	310	0.41	125	585	0.63	>335	–275	0.65	–215	
overcast day: <i>S. marginatus</i> – <i>T. laniflora</i>	320	0.40	130	460	0.62	>280	–140	0.65	–150	
<i>P. robustus</i> – <i>T. laniflora</i>	200	0.54	105	460	0.62	>280	–260	0.87	–175	
Cerrado (near Rio do Cipó, Minas Gerais)										
<i>S. marginatus</i> (dark green) – <i>Vernonia fruticulosa</i> Mart.	220	0.61	135	480	0.63	>295	–260	0.97	–160	
<i>S. marginatus</i> (yellow green) – <i>V. fruticulosa</i>	200	0.39	75	480	0.63	>295	–280	0.62	–220	
– <i>V. fruticulosa</i> (non parasitized)	–	–	–	420	0.61	>255	–	–	–	
Cerrado (Brasília)										
Site 1: Centro Olímpico										
<i>P. ovata</i> – <i>P. ramiflora</i>	305	0.48	160	365	0.28	100	–60	1.71	60	
<i>P. ovata</i> – <i>S. ferrugineus</i> new leaves	250	0.50	125	300	0.63	180	–55	0.79	–60	
old leaves	250	0.50	125	240	0.62	145	10	0.81	–20	
Site 2: Experimental Station										
<i>P. ovata</i> – <i>D. violacea</i>	430	0.48	210	370	0.58	210	60	0.83	0	
<i>P. ovata</i> – <i>B. coccolobifolia</i>	245	0.53	135	180	0.67	95	65	0.79	40	
<i>P. ovata</i> – <i>Q. parviflora</i>	320	0.57	>180	180	0.60	105	140	0.95	75	
Site 3: Parque Nacional										
<i>P. ovata</i> – <i>K. coriacea</i>	265	0.59	155	340	0.53	185	–75	1.11	–30	
<i>P. ovata</i> – <i>V. rufa</i>	280	0.62	175	210	0.57	120	70	1.09	55	
Gallery Forest (Brasília, IBGE)										
<i>P. ovata</i> – <i>C. cruiva</i>	195	0.60	110	390	0.61	230	–195	0.98	–125	
<i>P. ovata</i> – <i>I. cf. affinis</i>	210	0.66	140	245	0.66	150	–35	1.00	–15	
<i>P. crassifolium</i> – <i>I. cf. affinis</i>	100	0.53	60	120	0.67	85	–20	0.79	–25	
<i>P. crassifolium</i> – <i>M. chamissois</i>	200	0.53	100	220	0.59	130	–20	0.90	–30	

Light-dependence curves of mistletoes and their hosts

Light-dependence curves of ETR and effective quantum yield ($\Delta F/F'_m$) of photosynthesis were obtained for many mistletoe/host pairs as summarized in Table 2. A few selected examples are shown in Fig. 2. The host plant of the mistletoes at the rupestrian field site showed the highest maximum ETR (over 250 up to 375 $\mu\text{mol m}^{-2}\text{s}^{-1}$; Fig. 2A, Table 2) although another species measured in the rupestrian field, namely *Mimosa nagueirei*, even had an $ETR < 400 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Fernandes et al. 1997). Another mistletoe-host the Asteraceae *Vernonia fruticulosa* at an open road-side site in the cerrado at the base of Serra do Cipó, and even *Clusia cruiva* in the gallery forest also had high ETR_{max} (over 250 and over 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively). In the mistletoes an ETR_{max} over 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$ was only reached in one case. Overall the range of ETR_{max} was much smaller in the mistletoes (60–210 μmol

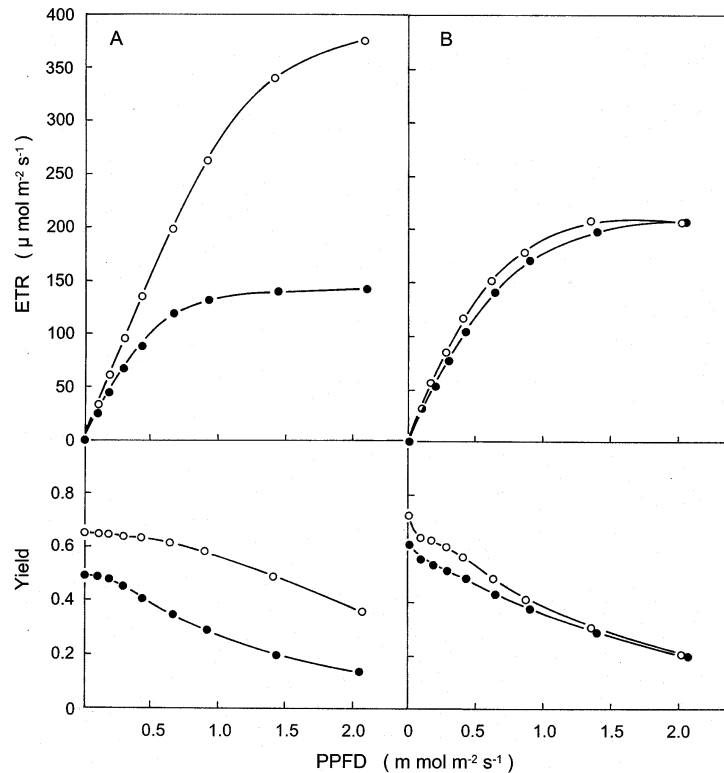
$\text{m}^{-2}\text{s}^{-1}$) than in their hosts (85–375 $\mu\text{mol m}^{-2}\text{s}^{-1}$). Thus, the large difference between parasites and hosts in the rupestrian field seems to be a matter of the specific hosts. With the smaller PPFD and effective quantum yield at half saturation of ETR and the lower ETR_{max} the mistletoes behave like shade plants in comparison to the sun-plant characteristics of the host. In the other less exposed sites this strong difference disappears due to the less pronounced sun-plant characteristics of the hosts.

Carbon isotope ratios and calculated internal CO_2 partial pressures of leaves and leaf-temperature differences in mistletoe/host pairs

Carbon isotope ratios of all mistletoes and hosts studied showed that all taxa were C_3 -plants, including *C. cruiva* in the gallery forest at IBGE, i.e. the species of a genus

Fig. 2 Selected examples of light-dependence curves of mistletoes and their hosts.

(A) *Psittacanthus robustus* (mistletoe; closed symbols) and *Trembleya laniflora* (host; open symbols) in the Campo rupestre (Serra do Cipó). (B) *Phthirusa ovata* (mistletoe; closed symbols) and *Dalbergia violacea* (host; open symbols) in the cerrado of the Experimental Station, University of Brasília



comprising many CAM and C₃/CAM intermediate species (Lüttge 1996). For all pairs measured the host values of $\delta^{13}\text{C}$ were always less negative than the parasite values.

Among C₃-plants more negative $\delta^{13}\text{C}$ values indicate larger long-term average stomatal conductance and transpirational loss of water. Larger transpiration should lead to increased transpirational cooling of the leaves, and indeed, this prediction from the long-term average behaviour given by the carbon-isotope analyses of leaf biomass is also borne out by the instantaneous determinations of actual leaf temperatures (L_T) during chlorophyll fluorescence measurements. Leaf temperatures in the present study ranged from 23.5 ± 1.1 to 29.2 ± 0.5 and 25.1 ± 0.1 to $32.5 \pm 0.3^\circ\text{C}$ in parasites and hosts, respectively. L_T was consistently lower in the leaves of mistletoes as compared to the leaves of hosts. Only in a few cases was L_T equal in mistletoes and hosts, but this only occurred at low absolute irradiance (compare Table 3 with Table 1 for PPFD at the level of mistletoe leaves). The lower L_T of mistletoes in some cases can be explained by lower irradiance received by the leaves of mistletoes when these are shaded by the host. However, mistletoe L_T was also lower than host L_T in cases where the mistletoe leaves received similar or higher average irradiance than the host leaves. The lower L_T in the mistletoes then must have been due to higher transpirational cooling. In many cases these temperature differences were large enough to be sensed by touching the leaves with the fingers. The larger stomatal conductance of mistletoes as compared to their hosts also implies that internal CO₂-partial pressure of mistletoe leaves was higher than that of host leaves (Eq. 2; Table 3).

Mistletoes on aluminium accumulating and non-accumulating hosts

The cerrado soils are very rich in aluminium. Some of the host plants are known to be strong Al-accumulators, namely *Qualea parviflora*, *Vochysia rufa* and *Miconia chamissois* (Haridasan 1982). The other host plants (Tables 1–3) of this study were non-accumulators. However, comparisons show that there were no significant differences in potential quantum yield of dark adapted leaves (F_v/F_m) and leaf temperatures (data not presented) and $\delta^{13}\text{C}$ -values (Table 3) for a given mistletoe species, e.g. *Phthirusa ovata* or *Phoradendron crassifolium*, on Al-accumulating and non-accumulating hosts. Since the mistletoes receive much more Al on Al-accumulating than on non-accumulating hosts (data not shown), this implies that their photosynthetic apparatus and stomatal regulation are well adapted to increased Al-levels as there is no increased photoinhibition (no reduced F_v/F_m) or reduced transpirational cooling (no less negative $\delta^{13}\text{C}$ -values, no increased leaf temperatures) in the mistletoes on the Al-accumulating in relation to the non-accumulating hosts.

General discussion

Is it now well established that in addition to water and mineral ions, mistletoe parasites also receive more or less considerable amounts of photosynthetic products from their hosts, and in extreme cases mistletoes have even become

Table 3 Comparison of carbon isotope ratios ($\delta^{13}\text{C}$, PDB), calculated internal CO_2 partial pressures (p^{iCO_2}) and leaf temperatures (L_T) of mistletoe/host pairs at different sites in Brazil. In the sites and species column the first species name indicates that of the mistletoe parasite

the second one that of the host. Δ , mistletoe minus host values. Leaf temperatures are those obtained during the measurements of Table 1. Values of $\delta^{13}\text{C}$ marked by asterisks are averages of two samples, otherwise values are for single samples analysed

Sites and Species (Parasite – Host)	$\delta^{13}\text{C}$ (‰)			p^{iCO_2} (Pa/MPa)			Δ L_T (°C)
	Parasite	Host	Δ	Parasite	Host	Δ	
Rupestrian field (Serra do Cipó, Minas Gerais)							
Site 1: <i>S. marginatus</i> – <i>T. laniflora</i>	–31.96	–29.25	–2.71	306	263	43	–4.8
Site 2: <i>S. marginatus</i> – <i>T. laniflora</i>	–31.47	–27.50	–3.97	298	235	63	–2.3
Site 1: <i>P. robustus</i> – <i>T. laniflora</i>	–31.56	–28.25	–3.31	300	247	53	–2.7
Site 2: <i>P. robustus</i> – <i>T. laniflora</i>	–29.53	–27.90	–1.63	268	242	26	–5.4
Cerrado (near Rio do Cipó, Minas Gerais)							
<i>S. marginatus</i> (yellow-green) – <i>V. fruticosa</i>	–32.09*	–29.23	–2.86	308	263	45	
<i>S. marginatus</i> (dark-green) – <i>V. fruticosa</i>	–31.83	–26.35	–5.48	304	217	87	
Cerrado (Brasília)							
Site 1: Centro Olímpico							
<i>P. ovata</i> – <i>P. ramiflora</i>	–31.36	–28.65	–2.71	297	254	43	–2.9
<i>P. ovata</i> – <i>S. ferrugineus</i>	–31.63	–29.46	–2.17	301	266	35	–0.9
Site 2: Experimental Station							
<i>P. ovata</i> – <i>D. violacea</i>	–32.26	–25.57	–6.69	311	205	106	–2.8
<i>P. ovata</i> – <i>B. gocolobifolia</i>	–31.97	–29.76	–2.21	306	271	35	–1.5
<i>P. ovata</i> – <i>Q. parviflora</i>	–31.47	–28.69	–2.78	298	254	44	–0.6
Site 3: Parque Nacional							
<i>P. ovata</i> – <i>K. coriacea</i>	–33.48	–27.63	–5.85	330	238	92	–1.7
<i>P. ovata</i> – <i>V. rufa</i>	–31.35	–26.49	–4.86	296	220	76	–1.4
Gallery Forest (Brasília, IBGE)							
Site 1: Gallery Forest							
<i>P. ovata</i> – <i>C. cruiva</i>	–31.90	–26.72*	–5.18	305	223	82	+0.1
<i>P. ovata</i> – <i>I. cf. affinis</i>	–32.37*	–30.73*	–1.64	313	287	26	–0.6
<i>P. ovata</i> – <i>M. chamissois</i>	–31.62	–29.77	–1.85	301	271	30	
<i>P. crassifolium</i> – <i>I. cf. affinis</i>	–33.37	–30.57	–2.80	329	284	45	–1.4
<i>P. crassifolium</i> – <i>M. chamissois</i>	–31.97	–30.68	–1.29	306	286	20	–1.8
<i>P. crassifolium</i> – <i>T. guianensis</i>	–29.33	–26.14	–3.19	264	214	50	–1.2
<i>P. crulsii</i> – <i>M. chamissois</i>	–32.59	–28.43	–4.16	316	250	66	
Site 2: Ecotone Gallery Forest – Cerrado							
<i>P. crulsii</i> – <i>T. guianensis</i>	–27.97	–26.97	–1.00	243	227	16	–2.4

holoparasites and are entirely dependent on their hosts (see Introduction). Thus, one might have expected that mistletoes could afford a lower photosynthetic capacity than the leaves of their hosts. The present chlorophyll fluorescence measurements of mistletoe/host-pairs apparently do not bear out such a relationship between parasite and host photosynthesis. In only a few cases did the host show a superior photosynthetic capacity, but this can be explained by a particular adaptation of the host to high irradiance in an open habitat. It is not a general feature of host/mistletoe-relations because largely photosynthetic capacity of host and parasite leaves appeared to be similar. However, the carbon isotope analyses show that mistletoes have a larger long-term average stomatal conductance than the host leaves. This is already well known (Ziegler 1986; Richter et al. 1995) and a prerequisite for the mistletoes to drag the host transpiration stream with dissolved mineral nutrients to their own stems and leaves (Schulze et al. 1984). It has, however, additional consequences. One of them is the fact that mistletoe photosynthesis operates at higher intercellular leaf CO_2 -partial pressures (p^{iCO_2}) than host photosynthesis. The present carbon isotope data suggest that on average p^{iCO_2} in mistletoes was 52 ± 25 (21) Pa/MPa larger than that of hosts (Table 3). Thus, host leaves have a

handicap as compared to parasites. Achievement of similar ETR and effective quantum yields ($\Delta F/F'_m$) by mistletoe leaves as compared to hosts leaves may then well be due to compensation of lower intrinsic capacity by higher substrate (CO_2) concentration. When mistletoes have similar rates of photosynthesis at larger stomatal conductance this also implies that they have smaller water-use-efficiencies than hosts.

Another consequence of higher stomatal conductance of mistletoes dragging mineral solutes towards the mistletoe leaves is that also toxic metals dissolved in the transpiration stream should accumulate in the mistletoes. Thus, the mistletoes must receive much more Al from Al-including hosts than from non-includers on the Al-rich cerrado soils. Since there were no differences between mistletoes of given species on the two types of hosts, the mistletoes must be quite Al-resistant. Finally, the consistently lower mistletoe leaf temperature as compared to host leaf temperature, of course, is also a consequence of higher stomatal conductance of the mistletoes. It is an intriguing question if this cooling is only an unavoidable side effect of the higher transpiration of the parasites or if it has other advantages for the mistletoes, e.g. reducing stress in a hot environment.

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