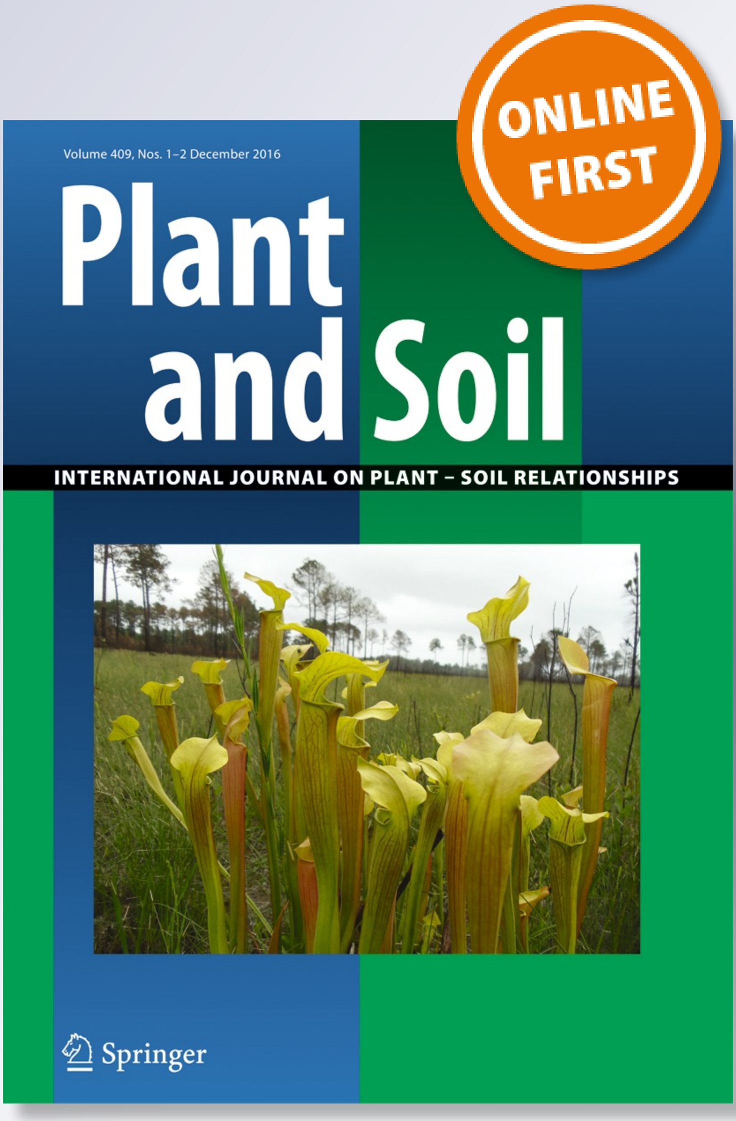
Leaf trait adaptations of xylem-tapping mistletoes and their hosts in sites of contrasting aridity

Marina C. Scalon & Ian J. Wright

Plant and Soil
An International Journal on Plant-Soil Relationships

ISSN 0032-079X

Plant Soil
DOI 10.1007/s11104-016-3151-3



Plant Soil
DOI 10.1007/s11104-016-3151-3

REGULAR ARTICLE

Leaf trait adaptations of xylem-tapping mistletoes and their hosts in sites of contrasting aridity

Marina C. Scalon · Ian J. Wright

Received: 8 July 2016 / Accepted: 13 December 2016

Abstract
Background and aims Xylem-tapping mistletoes may experience relaxed selective pressure to use water efficiently during photosynthesis because of lower per-unit costs for water acquisition than experienced by host plants. As a result, we hypothesised that mistletoes would exhibit parallel but dampened leaf-level adaptations and responses to aridity, compared to those seen in hosts.
Methods Photosynthetic traits, leaf dark respiration, nutrient concentrations and specific leaf area (SLA) were measured on 42 mistletoe-host species-pairs sampled from five sites in Australia and Brazil that vary widely in aridity.
Results Mistletoes exhibited similar trait-shifts to hosts in relation to site aridity. In both groups, arid-site species showed stronger control over stomatal water loss, larger drawdown of CO_2 during photosynthesis (lower c_i: c_a), higher leaf N and P concentrations per unit leaf area, and lower SLA. Nevertheless, mistletoes were profligate water users compared to their hosts and showed substantially less efficient use of water during photosynthesis. On average, mistletoes showed twice higher leaf dark respiration rates at a given photosynthetic capacity, suggesting relatively higher leaf maintenance costs for these parasitic plants.
Conclusions Despite fundamental differences in lifestyle and in photosynthetic traits, mistletoes exhibit trait responses and adaptations to site aridity in parallel and to approximately the same extent as their hosts.

Keywords Photosynthesis · Leaf nutrient concentration · Dark respiration · Loranthaceae · Hemi-parasite · Water use efficiency

Responsible Editor: Hans Lambers .

M. C. Scalon · I. J. Wright
Department of Biological Sciences, Macquarie University, Sydney, Australia

M. C. Scalon (✉)
Laboratório de Ecofisiologia Vegetal, Departamento de Botânica, Instituto de Ciências Biológicas, Universidade de Brasília, Caixa Postal 04457, Brasília, DF 70904-970, Brazil
e-mail: marina_scalon@yahoo.com.br

Present Address:
M. C. Scalon (✉)
Departamento de Botânica, Universidade de Brasília, Brasília, Brazil

Introduction

There is an extensive literature demonstrating that, in the short term (e.g., minutes to hours to days), plants maximise photosynthetic carbon gain in relation to transpirational water loss via modifying stomatal behaviour in relation to atmospheric humidity (Cowan and Farquhar 1977; Givnish 1986; Farquhar et al. 1989; Medlyn et al. 2011). On longer (ecological) time-scales, we might instead focus on functional trait differences among species and the manner in which these traits vary with site aridity. From this view point, two of the most striking leaf-level adaptations to higher aridity in woody plants are: (1) they tend to have lower specific leaf area (SLA, the ratio of leaf area per dry mass; Niinemets 2001; Wright et al. 2004a); and (2) they tend to deploy leaves with high nitrogen concentration per area (N_{area}; Cunningham et al. 1999; Wright et al. 2004a; Prentice et al. 2011). Lower SLA, due to thicker leaf laminae or higher concentrations of cell wall material, is thought to reflect the need for mechanical strengthening in leaves of evergreen arid zone species (Onoda et al. 2011). The increase in N_{area}, at least partially achieved via deeper mesophyll layers (also contributing to lower SLA), is generally associated with greater CO_2 drawdown during photosynthesis (i.e., lower intercellular CO_2 concentration - c_i). Through this process plants can achieve a given carbon assimilation rate (A_{area}) with a lower stomatal conductance to both CO_2 and water (g_s), thus economising on water use (Wright et al. 2001; Prentice et al. 2014).

Mistletoes are well known to be profligate users of water (Marshall and Ehleringer 1990; Marshall et al. 1994). Mistletoes are photosynthetic hemi-parasitic plants that attach via a modified root (haustorium) to the xylem stream of their host, from where they access water and nutrients. By not needing to invest in roots, the energetic per-unit costs for acquiring water and nitrogen should be presumably very low in mistletoes; at least, far lower than that experienced by their hosts. They usually exhibit higher transpiration rates and g_s than their hosts, yet achieve lower A_{area}, resulting in a very low water use efficiency (the ratio of A_{area} to transpiration; Ullmann et al. 1985). Various hypotheses have been proposed to explain this pattern. The most recognized one is the 'N-parasitism hypothesis' (Schulze et al. 1984), which posits that mistletoes are most strongly limited by access to nitrogen, hence they operate at very high transpiration rates in order to acquire sufficient N from the host xylem stream. Following a similar principle is the C-parasitism hypothesis (Marshall and Ehleringer 1990), based on reports of partial heterotrophy (i.e., part of the carbon in the mistletoes is actually transferred from the host xylem, in the form of amino acids; Marshall et al. 1994). The C-parasitism hypothesis predicts that higher transpiration rates would be necessary, not only to acquire N, but also to obtain heterotrophic carbon. It is generally thought that the higher transpiration rates are achieved via operating at lower leaf water potentials and/or by having a high hydraulic conductivity (Hsiao 1973, Aston and Lawlor 1979).

While the per-unit cost to acquire nitrogen might be lower for mistletoes than their hosts, presumably mistletoes and hosts suffer similar per-unit maintenance costs for leaf N, since there is no reason to believe that they differ in the need to continually break down and resynthesise nitrogen-rich proteins such as Rubisco. Protein turnover accounts for quite a considerable respiration cost to plants (Amthor 2000). Thus, considering both the acquisition and maintenance costs of water and nitrogen, one might argue that nitrogen is relatively cheaper for mistletoes than for their hosts, but the cost of water acquisition is especially cheap. Tempering that to some degree, presumably there is a cost to maintaining lower leaf water potentials, e.g. via greater investment in osmolytes. In any case, differences between the relative costs for water and nitrogen experienced by mistletoes and their hosts should have implications for the manner in which these resources are used during photosynthesis (Wright et al. 2003; Prentice et al. 2014), and also for how water and N use vary with site properties, especially with site aridity.

A complementary question is the degree to which mistletoes do or do not show stomatal responses to varying atmospheric humidity. Early work suggested that mistletoes showed only limited stomatal control (Schulze et al. 1984; Marshall et al. 1994), but more recent studies have shown close coordination of host and mistletoe stomatal behaviour during the day (Bowie and Ward 2004; Scalon et al. 2016a). From a global dataset of leaf traits including carbon isotope ratios, Scalon and Wright (2015) showed that mistletoes seem to become more conservative in their water use as site aridity increases. Moreover, universal parasitic theories suggest that obligatory parasites need to balance the advantage of higher virulence (e.g. decrease in host fitness via profligate water use by the parasite) with the need to prevent the death of the host (Anderson and May 1982). In summary, it is still unknown what sort of trait responses and adaptations mistletoes generally show in relation to site aridity, and how coordinated these responses are with those of their hosts. In this study, we explored these issues using a comparative, multi-species framework. We sampled 42 mistletoe-host pairs across four sites in Australia and one in Brazil that varied widely in moisture index (ratio of annual precipitation to potential evapotranspiration). We also used this opportunity to test for general trait differences between mistletoes and hosts across all species-pairs, and among sites.

In general we expected that mistletoes would exhibit qualitatively similar trait responses or adaptations to aridity as those seen in host plants (specifically, lower SLA, higher N_{area}, lower $c_i : c_a$), but that they would be noticeably dampened, because of the relaxed selective pressure to use water efficiently during photosynthesis (Stewart and Press 1990). In addition, we also expected that mistletoes, compared to their hosts, would operate at higher $c_i : c_a$ and thus, at higher g_s for a given A_{area} (using more water per unit of photosynthetically-fixed carbon); and, possibly, at higher g_s, absolutely.

Material and methods

Our dataset concerns 42 mistletoe-host (M-H) species-pairs sampled from five sites in Australia and Brazil. The 42 M-H species-pairs consist of 18 different mistletoe species parasitising 33 different host species (themselves representing 12 plant families; Table 1). We chose study sites that varied widely in vegetation type, annual precipitation and moisture index (MI; Table 2), and where we were able to sample six or more different M-H species-pairs (of which we then sampled four to seven individuals). Geographical coordinates were used to retrieve the mean annual temperature (MAT) and mean annual precipitation (MAP) from the CRU CL2.0 global climate dataset (New et al. 2002). Potential evapotranspiration (PET) was estimated following Wang et al. (2012) and annual moisture index (MI) was calculated as the ratio between MAP and PET (Wang et al. 2012). All sites were located in low fertility soils according to governmental reports (NPWS 1998, 2005) and past publications (Scalon et al. 2016b). Preliminary analyses (not shown) justified the approach, followed for the analyses presented in this paper, in which the sites were simply divided into dry (MI < 0.3) and wet (MI > 0.7) site categories.

Site descriptions

Wet sites

Australian savanna (7 M-H pairs) The site was located in Howard Springs National Park, approximately 35 km southeast of Darwin (130°45'E, 12°30'S). It consists of a typical Australian tropical savanna with very marked seasonality, where ca. 95% of the ~1700 mm mean annual rainfall is restricted to the wet season (December to March). The soil in the area is well-drained, highly weathered, laterised and low in nutrients (Hutley et al. 2000). The vegetation in the study site consists of open-forest dominated by *Eucalyptus tetrodonta* (F. Muell.) and *Eucalyptus miniata* (Cunn. Ex Schauer), and an understory of small trees, shrubs and C4 grasses. Mistletoes in the site tend to occur on the most abundant species (listed in Table 2).

Cerrado (Brazilian savanna) (9 M-H pairs) The site was located in the Natural Reserve of the Roncador belonging to the Brazilian Institute of Geography and Statistics (RECOR/IBGE), 35 km south of Brasilia-DF, Brazil (47°53'W, 15°56'S). Soil nutrient availability usually limits tree growth and density, mainly because of the low availability of P and Ca associated with high soil acidity (pH around 5.5), high Al availability and fire disturbance (Eiten 1972). The average annual precipitation in this area is approximately 1500 mm with a pronounced dry season from May through September and a mean annual temperature that ranges from 20 to 26 °C; the predominant soils are deep and well-drained Oxisols (Oliveira-Filho et al. 1989). The vegetation in the area is dominated by *Eremanthus glomerulatus* Less.*, Schefflera macrocarpa* (Cham. & Schltdl.) Frodin*, Ouratea hexasperma* (A. St.-Hil.) Baill., and *Vellozia squamata* Pohl, and the most representative families are Fabaceae and Vochysiaceae.

Australian closed woodland (6 M-H pairs) The two sub-sites within this vegetation type were both located in eastern New South Wales, one in Ku-ring-gai Chase National Park (33°63'S, 151°26'E) and one, ca. 55 km south, in Royal National Park (34°17'S, 151°05'E). Both sites occur on low-nutrient sandstone-derived soils, have very similar long-term climate averages, and have canopies dominated by Myrtaceous trees. In Royal NP the site is located on a sheltered sandstone slope and the vegetation is dominated by red gum (*Angophora costata* (Gaertn.) Britten) and various *Eucalyptus* species (Tozer et al. 2010). In Kuring-gai Chase NP the site is also located on a sheltered sandstone slope and the vegetation is dominated by forest grey box (*Eucalyptus moluccana* Roxb.), spotted gum (*Eucalyptus maculata* Hook.), and scribbly gum (*Eucalyptus haemastoma* Sm.), and commonly classified as a low eucalypt woodland (NPWS 2002).

Dry sites

Australian chenopod shrubland (8 M-H pairs) Plants were sampled within Whyalla National Park and the immediate surrounds, ca. 10 km north of Whyalla,

Table 1 List of the studied mistletoe-host pairs species at each site location

Site	Mistletoe	Host	Host Family
Wet sites			
Australian Savanna (Darwin) $n = 7$	*Amyema sanguinea*	*Corymbia porrecta*	Myrtaceae
	Amyema sanguinea	*Eucalyptus miniata*	Myrtaceae
	Amyema sanguinea	*Eucalyptus tetrodonta*	Myrtaceae
	Amyema sanguinea	*Corymbia bleeseri*	Myrtaceae
	Amyema miquelii	*Eucalyptus miniata*	Myrtaceae
	Dendrophthoe odontocalyx	*Grevillea pteridifolia*	Proteaceae
	Decaisnina signata	*Xanthostemon paradoxus*	Myrtaceae
Brazilian Savanna (Brasília) $n = 9$	*Phoradendron sp.*	*Miconia albicans*	Melastomataceae
	Struthanthus polyanthus	*Miconia albicans*	Melastomataceae
	Psittacanthus robustus	*Miconia albicans*	Melastomataceae
	Phthirusa ovata	*Miconia albicans*	Melastomataceae
	Psittacanthus robustus	*Qualea grandiflora*	Vochysiaceae
	Psittacanthus robustus	*Qualea parviflora*	Vochysiaceae
	Psittacanthus robustus	*Qualea multiflora*	Vochysiaceae
	Phthirusa ovata	*Dalbergia miscolobium*	Fabaceae
	Phthirusa ovata	*Styrax ferrugineus*	Styracaceae
Closed woodland (Sydney) $n = 6$	*Muellerina eucalyptoides*	*Eucalyptus haemastoma*	Myrtaceae
	Muellerina eucalyptoides	*Eucalyptus moluccana*	Myrtaceae
	Muellerina eucalyptoides	*Eucalyptus spp.*	Myrtaceae
	Amyema congener	*Allocasuarina littoralis*	Casuarinaceae
	Dendrophtoe vitellina	*Eucalyptus sp.*	Myrtaceae
	Dendrophtoe vitellina	*Angophora costata*	Myrtaceae
Dry sites			
Chenopod shrubland (Whyalla) $n = 8$	*Amyema quandang*	*Acacia papyrocarpa*	Fabaceae
	Lysiana exocarpii	*Eremophila longifolia*	Scrophuliaceae
	Lysiana exocarpii	*Acacia sp.*	Fabaceae
	Lysiana exocarpii	*Pittosporum angustifolium*	Pittosporaceae
	Lysiana exocarpii	*Myoporum platycarpum*	Scrophuliaceae
	Amyema miraculosa	*Myoporum platycarpum*	Scrophuliaceae
	Amyema preissii	*Acacia victoriae*	Fabaceae
	Lysiana exocarpii	*Santalum acuminatum*	Santalaceae
Semi-arid woodland (Bourke) $n = 12$	*Amyema miraculosa*	*Eremophila longifolia*	Scrophuliaceae
	Amyema miraculosa	*Myoporum platycarpum*	Scrophuliaceae
	Amyema miraculosa	*Eremophila mitchellii*	Scrophuliaceae
	Lysiana exocarpii	*Alectryon oleifolius*	Sapindaceae
	Amyema lucasii	*Flindersia maculosa*	Rutaceae
	Amyema preissii	*Acacia aneura*	Fabaceae
	Amyema preissii	*Senna eremophila*	Fabaceae
	Amyema preissii	*Flindersia maculosa*	Rutaceae
	Amyema mandeinii	*Acacia harpophylla*	Fabaceae
	Amyema mandeinii	*Acacia aneura*	Fabaceae
	Lysiana linearifolia	*Eremophila mitchellii*	Scrophuliaceae
	Lysiana exocarpii	*Acacia aneura*	Fabaceae

Table 2 Site locations and climates. Mean annual precipitation (MAP) and mean annual temperatures (MAT) were obtained from the CRU CL2.0 global gridded dataset (New et al. 2002). Mean annual evapotranspiration (PET) was estimated following Wang et al. (2012) and moisture index was calculated as the ratio between MAP and PET

Site vegetation	Location	Coordinates	MAT (°C) (Min-Max)	MI* (wet/dry)	(mm)	PET (mm)
Wet sites						
Australian Savanna	Howard Springs (Darwin, NT, Australia)	12°30’S 130°45’E	27.6 (23.2–32.0)	0.78 (wet)	1669	2147
Brazilian Savanna	IBGE Ecological Reserve (Brasília, DF, Brazil)	15°55’S 47°51’E	25.8 (14.4–31.2)	1.03 (wet)	1478	1434
Closed woodland	Ku-ring-gai NP Royal NP (Sydney, NSW, Australia)	33°63’S 151°26’E 34°17’S 151°05’E	17.2 (13.7–21.7)	0.95 (wet)	1267	1331
Dry sites						
Chenopod shrubland	Whyalla Park (Whyalla, SA, Australia)	32°94’S 137°53’E	17.9 (11.4–23.7)	0.19 (dry)	278	1465
Semi-arid woodland	Gundabooka NP (Bourke, NSW, Australia)	30°42’S 145°56’E	19.8 (13.1–28.0)	0.15 (dry)	294	1888

*MI = MAP/PET

South Australia (32°94’S, 137°53’E). The vegetation there is chenopod shrubland dominated by Bladder Saltbush (*Atriplex vesicaria* Hewart ex Benth.) and Pearl Bluebush (*Maireana sedifolia* (F. Muell.) Paul G. Wilson) with scattered trees, such as western myall trees (*Acacia papyrocarpa* Benth.) and sugarwood (*Myoporum platycarpum* R. Br.), both which are potential hosts for mistletoes. The climate is semi-arid (MAP =278 mm), averaging 300 clear and sunny days per year, and the soils are deep and stratified, classified as clay sand soils (NPWS 1998).

Australian semi-arid woodland (12 M-H pairs) The site was located at Gundabooka National Park, north-western New South Wales (30°42’S, 145°56’E), and approximately 50 km south of Bourke. The climate of the region is semi-arid, with low annual rainfall (294 mm) and high temperatures in summer (NPWS 2005). The vegetation consists of an open woodland community dominated by Mulga (*Acacia aneura* F. Muell. ex Benth.), Ironwood (*Acacia excelsa* Benth.) and Leopardwood (*Flindersia maculosa* (Lindl.) Benth.), and soils are sandy earths with sandy and loamy topsoils (NPWS 2005). The region has been severely impacted by feral goat grazing affecting vegetation and soil (Russell et al. 2011). In most areas of the park, the topsoil horizon has been lost, and now the park has a high abundance of less palatable shrubs, such as *Eremophila*, *Senna* and *Dodonaea* species (NPWS 2005). Mistletoes in the area occur at a very high density and parasitizing most of the dominant species.

We note that for the savanna and cerrado sites, the very low rainfall during the dry season might make one consider the sites ‘dry’ rather than ‘wet’, for that part of the year. However, because evergreen tree species have reliable access to deep stores of soil water, very substantial photosynthetic rates and canopy-level transpirational fluxes are observed during the dry season (Eamus et al. 1999; O’Grady et al. 1999; Eamus and Prior 2001), suggesting that the dry season is not as ‘dry’ as one might expect based on rainfall alone. Hence, for the purposes of this study we felt confident in grouping the sites ‘wet’ and ‘dry’, as described above.

Trait measurements

All trait measurements, including gas exchange measurements, were made on four to seven individuals of each mistletoe-host pair. In the field, we simultaneously measured photosynthetic rate (A_{area}), stomatal conductance (g_s), and transpiration rates (E) at (presumed) saturating light intensity of 2000 μmol quanta m^{-2} s^{-1}, and 400 ppm CO2 concentration, using either a LI-6400 LiCor Inc. (Australian sites) or a LCpro ADC Bioscientific Ltd. (Brazilian site). Both types of equipment consist of an enclosed infra-red gas analyser system with similar principles, and they give analogous measurements. The measurements were made during the morning, between 8:00 and 11:30 am, on one canopy sun-exposed mature leaf from each individual. Measurements were made during well-watered periods of the growing season at each site, so measured photosynthetic rates should reasonably be considered as being close to maximal. Leaf-to-air vapour pressure deficit in the cuvette (VpdL) varied from 0.91 to 2.77 kPa in wet sites (mean ± sd: 1.55 ± 0.58 kPa), and from 2.02 to 4.29 kPa in dry sites (mean ± sd: 3.25 ± 0.66 kPa).

After a maximum period of 6 h, leaf dark respiration ($R_{d\text{-}area}$) was measured in the laboratory on healthy mature leaves from detached branches that were maintained hydrated in a cooler. Measurements were taken at 25 °C when possible, or in some cases (Cerrado and Australian Savanna) measured at between 26.8 and 35.1 °C, with these measurements transformed to 25 °C using the empirically-derived formula for temperature dependence of respiration rate described by (Atkin et al. 2005):

$$R_2 = R_1\{3.09 - 0.0435[(T_2 + T_1)/2]\}^{[(T_2 - T_1)/10]} \quad (1)$$

where R_1 and T_1 are the respiration rate and temperature measured, and R_2 and T_2 are the respiration rate and temperature of interest (25 °C), respectively.

In addition, five fully-expanded mature leaves were collected from each individual, scanned, and the area was measured using the software Image J (Abràmoff et al. 2004). After drying for 72 h, the leaves were weighed and specific leaf area (SLA) was calculated as the ratio of fresh area to dry mass. The dried leaves were ground and Australian samples were sent to the Analytical Service Unit from the School of Agriculture and Food Science at The University of Queensland for N and P determination by LECO TruSpec CHN combustion analyser and ICP-OES technique, respectively. Brazilian samples were sent to Laboratorio de Agroquimica e Meio Ambiente at Universidade Estadual de Maringa (PR/Brazil) for N and P determination by Kjeldahl digestion and UV-Vis spectroscopy, respectively.

Data analyses

As appropriate, mass- and area-basis trait measurements were interconverted via SLA. Individual measurements were averaged for each species-pair-site combination, and all data were log-transformed in order to meet the assumption of approximate normality (Kolmogorov-Smirnov test, $P < 0.05$ for all variables). Because of the intrinsically paired nature of the data, we used paired t-tests to test for systematic differences between individual traits in mistletoes and their hosts. To test for trait differences in relation to habit (parasite or host) and site aridity (wet or dry) we used two-way analysis of variance (ANOVA). We also fitted standardized major axis (SMA) slopes to describe bivariate relationships between key traits and to compare the slope homogeneity and elevation shifts of these relationships between dry and wet sites, and between mistletoes and hosts. The software R v. 2.13 (R Development Core Team 2008) was used to perform all statistical analysis, and the package SMATR version 3 (Warton et al. 2012) to test for SMA slopes differences. Statistical tests were considered to be significant when $P < 0.05$.

Results

Trait patterning with site aridity

Overall, our results indicated that mistletoes exhibited clear trait-shifts to aridity, in parallel and to approximately the same extent as host species (Fig. 1, Table 3). In both mistletoes and hosts, species at dry sites had higher N_{area} and P_{area}. Inspection of boxplots in Fig. 1 shows that, in host species, the higher N_{area} at dry sites (Fig. 1e) was achieved both via lower SLA (Fig. 1i) and higher N_{mass} (Fig. 1d), but in mistletoes more so via lower SLA (i.e., there was no significant difference in N_{mass} between dry- and wet-site mistletoe species). In both mistletoes and hosts, the higher P_{area} seen in dry-site species (Fig. 1h) was clearly due both to their lower SLA and to their higher P_{mass} (Fig. 1g).

In both mistletoes and hosts, dry-site species showed greater CO_2 drawdown during photosynthesis (lower $c_i : c_a$; Fig. 1c), in support of the contention that higher N_{area} is implicated in decreasing photosynthetic water use. As a result, we expected that species from dry sites would show lower g_s at a given A_{area}, but in fact, we found stronger-than-expected patterning with aridity such that, in both mistletoes and hosts, dry-site species were operating *both* at lower g_s and at lower A_{area} (Figs 1a, f and 2a).

Shifts in leaf dark respiration rate, $R_{d\text{-}area}$, mirrored those in A_{area}, $R_{d\text{-}area}$ being significantly lower at dry sites in mistletoes while, in hosts, the apparent decrease was not supported statistically.

Trait differences between mistletoes and their hosts

Considering all species, there were several notable trait differences between mistletoes and hosts (Table 3). Mistletoes averaged 1.4-fold lower SLA, 1.4-fold higher N_{area}, 2.5-fold higher P_{area}, 2-fold higher P_{mass}, 1.5-fold higher $c_i : c_a$, 1.5-fold lower A_{area}, and 2.4-fold higher

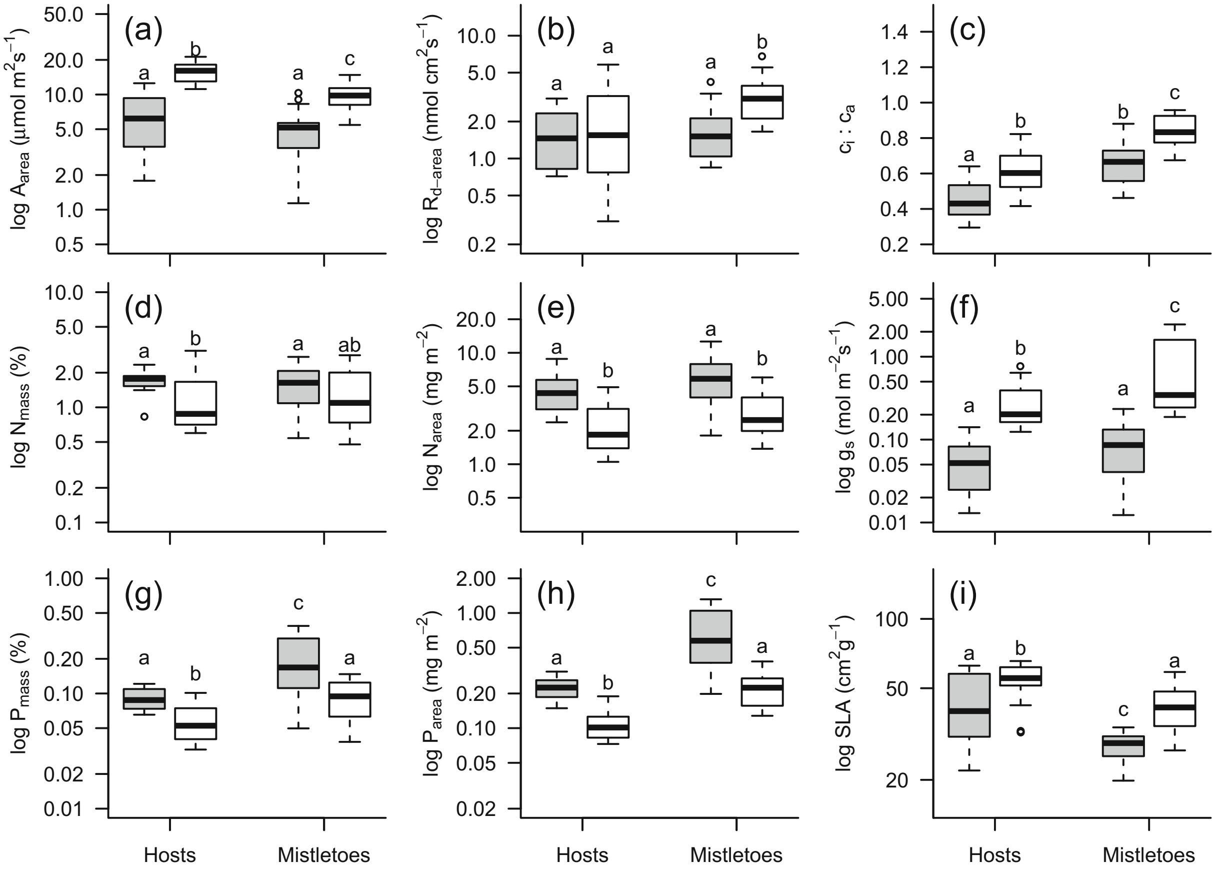


Fig. 1 Boxplots of traits for mistletoes and hosts sampled at 'dry' (*grey boxes*) and 'wet' sites (*white boxes*): leaf carbon assimilation rate (A_{area}); leaf dark respiration rate ($R_{d\text{-}area}$); internal to ambient CO_2 ratio ($c_i : c_a$); leaf nitrogen concentration (N_{area} and N_{mass}); stomatal conductance to water (g_s); leaf phosphorus concentration (P_{area} and P_{mass}); and specific leaf area (SLA). Distinct letters denote statistically significant differences (ANOVA, $P < 0.05$; Table 4)

stomatal conductance than their hosts (paired t-tests, $P < 0.01$ for all tests).

Divided by rainfall zone, mistletoes on average showed 1.6-fold higher (wet sites) and 1.2-fold higher (dry sites) stomatal conductance at a given A_{area}, compared to hosts (differences in slope elevation both $P < 0.001$; Fig. 2a). Mistletoes also showed higher dark respiration relative to photosynthetic rates than hosts, $R_{d\text{-}area}$ for a given A_{area} being on average 2.7-fold higher at wet sites and 1.3-fold higher at dry sites (Fig. 2b). Considered as a ratio, overall, $R_{d\text{-}area} : A_{area}$ was twice as high in mistletoes than in hosts (mean ± SD: 0.39 ± 0.21 versus 0.20 ± 0.09; paired t-test, $P < 0.001$).

These mean trait differences between hosts and mistletoes were generally consistent across sites (Table 3). In each of the study sites, compared to their hosts, mistletoes showed higher N_{area}, P_{area}, P_{mass} and g_s; lower SLA and A_{area}, and similar $R_{d\text{-}area}$ and N_{mass}. The few exceptions were at the Cerrado site, where mistletoes showed higher $R_{d\text{-}area}$; at Sydney closed woodland, where mistletoes and hosts exhibited similar N_{area} and g_s; and at Gundabooka semi-arid woodland, with similar A_{area} and g_s (Table 3).

Two-way ANOVA showed an individual significant effect of site (wet or dry) for every trait studied, and of habit (host or mistletoes) for most of the traits, except N_{mass} (Table 4). The effect of the two-way interaction between site and habit was restricted to A_{area}, g_s, and leaf P concentration (P_{area} and P_{mass}), suggesting that increasing aridity affected mistletoes and hosts differently for these traits. However, the non-significant interaction between site and habit for SLA, leaf N concentration (N_{area} and N_{mass}) and $R_{d\text{-}area}$ suggests the opposite; i.e., plants were affected in similar ways for these traits, irrespective of being mistletoe or host.

Table 3 Trait mean (± SD) for mistletoes (M) and host plants (H) and the mistletoe: host ratio for the different (M:H) studied sites and the total average value. Pair-wise differences between mistletoes and hosts are indicated by the symbol * within each site considered (paired t-tests, $P < 0.05$)

	Wet sites									Dry sites						Total		
	Australian Savanna			Brazilian Savanna			Closed woodland			Chenopod shrubland			Semi-arid woodland					
Trait	M	H	M:H	M	H	M:H	M	H	M:H	M	H	M:H	M	H	M:H	M	H	M:H
N_{area}	2.4 (0.4)	1.5 (0.3)	1.7*	4.6 (1.0)	3.1 (0.4)	1.5*	1.8 (0.3)	1.7 (0.5)	1.1	5.8 (2.2)	4.4 (1.7)	1.3*	6.4 (3.0)	4.7 (1.8)	1.4*	4.7 (2.6)	3.3 (1.8)	1.4*
P_{area}	0.23 (0.07)	0.09 (0.02)	2.6*	0.3 (0.06)	0.12 (0.04)	2.3*	0.15 (0.02)	0.09 (0.02)	1.7*	0.83 (0.4)	0.25 (0.04)	3.3*	0.36 (0.35)	0.21 (0.05)	1.7*	0.5 (0.4)	0.2 (0.1)	2.8*
SLA	40.6 (12.8)	56.1 (8.5)	0.7*	46.2 (5.7)	64.9 (15.3)	0.7*	33.9 (7.3)	46.5 (14.3)	0.7*	27.5 (2.9)	38.9 (11.8)	0.7*	28.7 (4.5)	44.6 (15.2)	0.6*	35.0 (10.0)	50.1 (16.0)	0.7*
A_{area}	10.6 (1.5)	17.6 (2.7)	0.6*	10.1 (2.4)	13.4 (2.1)	0.8*	6.6 (1.5)	17.1 (2.5)	0.4*	6.7 (2.3)	9.5 (2.0)	0.7*	3.9 (1.5)	4.6 (2.6)	0.8	7.3 (3.3)	11.2 (5.6)	0.6*
R_{area}	4.61 (1.34)	3.56 (1.12)	1.3	2.39 (0.89)	1.49 (0.34)	1.7*	2.82 (0.73)	2.18 (1.23)	1.3	2.67 (0.91)	2.42 (0.49)	1.1	1.19 (0.29)	1.11 (0.44)	1.1	2.52 (1.4)	1.85 (1.2)	1.4
g_s	1.80 (0.52)	0.52 (0.15)	3.5*	0.24 (0.04)	0.17 (0.05)	1.4*	0.41 (0.12)	0.30 (0.12)	1.4	0.15 (0.04)	0.09 (0.02)	1.7*	0.05 (0.03)	0.03 (0.02)	1.7	0.46 (0.66)	0.19 (0.18)	2.4*
c_i:c_a	0.93 (0.02)	0.76 (0.06)	1.2*	0.77 (0.05)	0.56 (0.05)	1.4*	0.86 (0.05)	0.53 (0.12)	1.6*	0.75 (0.09)	0.53 (0.08)	1.4*	0.59 (0.09)	0.39 (0.08)	1.5*	0.75 (0.14)	0.54 (0.14)	1.4*
N_{mass}	0.95 (0.29)	0.81 (0.17)	1.2	2.08 (0.48)	1.95 (0.58)	1.1	0.60 (0.14)	0.71 (0.09)	0.8	1.57 (0.59)	1.54 (0.37)	1.0	1.76 (0.74)	1.84 (0.27)	1.0	1.49 (0.72)	1.48 (0.59)	1.0
P_{mass}	0.09 (0.03)	0.05 (0.02)	1.8*	0.12 (0.01)	0.08 (0.02)	1.5*	0.05 (0.01)	0.04 (0.01)	1.3*	0.23 (0.12)	0.09 (0.02)	2.6*	0.17 (0.09)	0.09 (0.02)	1.9*	0.14 (0.09)	0.07 (0.03)	2.0*
N:P	11.2 (2.92)	15.8 (2.79)	0.7	17.6 (5.69)	26.7 (9.07)	0.65	11.6 (2.01)	18.1 (3.69)	0.6*	10.6 (10.2)	16.9 (5.53)	0.6	15.0 (12.8)	22.1 (5.27)	0.7	13.6 (8.81)	20.4 (6.75)	0.7
$R_{d\text{-}area}$:A_{area}	0.44 (0.15)	0.21 (0.07)	2.1*	0.24 (0.07)	0.16 (0.03)	1.5*	0.46 (0.19)	0.13 (0.07)	3.5*	0.46 (0.25)	0.26 (0.06)	1.8*	0.39 (0.41)	0.27 (0.09)	1.4	0.39 (0.21)	0.20 (0.11)	2.0*

Discussion

Our overarching question in this research was whether mistletoes exhibited photosynthetic trait adaptations to aridity comparable to those seen in hosts (recognising that any observed "adaptations" could in fact reflect a mixture of true genetic adaptation, phylogenetic niche conservatism and within-species acclimation, in unknown proportions). To ask this question we first tested whether or not host species exhibited the chief expected adaptations to site aridity (higher N_{area}, lower SLA, lower c_i : c_a), which in fact, they generally did. Dry-site hosts also showed generally higher P_{area}, as reported previously by Wright et al. (2001) in a survey of 79 sclerophyllous species in eastern Australia. Counter to expectations (from Wright et al. 2001; Wright et al. 2006; Atkin et al. 2015), there was no evidence of higher leaf respiration at dry sites (absolutely, or relative to photosynthetic rates), among host plants.

We expected to see similar trait shifts in mistletoes, but for this to be noticeably dampened compared to what was seen in hosts – as suggested by Stewart and Press (1990) to be generally true of leafy parasites. However, as it turned out our overall answer was that mistletoes showed the same types of aridity-related shifts in leaf traits as their hosts, and that these shifts were of the same general magnitude. This trend was demonstrated at a considerable level of generality, considering 42 species-pairs from five sites on two continents. This finding was unexpected and needs to be reconciled with the idea that water could be much "cheaper" for mistletoes, which on the face of it suggests there should be little selective pressure for them to use it efficiently. Below, we discuss this, the general matter of leaf nutrient adaptations to aridity, and lastly the finding that respiration in relation to photosynthesis was twice higher in mistletoes than in their hosts.

Similar trait adaptation to aridity in mistletoes and hosts

Overall, we found clear evidence that mistletoes are profligate water users compared to their hosts, at dry and wet sites. This pattern was shown from instantaneous measurements of photosynthesis, with mistletoes maintaining generally higher stomatal conductance to water (g_s) and higher c_i: c_a at all five study sites, and thus also operating with higher transpiration rates, and lower water use efficiency (ratio of A_{area} to transpiration).

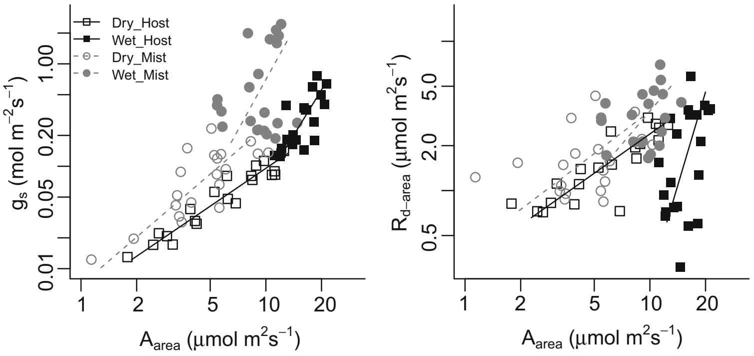


Fig. 2 Relationships between stomatal conductance (g_s) and leaf dark respiration rate ($R_{d\text{-area}}$) to leaf carbon assimilation rate (A_{area}) for mistletoes (*circles*, *dashed lines*) and their hosts (*squares, continuous line*). **a** Common standardized major axis (SMA) slopes were fitted within wet sites (*filled symbols*, MI > 0.7): 0.32 (95% CI 0.25, 0.42), and within dry sites (*empty symbols*, MI < 0.3): 0.78 (0.67, 0.88). These slopes differed significantly in elevation between mistletoes and hosts (wet/ dry sites: Wald statistic: 68.3/ 30.97; $P < 0.001$), meaning that mistletoes achieved a given A_{area} at far higher g_s. **b** Common SMA slopes were fitted within wet sites (circles, MI > 0.7): 1.99 (95% CI 1.44, 2.76), and within dry sites (squares, MI < 0.3): 0.89 (0.71, 1.11). These differed significantly in elevation between mistletoes and hosts (wet/ dry sites: Wald statistic: 33.07/ 4.52; $P < 0.05$), meaning that mistletoes achieved a given A_{area} at far higher $R_{d\text{-area}}$

We did not find evidence of dampened responses to aridity between mistletoes and hosts in terms of water use. Our results accord with those of Ullmann et al. (1985) who, considering a wide range of mistletoes and hosts across a transect in central Australia, observed that, while daily average leaf conductance was uniformly higher in mistletoes, diurnal time courses of stomatal regulation were seemingly tightly coordinated in mistletoe-host pairs. From our results and from some complementary findings elsewhere (e.g., Ullmann et al. 1985; Bowie and Ward 2004; Scalon and Wright 2015; Scalon et al. 2016a), we could confirm that mistletoe stomatal behaviour was responding to environmental influences. Mistletoes and hosts are connected hydraulically. As a consequence, the need for mistletoes to maintain lower leaf water potential and higher transpiration rates in order to extract water and nutrients from hosts might impose a series of limitations and costs, such as the need to invest in cavitation protection and/or embolism refilling strategies, and to expend energy on maintaining cell turgor (Nardini et al. 2011, 2012).

The extent to which aridity responses in mistletoes are mediated by host-induced responses is unclear; e.g., there are some reports that stomatal closure in mistletoes is partially controlled by chemical signals (e.g. ABA) produced by the host roots, which are then transferred to mistletoes via the host xylem (Ihl et al. 1987). We were unable to explore this possibility based on our own work. Nevertheless, we note that there is also conflicting evidence against the ABA-mechanism for the mistletoe *Viscum album*, for which Escher et al. (2008) corroborated strong control by the mistletoe over the influx of ABA from the host.

Higher N_{area} and P_{area} at arid sites

We found that species from drier sites, whether mistletoes or hosts, had generally 2-fold higher N_{area} and 2.5-fold higher P_{area} than wet-site species, due both to lower SLA at drier sites, and generally higher nutrient concentrations per leaf mass. It is well known that woody species in arid and high irradiance regions tend to have higher N_{area} (Cunningham et al. 1999; Wright et al. 2001; Wright et al. 2005; Prentice et al. 2011). This is at least partly associated with an enhanced ability to drawdown CO_2 during photosynthesis (lower $c_i : c_a$), and thus, to being more economical in photosynthetic water use (Wright et al. 2003; Prentice et al. 2014). Note however, dry-site species do not necessarily use less water per unit photosynthetic carbon fixed than wet-site species, since it depends on the relative magnitude of the between-site shift in g_s versus that in atmospheric VPD, transpiration being a function of both. What is far less understood, however, is the significance of higher P_{area} at lower rainfall sites – as seen here and previously also in New South Wales, Australia (Wright et al. 2001) and globally for woody species (Wright et al. 2004b). Here, the higher P_{area} at more arid sites was driven both by lower SLA and by higher P_{mass}.

Table 4 *F*-values and *P*-values for two-way ANOVA on the influence of site moisture class (wet or dry) and habit (mistletoe or host) on leaf functional traits

Trait	Source of variation	df	*F*	*P*
A_{area}	Site	1	117.96	< 0.001
	Habit	1	39.73	< 0.001
	Site*Habit	1	13.88	< 0.001
	Residuals	80		
N_{area}	Site	1	45.82	< 0.001
	Habit	1	10.688	< 0.001
	Site*Habit	1	0.644	0.425
	Residuals	80		
g_s	Site	1	28.05	< 0.001
	Habit	1	8.909	0.004
	Site*Habit	1	6.610	0.012
	Residuals	80		
$R_{d\text{-}area}$	Site	1	18.56	< 0.001
	Habit	1	4.44	0.038
	Site*Habit	1	2.175	0.144
	Residuals	80		
P_{area}	Site	1	45.53	< 0.001
	Habit	1	46.38	< 0.001
	Site*Habit	1	16.63	< 0.001
	Residuals	80		
SLA	Site	1	32.131	< 0.001
	Habit	1	36.943	< 0.001
	Site*Habit	1	0.101	0.752
	Residuals	80		
N_{mass}	Site	1	8.698	0.04
	Habit	1	0.004	0.953
	Site*Habit	1	0.225	0.676
	Residuals	80		
P_{mass}	Site	1	24.783	< 0.001
	Habit	1	26.911	< 0.001
	Site*Habit	1	6.855	0.011
	Residuals	80		

Leaf phosphorus is found in molecules such as ATP and NADPH. Generally speaking, higher leaf P enables a higher carboxylation capacity for a given leaf N (Reich et al. 2009; Ellsworth et al. 2015) and perhaps, simply for this reason, combining higher leaf P with higher leaf N_{area} could consist of an advantageous ecological strategy at more arid sites, where this would mean losing less water for a given rate of carbon gain. Indeed, there are reports of a role for leaf P in enhancing water use efficiency but, to our knowledge, no general mechanism has yet been established. For example, in *Quercus ilex* forest subjected experimentally to lower soil moisture, leaf P_{mass} increased, while P concentration in roots and stems decreased, suggesting that plants were mobilising P towards leaves, presumably to improve water use efficiency (Sardans and Peñuelas 2007). Similarly, in experiments with *Eucalyptus grandis* it has been shown that P fertilization enhances growth and water use efficiency for droughted seedlings (Graciano et al. 2005). Finally, in a recent global analysis, Maire et al. (2015) found that species from higher-P soils tended to have higher 'intrinsic' water use efficiency (the ratio of of A_{area} to g_s). This topic remains little understood but potentially of significant interest for Australia and Brazil where P is generally considered the most limiting soil nutrient, and where rainfall is low or seasonally restricted in many areas. Our results here serve to illustrate that high P_{area} in arid regions may be an even more general trend than previously suspected, found even in hemi-parasitic mistletoes.

Moreover, following the principle behind the N-parasitism hypothesis, if there is indeed some specific limiting nutrient driving the high transpiration rates in mistletoes leaves, in the systems we investigated it might be more sensible to consider P as this limiting resource, rather than N. This inference is not only based on the results we found here, but also previous results showed by Scalon and Wright (2015), where no general support was found for the N-parasitism globally, and from Scalon et al. (2016b), who suggested that N is not a limiting nutrient for Australian and Brazilian mistletoes, N not being resorbed from senescing leaves while, in contrast, P is generally resorbed.

High leaf respiration rates in mistletoes

In a previous study concerning several dozen woody perennials in Australia, Wright et al. (2001) showed that dry-site species had higher leaf respiration rates, both absolutely and at a given photosynthetic rate. This trend was later generalised to global scale (Wright et al. 2006; with some additional support from Atkin et al. 2015), and interpreted as reflecting the higher cost of "doing business" at arid, high irradiance sites. Mechanisms invoked included higher respiratory costs of repairing UV-related damage to photosystem II; production of protective pigments, such as xanthophyll; various costs associated with dealing with photoinhibition; and respiratory costs associated with maintaining solute gradients, which should be especially important at arid sites (Wright et al. 2006).

Actually, here we did not find any support for such a pattern (or interpretation), with mistletoes and hosts showing both lower $R_{d\text{-area}}$ and lower A_{area} at drier sites. Here the lower A_{area} at drier sites was clearly related to lower g_s, and presumably also a contribution from factors thought common in arid and semi-arid environments, e.g. higher leaf-internal CO_2 diffusion limitations, and down-regulation of photosynthesis by metabolic impairment (Flexas et al. 2004). In general, one would expect lower respiration rates to be paired with lower photosynthetic rates because major contributors to photosynthesis (and related processes) have significant respiration costs: e.g. continual turnover of photosynthesis-related proteins (most notably, but not only Rubisco), and phloem loading of photosynthates (Amthor 2000). Therefore, on this basis, our results (lower $R_{d\text{-area}}$ at drier sites) make sense; it is just the discrepancy with the results from Wright et al. (2001) and Wright et al. (2006) that we are unable to reconcile.

Putting site aridity aside, the other key result here was that mistletoes showed considerably higher $R_{d\text{-area}}$: A_{area} ratio, suggesting 2-fold higher maintenance costs at a given rate of carbon gain (indeed, mistletoes showed generally lower A_{area} but similar $R_{d\text{-area}}$ to their hosts; Table 3). Various studies have shown that mistletoes usually show lower photosynthetic rates compared to their hosts (Ehleringer et al. 1986; Marshall et al. 1994; Glatzel and Geils 2009). This lower A_{area} may be caused by differences in mesophyll structure (e.g. undifferentiated mesophyll decreasing mesophyll conductance; Stewart and Press (1990)), low chlorophyll concentration (Tuquet and Sallé 1996; Strong et al. 2000) and low Rubisco and photosystem II activity (Strong et al. 2000; Chen et al. 2013). However, less well understood is why mistletoes show such high respiration rates for a given photosynthetic capacity and, indeed, how such a strategy is even feasible; i.e., how it results in sufficient net carbon gain to support their growth.

Possible factors leading to higher $R_{d\text{-area}}$ at a given A_{area} include: (1) heterotrophy itself, there being energetic costs to using host-derived carbon, as for any carbon substrates (Amthor 2000); and (2) maintenance of large ion gradients between cellular compartments. Mistletoes have limited sinks and can accumulate disproportional amounts of some nutrients in their leaves. There are reports of disproportional hyperaccumulation of ions and heavy metals, such as potassium (Lamont and Southall 1982; Schulze et al. 1984; Scalon et al. 2013) and aluminium (Scalon et al. 2013). Indeed, dealing with nutrient imbalances might be one of the most substantial metabolic challenges for mistletoes. In addition, mistletoes need to maintain lower leaf water potentials than found in host leaves in order to maintain high transpiration rates. Popp et al. (1995) showed evidence that the higher leaf succulence of two African mistletoes species was an adaptation to keep ion concentration at a tolerable level. Moreover, it has been proposed that selective intake of nitrogen-containing compounds, such as polyols, proline, and glycine betaine may be an important advantage for the parasite (Tennakoon and Pate 1996; Frost et al. 2003) because these compounds act as osmoprotectants (i.e., protect the cell from the consequences of osmotic stress; Sakamoto and Murata (2002)). Therefore, mistletoes may need to find a balance between maintaining higher osmolarity, to guarantee lower water potential and the continuous flow of the host xylem, with the considerable costs associated with it.

Conclusions

In this study, we focused on adaptations to aridity in mistletoes and their host. Our results indicate that, even though mistletoes are profligate water users, they showed the same aridity-related shifts in leaf traits as their hosts, and with the same general magnitude. Perhaps in these systems the high transpiration rates of mistletoes can best be understood as driven by the need to obtain both carbon and phosphorous from their hosts, rather than nitrogen. That said, there is likely a trade-off between mistletoes maintaining higher osmolarity, to guarantee lower water potential and the continuous flow of the host xylem, with the considerable costs associated with it, resulting in notably high respiration rates for a given photosynthetic capacity. Finally, our findings address mistletoe and host adaptations along environmental gradients, delivering important new data of plant traits across the globe.

Acknowledgements MCS was supported by a scholarship from 'Conselho Nacional do desenvolvimento Cientifico e Tecnologico' (CNPq) and by Macquarie University. IJW acknowledges support from the Australian Research Council. We acknowledge Australian National Parks offices, RECOR/IBGE, Lindsay

Hutley and Augusto Cesar Franco for logistic support. We thank New South Wales and South Australia National Parks and Wildlife Services (license numbers SL100326 and M26025-1, respectively) for permits. We also thank Izabelly Sant'Ana, Allyson Eller, Julieta Garcia-Russell, Julia Cooke and Fabricius Domingos for the valuable help in the field.

Author contributions MCS and IJW conceived and designed the study. MCS conducted fieldwork, performed statistical analyses, and wrote the manuscript with help from IJW.

References

Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. Biophoton Int 11:36–43

Amthor JS (2000) The McCree-de wit-penning de Vries-Thornley respiration paradigms: 30 years later. Ann Bot 86:1–20

Anderson RM, May RM (1982) Coevolution of hosts and parasites. Parasitology 85(Pt 2):411–426

Aston MJ, Lawlor DW (1979) The relationship between transpiration, root water uptake, and leaf water potential. J Exp Bot 30:169–181

Atkin OK, Bruhn D, Hurry VM, Tjoelker MG (2005) The hot and the cold: unravelling the variable response of plant respiration to temperature. Funct Plant Biol 32:87–105

Atkin OK, Bloomfield KJ, Reich PB, Tjoelker MG, Asner GP, Bonal D, Bonisch G, Bradford MG, Cernusak LA, Cosio EG, Creek D, Crous KY, Domingues TF, Dukes JS, Egerton JJ, Evans JR, Farquhar GD, Fyllas NM, Gauthier PP, Gloor E, Gimeno TE, Griffin KL, Guerrieri R, Heskel MA, Huntingford C, Ishida FY, Kattge J, Lambers H, Liddell MJ, Lloyd J, Lusk CH, Martin RE, Maksimov AP, Maximov TC, Malhi Y, Medlyn BE, Meir P, Mercado LM, Mirotchnick N, Ng D, Niinemets U, O'Sullivan OS, Phillips OL, Poorter L, Poot P, Prentice IC, Salinas N, Rowland LM, Ryan MG, Sitch S, Slot M, Smith NG, Turnbull MH, VanderWel MC, Valladares F, Veneklaas EJ, Weerasinghe LK, Wirth C, Wright IJ, Wythers KR, Xiang J, Xiang S, Zaragoza-Castells J (2015) Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. New Phytol 206:614–636

Bowie M, Ward D (2004) Water and nutrient status of the mistletoe Plicosepalus acaciae parasitic on isolated Negev Desert populations of Acacia Raddiana differing in level of mortality. J Arid Environ 56:487–508

Chen L, Huang L, Li X, You S, Yang S, Zhang Y, Wang W (2013) Water and nutrient relationships between a mistletoe and its mangrove host under saline conditions. Funct Plant Biol 40: 475–483

Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment: stomatal function in the regulation of gas exchange. In: Jennings DH (ed) Symposium of the Society of Experimental Botany. Cambridge University Press, Cambridge, pp. 471–505

Cunningham SA, Summerhayes B, Westoby M (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecol Monogr 69:569–588

Eamus D, Prior L (2001) Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. Adv Ecol Res 32: 113–197

Eamus D, Myers B, Duff G, Williams D (1999) Seasonal changes in photosynthesis of eight savanna tree species. Tree Physiol 19:665–671

Ehleringer JR, Cook CS, Tieszen LL (1986) Comparative water use and nitrogen relationships in a mistletoe and its host. Oecologia 68:279–284

Eiten G (1972) The cerrado vegetation of Brazil. Bot Rev 38:201–341

Ellsworth DS, Crous KY, Lambers H, Cooke J (2015) Phosphorus recycling in photorespiration maintains high photosynthetic capacity in woody species. Plant Cell Environ 38:1142–1156

Escher P, Peuke AD, Bannister P, Fink S, Hartung W, Jiang F, Rennenberg H (2008) Transpiration, CO_2 assimilation, WUE, and stomatal aperture in leaves of *Viscum album* (L.): effect of abscisic acid (ABA) in the xylem sap of its host (*Populus euamericana*). Plant Physiol Biochem 46:64–70

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Biol 40: 503–537

Flexas J, Bota J, Cifre J, Escalona MJ, Galmés J, Gulías J, Lefi EK, Martínez-Cañellas FS, Moreno TM, Ribas-Carbó M (2004) Understanding down-regulation of photosynthesis under water stress: future prospects and searching for physiological tools for irrigation management. Ann Appl Biol 144:273–283

Frost A, Lopez-Gutierrez JC, Purrington CB (2003) Fitness of *Cuscuta salina* (Convolvulaceae) parasitizing *Beta vulgaris* (Chenopodiaceae) grown under different salinity regimes. Am J Bot 90:1032–1037

Givnish TJ (1986) Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp. 25–55

Glatzel G, Geils BW (2009) Mistletoe ecophysiology: host–parasite interactions. Botany 87:10–15

Graciano C, Guiamét JJ, Goya JF (2005) Impact of nitrogen and phosphorus fertilization on drought responses in *Eucalyptus grandis* seedlings. Forest Ecoly Manag 212:40–49

Hsiao TC (1973) Plant responses to water stress. Annu Rev Plant Biol 24:519–570

Hutley L, O'grady A, Eamus D (2000) Evapotranspiration from eucalypt open-forest savanna of northern Australia. Funct Ecol 14:183–194

Ihl B, Jacob F, Meyer A, Sembdner G (1987) Investigations on the endogenous levels of abscisic acid in a range of parasitic phanerogams. J Plant Growth Regul 5:191–205

Lamont BB, Southall KJ (1982) Distribution of mineral nutrients between the mistletoe, *Amyema preissii*, and its host, *Acacia acuminata*. Ann Bot 49:721–725

Maire V, Wright IJ, Prentice IC, Batjes NH, Bhaskar R, van Bodegom PM, Cornwell WK, Ellsworth D, Niinemets Ü, Ordonez A, Reich PB, Santiago LS (2015) Global effects of soil and climate on leaf photosynthetic traits and rates. Glob Ecol Biogeogr 24:706–717

Marshall JD, Ehleringer JR (1990) Are xylem-tapping mistletoes partially heterotrophic? Oecologia 84:244–248

Marshall J, Ehleringer J, Schulze ED, Farquhar G (1994) Carbon isotope composition, gas exchange and heterotrophy in Australian mistletoes. Funct Ecol 8:237–241

Medlyn BE, Duursma RA, Eamus D, Ellsworth DS, Prentice IC, Barton CVM, Crous KY, de Angelis P, Freeman M, Wingate L (2011) Reconciling the optimal and empirical approaches to modelling stomatal conductance. Glob Chang Biol 17: 2134–2144

Nardini A, Gullo MA, Salleo S (2011) Refilling embolized xylem conduits: is it a matter of phloem unloading? Plant Sci 180: 604–611

Nardini A, Pedà G, Rocca NL (2012) Trade-offs between leaf hydraulic capacity and drought vulnerability: morpho-anatomical bases, carbon costs and ecological consequences. New Phytol 196:788–798

New M, Lister D, Hulme M, Makin I (2002) A high-resolution data set of surface climate over global land areas. Clim Res 21:1–25

Niinemets Ü (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82:453–469

NPWS (1998) Whyalla Conservation Park management plan. In: SADoEaN Resources (ed) . Department For Environment, Heritage & Aboriginal Affairs, Whyalla

NPWS (2002) Ku-ring-gai Chase National Park and Lion Island, Long Island and Spectacle Island Nature Reserves. Office of Environment and Heritage

NPWS (2005) Gundabooka National Park and Gundabooka state conservation area plan of management. In: DoEa Conservation (ed) . NSW National Parks and Wildlife Service, Sydney

O'Grady AP, Eamus D, Hutley LB (1999) Transpiration increases during the dry season: patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiol 19:591–597

Oliveira-Filho ATD, Shepherd GJ, Martins FR, Stubblebine WH (1989) Environmental factors affecting physiognomic and floristic variation in an area of cerrado in Central Brazil. J Trop Ecol 5:413–431

Onoda Y, Westoby M, Adler PB, Choong AMF, Clissold FJ, Cornelissen JHC, Diaz S, Dominy NJ, Elgart A, Enrico L et al (2011) Global patterns of leaf mechanical properties. Ecol Lett 14:301–312

Popp M, Mensen R, Richter A, Buschmann H, Willert DJ (1995) Solutes and succulence in southern African mistletoes. Trees-Struct Funct 9:303–310

Prentice IC, Meng T, Wang H, Harrison SP, Ni J, Wang G (2011) Evidence of a universal scaling relationship for leaf CO2 drawdown along an aridity gradient. New Phytol 190:169–180

Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ (2014) Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. Ecol Lett 17:82–91

R Development Core Team (2008) R: A language and environment for statistical computing. In: RFfS Computing (ed) Vienna

Reich PB, Oleksyn J, Wright IJ (2009) Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. Oecologia 160:207–212

Russell BJ, Letnic M, Fleming PJS (2011) Managing feral goat impacts by manipulating their access to water in the rangelands. Rangel J 33(2):143

Sakamoto A, Murata N (2002) The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. Plant Cell Environ 25:163–171

Sardans J, Peñuelas J (2007) Drought changes phosphorus and potassium accumulation patterns in an evergreen Mediterranean forest. Funct Ecol 21:191–201

Scalon MC, Wright IJ (2015) A global analysis of water and nitrogen relationship between mistletoes and their hosts: broad-scale tests of old and enduring hypotheses. Funct Ecol 29:1114–1124

Scalon M, Haridasan M, Franco A (2013) A comparative study of aluminium and nutrient concentrations in mistletoes on aluminium-accumulating and non-accumulating hosts. Plant Biol 15:851–857

Scalon M, Rossatto D, Domingos F, Franco A (2016a) Leaf morphophysiology of a Neotropical mistletoe is shaped by seasonal patterns of host leaf phenology. Oecologia 180: 1103–1112

Scalon MC, Wright IJ, Franco AC (2016b) To recycle or steal? Nutrient resorption in Australian and Brazilian mistletoes from three low-phosphorus sites. Oikos. doi:10.1111/oik.03455

Schulze ED, Turner N, Glatzel G (1984) Carbon, water and nutrient relations of two mistletoes and their hosts: a hypothesis*. Plant Cell Environ 7:293–299

Stewart GR, Press MC (1990) The physiology and biochemistry of parasitic angiosperms. Annu Rev Plant Biol 41:127–151

Strong GL, Bannister P, Burritt D (2000) Are mistletoes shade plants? CO_2 assimilation and chlorophyll fluorescence of temperate mistletoes and their hosts. Ann Bot 85:511–519

Tennakoon K, Pate J (1996) Effects of parasitism by a mistletoe on the structure and functioning of branches of its host. Plant Cell Environ 19:517–528

Tozer M, Turner K, Simpson C, Keith D, Beukers P, MacKenzie B, Tindall D, Pennay C (2010) Native vegetation of southeast NSW: a revised classification and map for the coast and eastern tablelands. Royal Botanic Gardens, Sydney, National Herbarium of New South Wales.

Tuquet C, Sallé G (1996) Characteristics of chloroplasts isolated from two mistletoes originating from temperate (*Viscum album*) and tropical (*Tapinanthus dodoneifolius*) areas. Plant Physiol Biochem 34:283–292

Ullmann I, Lange O, Ziegler H, Ehleringer J, Schulze ED, Cowan I (1985) Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia. Oecologia 67:577–587

Wang H, Prentice I, Ni J (2012) Primary production in forests and grasslands of China: contrasting environmental responses of light-and water-use efficiency models. Biogeosci Discuss 9: 4285–4321

Warton DI, Duursma RA, Falster DS, Taskinen S (2012) Smatr 3– an R package for estimation and inference about allometric lines. Methods Ecol Evol 3:257–259

Wright IJ, Reich PB, Westoby M (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Funct Ecol 15:423–434

Wright IJ, Reich PB, Westoby M (2003) Least-cost input mixtures of water and nitrogen for photosynthesis. Am Nat 161:98–111

Wright IJ, Groom PK, Lamont BB, Poot P, Prior LD, Reich PB, Schulze ED, Veneklaas EJ, Westoby M (2004a) Leaf trait relationships in Australian plant species. Funct Plant Biol 31: 551–558

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M (2004b) The worldwide leaf economics spectrum. Nature 428:821–827

Wright IJ, Reich PB, Cornelissen JH, Falster DS, Groom PK, Hikosaka K, Lee W, Lusk CH, Niinemets Ü, Oleksyn J (2005) Modulation of leaf economic traits and trait relationships by climate. Glob Ecol Biogeogr 14:411–421

Wright IJ, Reich PB, Atkin OK, Lusk CH, Tjoelker MG, Westoby M (2006) Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites. New Phytol 169:309–319