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RESEARCH PAPER

A comparative study of aluminium and nutrient concentrations in mistletoes on aluminium-accumulating and non-accumulating hosts

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ABSTRACT

Mistletoes offer a unique model to study interactions among Al and nutrients in vascular plants, because they grow and reproduce on hosts with distinct Al uptake strategies. We investigated Al distribution and nutrient relations of mistletoes on Al-accumulating and non-accumulating hosts. We hypothesised that mistletoes would exhibit similar leaf nutrient and Al concentrations as their host plants, but a strong compartmentalisation of Al when growing on Al-accumulators. We measured concentrations of N, P, K, Ca, Mg, Cu, Fe, Mn, Zn in leaves and Al in leaves, seeds and branches of *Phthirusa ovata* and *Psittacanthus robustus* infecting *Miconia albicans*, an Al-accumulator, and *Ph. ovata* infecting *Byrsonima verbascifolia*, a non-Al-accumulator. High leaf concentrations of Al in *Ph. ovata* only occurred while parasitizing the Al-accumulating host; there was no accumulation in branches or seeds. In *P. robustus*, large concentrations of Al were found in leaves, branches and seeds. Mistletoe seed viability and leaf nutrient concentrations were not affected by Al accumulation. Passive uptake of Al, Ca, Mg, Mn and Cu in mistletoes was evidenced by significant correlations between mistletoes and host leaf concentrations, but not of N, P and K. Al was retranslocated to different plant organs in *P. robustus*, whereas it was mostly restricted to leaves in *Ph. ovata*. We suggest that Al might have some specific function in *P. robustus*, which only parasitizes Al-accumulator hosts, while the host generalist *Ph. ovata* can be considered a facultative Al-accumulator.

INTRODUCTION

Mistletoes are plants that grow on branches of trees or shrubs, establishing a connection with the host plant xylem to take up water and nutrients (Kuijt 1969; Tennakoon & Pate 1996). This connection occurs through a modified root, known as a haustorium (Nickrent 2002), which is capable of penetrating and transferring solutes from the host xylem to the parasite xylem (Riopel & Timko 1995; Calvin & Wilson 2006). In this context, to grow and reproduce, mistletoes have to not only successfully compete for part of the water and nutrients absorbed by the host but also, in many cases, be able to tolerate large differences in chemical composition of the xylem sap of different hosts (Glatzel & Geils 2008). This tolerance can be particularly critical in the savannas of central Brazil, locally known as cerrados, where a large number of potential host trees are Al-accumulators (Haridasan 1987).

Mistletoes often parasitize a variety of Al-accumulating and non-accumulating hosts (Monteiro *et al.* 1992; Cazetta & Galetti 2007), which naturally subject them to xylem saps of very contrasting Al and nutrient concentrations, and offer a unique model to study the effects of Al on absorption of other nutrients in vascular plants. Lüttge *et al.* (1998) reported that the mistletoe *Phthirusa ovata* (Pohl) Eichler maintained high Al concentrations in its leaves only when attached to an Al-accumulating host, but not when attached to a non-accumulating host. High Al concentrations did not affect absorption of other nutrients or photosynthetic functions. However, they did not report any data on Al retranslocation to other organs from the leaves or make any comparison with other mistletoes that occur only on Al-accumulating host trees.

The majority of Al-accumulating plants occur in the humid tropics or in tropical savannas, where the soils are acidic and availability of Al is high (Haridasan 1982; Jansen *et al.* 2003a, b). Haridasan (1982) reported that the accumulation of Al did not hinder the absorption of other essential nutrients by savanna plants, and this seems to be the pattern on a global scale (Metali *et al.* 2011). Moreover, some species from the cerrados were shown to have normal development only in Al-rich soils (Haridasan 1988, 2008). *Miconia albicans* (Sw.) Triana (Melastomataceae) exhibited nutritional deficiency symptoms (chlorotic leaves and abnormal development) while growing on a soil with no available Al (Haridasan 1988). When these plants were transplanted to an acidic soil, the seedlings recovered their normal development, and the unique difference from the previous situation was the increase in Al leaf concentration; thus suggesting the possibility that Al plays an essential role in some specific metabolic function still to be described. In a recent report, Andrade *et al.* (2011) showed that the processes of storage of Al in leaf tissues differ among species of Vochysiaceae.

The aim of this study was to investigate the patterns of Al distribution and nutrient relations of mistletoes on Al-accumulating and non-accumulating hosts. Because mistletoes are directly connected to the xylem of the host, we predicted that mistletoes would exhibit similar leaf nutrient and Al concentrations to the host plants. For mistletoes growing on Al-accumulating hosts, we expected a strong compartmentalisation of Al in leaf tissues and lack of Al translocation to the phloem as a strategy to deal with high amounts of Al from the host xylem.

MATERIAL AND METHODS

The study was conducted in the Natural Reserve of the Roncador belonging to the Brazilian Institute of Geography and Statistics (RECOR/IBGE), located 35 km south of Brasília in the Federal District of Brazil (15º56′41′ S, 47º53′07′ W). The study site represents the most common physiognomy found in the cerrado region, known as cerrado *sensu stricto*, a seasonal savanna with a relatively continuous layer of perennial grasses and a discontinuous layer of trees and shrubs. The soil of the area is a deep, well-drained, strongly acid dystrophic latosol (pH around 4.2), with high aluminium (Al^{3+}) saturation (see Bucci *et al.* 2006 for a more detailed soil description). The climate of the region is tropical, classified as Aw according to Köppen's classification.

We sampled leaves and branches of nine individuals of the mistletoe *Phthirusa ovata* (Loranthaceae), five of them parasitizing *Miconia albicans* (Melastomataceae), an Al-accumulator species, and four parasitizing *Byrsonima verbascifolia* (L.) Rich. ex A. L. Juss. (Malphighiaceae), a non-Al-accumulating species. We also sampled five individuals of another mistletoe, *Psittacanthus robustus* Mart. (Loranthaceae), parasitizing *Miconia albicans*. We did not find any *P. robustus* parasitizing any non-Al-accumulating species. We collected three fully expanded leaves and three branches of each individual of mistletoe and its host during the rainy season, between December 2008 and January 2009. For hosts, we used leaves from healthy, non-infected branches. All individuals of mistletoes and hosts were at the mature stage, and host trunks had similar diameters at 30 cm above ground. Mistletoes did not differ in number of leaves within the same hosts (data not shown). We also collected seeds from six *Ph. ovata* parasitizing *M. albicans* (Melastomataceae), six parasitizing *B. verbascifolia* and six *P. robustus* (Loranthaceae) parasitizing *M. albicans*. Because not all mistletoes flowered within a single year, seeds were collected in January 2009 and January 2010.

All samples were oven dried and ground in a Wiley mill. Nitrogen (N) was determined by micro-Kjeldahl digestion and distillation (Allen 1974). Leaf concentrations of P, K, Ca, Mg, Mn, Cu, Zn, Fe and leaf, branch and seed concentrations of Al were determined after wet digestion with a tri-acid mixture of nitric, sulphuric and perchloric acid (10:1:2). Phosphorus was determined by colorimetry and the other nutrients by atomic absorption or emission spectrophotometry.

To assess the viability of mistletoe seeds, we performed a tetrazolium test for each host–mistletoe pair. In all cases, 10 seeds of each individual mistletoe plant were placed in a 1% triphenyltetrazolium chloride (TTC) solution and incubated in the dark at 25°C for 24 h. Seeds were recorded as viable when embryos were homogeneously stained (*i.e.* both radicle and cotyledons).

We used an LC*i* portable photosynthesis system (ADC BioScientific Ltd., Hoddesden, Herts, UK) to measure maximum photosynthetic rates in the same mistletoes that were sampled for Al and nutrient analyses. The leaf cuvette was fitted with a halogen dichroic lamp that delivered a photosynthetic photon flux density of 1260 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the leaf surface, which was sufficient to saturate photosynthesis in these plants. Measurements were taken in January 2009, at the peak of the wet season.

The software R version 2.3 (R Development Core Team 2005) was used for statistical analyses of the data. Normality was tested with the Shapiro–Wilk test, which is appropriate for small sample sizes. We compared the treatment means with analysis of variance (ANOVA) and performed *post-hoc* Tukey tests, assuming differences to be significant at $P < 0.05$. Pearson correlations were used to assess bivariate relationships, using data from each individual (n = 14).

RESULTS

Phthirusa ovata growing on the non Al-accumulating host *B. verbascifolia* did not have high concentrations of Al in the leaves. In contrast, leaf Al concentrations in both mistletoes growing on the Al-accumulating host *M. albicans* were above 1,000 $mg \cdot kg^{-1}$ (Table 1). The two mistletoes exhibited contrasting patterns of Al retranslocation to other plant organs when they were attached to Al-accumulating hosts. High Al concentrations were present in leaves, but not in branches or seeds of *Ph. ovata*, while high Al concentrations were present in all organs of *P. robustus* (Table 1).

Maximum photosynthetic rates and seed viability of the two mistletoes were not affected by leaf Al accumulation. *Ph. ovata* showed similar photosynthetic rates when growing on both hosts (mean ± SD on *B. verbascifolia*: 8.73 ± 5.01 $\mu mol\ m^{-2}\ s^{-1}$; on *M. albicans*: 8.43 ± 3.58 $\mu mol\ m^{-2}\ s^{-1}$; $P > 0.05$). There was also no difference in photosynthetic rates between the two mistletoe species growing on the same host (*P. robustus* on *M. albicans*: 7.06 ± 1.57 $\mu mol\ m^{-2}\ s^{-1}$; $P > 0.05$). Seeds of *Ph. ovata* had viability of 90–100% on *M. albicans* hosts and 80–100% on *B. verbascifolia* hosts, as determined with the tetrazolium test. Seed viability of *P. robustus* on *M. albicans* ranged from 80–100%.

Mistletoes had higher leaf K concentrations than hosts, but hosts and mistletoes did not differ in leaf N, Ca, Mg, Al and Mn concentration (Fig. 1). Differences between host and

Table 1. Al concentrations (mg kg^{-1}) in leaves, branches and seeds of mistletoes on Al-accumulator host (*Miconia albicans*) and non-accumulator host (*Byrsonima verbascifolia*). Data as mean ± SD.

organ	*Phthirusa ovata* on *Miconia albicans* (n)	*Psittacanthus robustus* on *Miconia albicans* (n)	*Phthirusa ovata* on *Byrsonima verbascifolia* (n)
leaf	10869 ± 7014 (5)	8679 ± 2208 (5)	260 ± 27 (4)
branch	156 ± 44 (5)	2173 ± 616 (5)	132 ± 23 (4)
seed	127 ± 19 (6)	2878 ± 946 (6)	122 ± 37 (6)

mistletoes for other nutrients were more pronounced when the Al accumulator *M. albicans* was the host plant. Both mistletoes presented higher leaf Cu but lower Fe concentrations than *M. albicans*, while *P. robustus* had lower leaf Zn and *Ph. ovata* higher leaf P concentrations than *M. albicans* (Fig. 1). Leaf Ca concentrations were higher in *Ph. ovata* attached to *B. verbascifolia* than to *M. albicans* (ANOVA: F = 5.60; $P < 0.05$).

We found significant positive correlations between mistletoes and hosts for Ca, Mg, Mn and Al, and a negative correlation for Cu (Fig. 2). Relationships were not significant for N, P, K, Fe and Zn. There was a significant correlation between Ca and Mg for mistletoes ($R^2 = 0.72$; $P < 0.05$, n = 14) and hosts ($R^2 = 0.66$; $P < 0.05$, n = 14; Fig. 3). The slopes of the two correlation lines were not significantly different (t = 1.18, $P = 0.25$). The relationship between leaf P and N concentrations was significant for the hosts ($R^2 = 0.52$; $P < 0.05$, n = 14) but not for the mistletoes (Fig. 4).

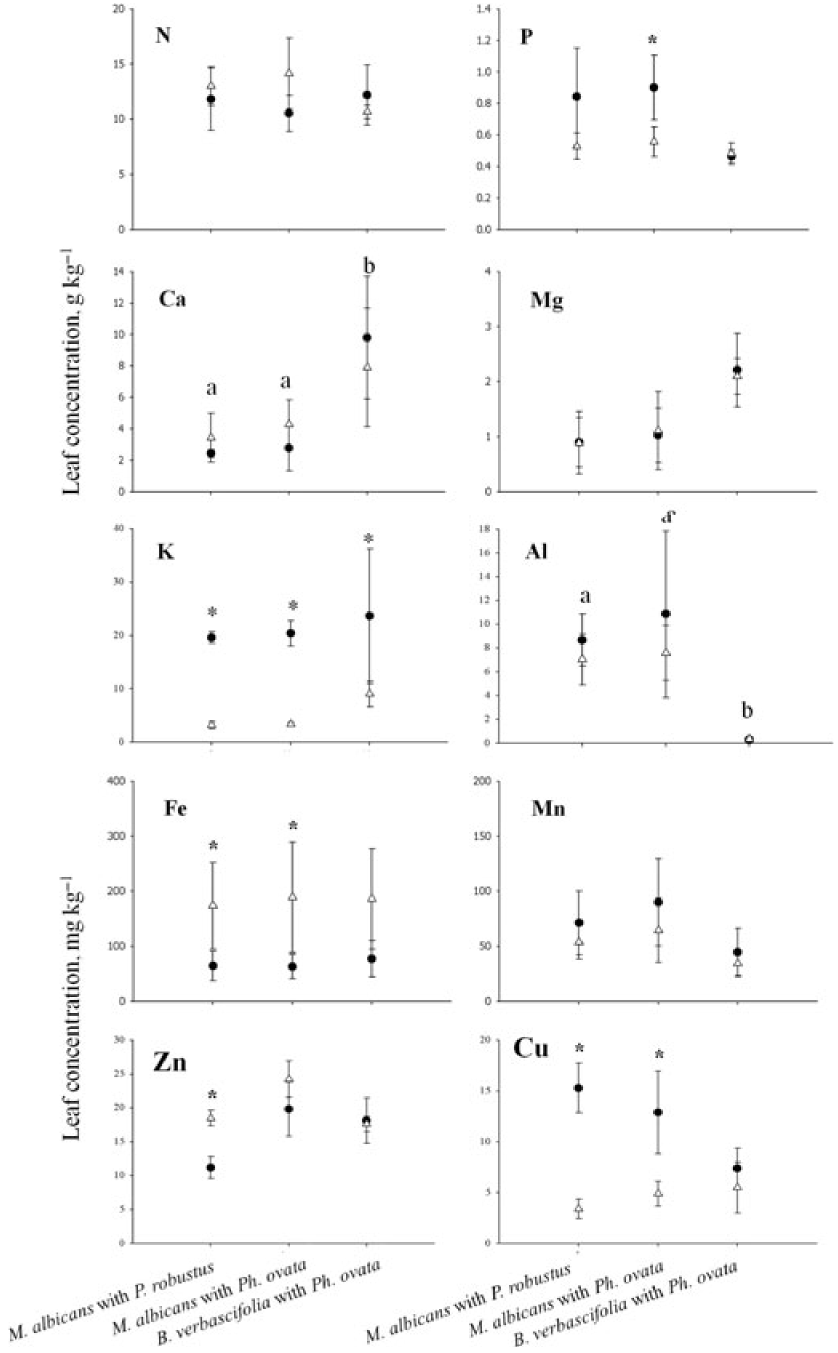

Fig. 1. Leaf concentrations (mean ± SD) of nutrients and Al in mistletoes (closed circles) and associated hosts (open triangles) in a cerrado in central Brazil. Different letters indicate significant differences among mistletoes, while asterisks indicate significant differences between the host and the associated mistletoe. (Tukey's test: $P < 0.05$).

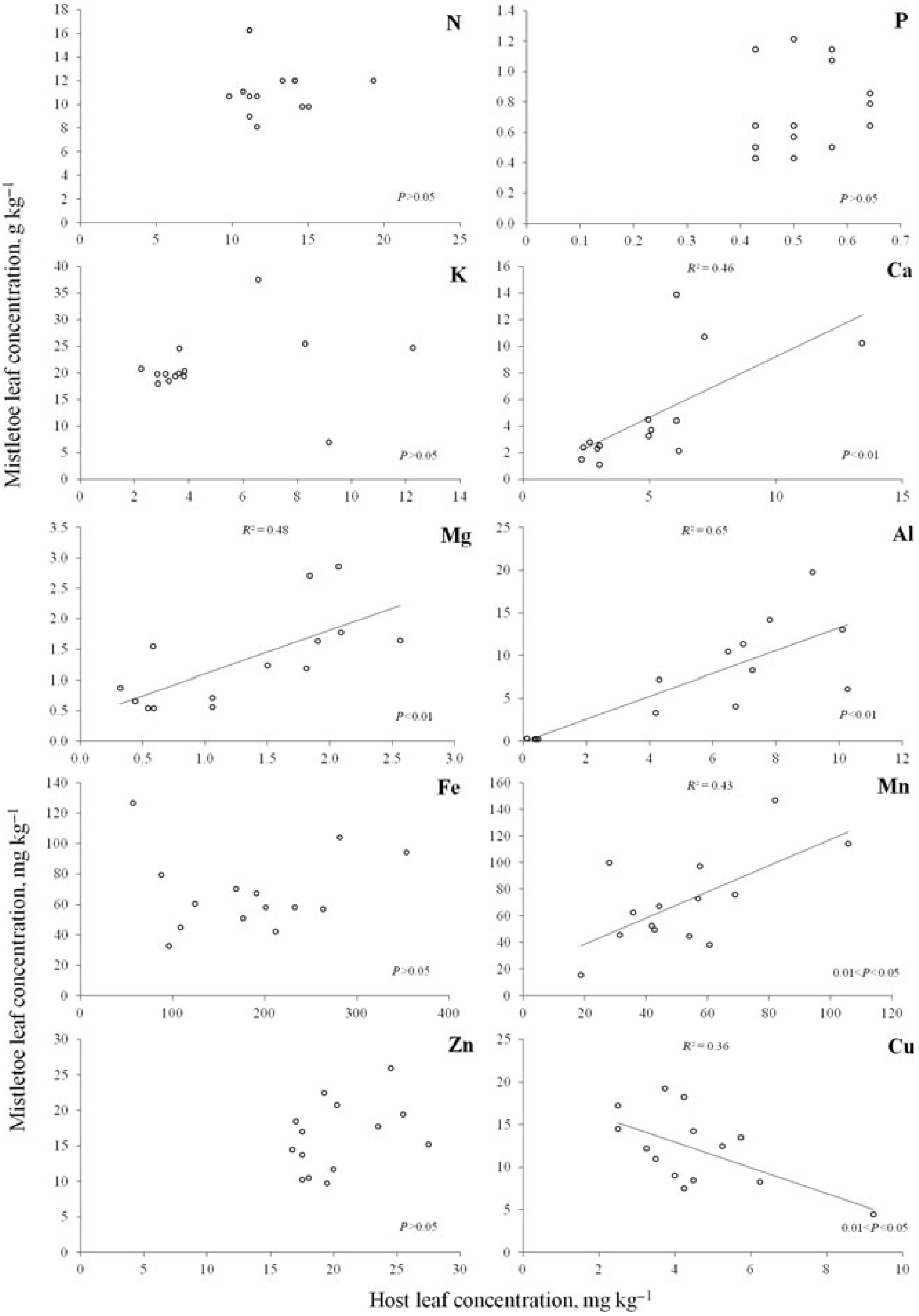

Fig. 2. Correlations between leaf concentrations of nutrients and Al in mistletoes and hosts in a cerrado in central Brazil. Each point corresponds to one mistletoe–host pair, n = 14.

DISCUSSION

Aluminium was found in high concentrations in leaves of *M. albicans*, and in the attached mistletoe parasites (Table 1). On the other hand, *Ph. ovata* growing on *B. verbascifolia* had negligible leaf Al concentrations, confirming earlier observations of Lüttge *et al.* (1998) that mistletoes present high concentrations of this element only on Al-accumulating hosts.

We cannot assert that the differences in leaf concentrations of some nutrients among *Ph. ovata* growing on Al-accumulating

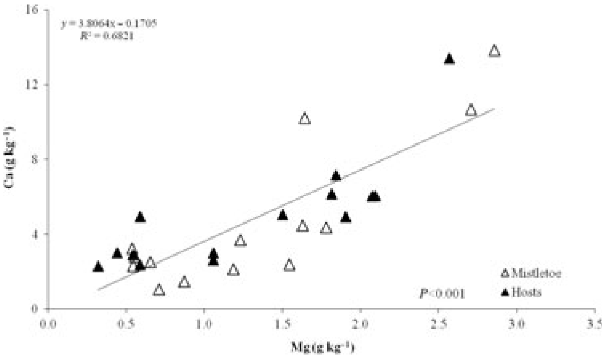

Fig. 3. Correlation between leaf concentrations of Ca and Mg in mistletoes (open triangles, $R^2 = 0.72$, $P < 0.05$) and hosts (closed triangles, $R^2 = 0.66$, $P < 0.05$) in a cerrado in central Brazil. Because the slopes of the regression lines were not significantly different ($t = 1.18$, $P = 0.25$), a single regression line was fitted to the data. Each point corresponds to one individual, n = 14 for hosts and mistletoes.

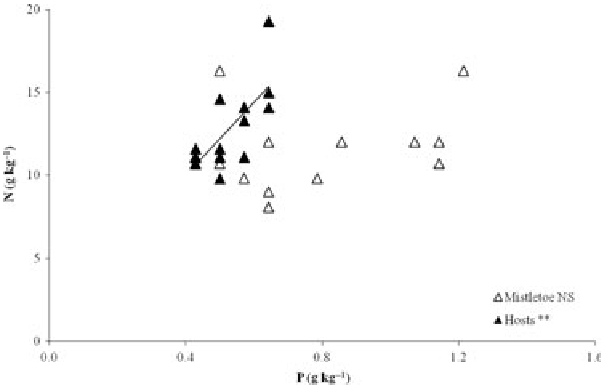

Fig. 4. Correlation between leaf concentrations of N and P in mistletoes (open triangles, not significant) and hosts (closed triangles, $R^2 = 0.52$, $P < 0.01$) in a cerrado in central Brazil. Each point corresponds to one individual, n = 14 for hosts and mistletoes.

and non-accumulating hosts, such as higher foliar concentrations of Ca and Mg on the non-accumulating host, are associated with contrasting concentrations of Al in the leaves. This probably reflects differences in foliar nutrient concentrations of the two hosts, given the significant positive correlations between mistletoes and hosts for Ca and Mg (Fig. 3). However, *Ph. ovata* maintained similar photosynthetic rates when growing on both hosts, suggesting that the presence of Al stored in the leaves did not affect individual productivity.

The fact that *Ph. ovata* did not have much Al in its seeds or branches indicates that Al was not retranslocated from the leaves to other organs through the phloem. This is consistent with Al immobilisation mechanisms *via* compartmentalisation in the leaves (Ma *et al.* 2001; Watanabe & Osaki 2002). While Al was mostly restricted to the leaves in *P. ovata*, Al did accumulate in leaves, branches and seeds of *P. robustus*. There is considerable interspecific variability in Al tolerance (Ma *et al.* 2001), and even within different genotypes of the same species (Delhaize & Ryan 1995). These contrasting Al distribution patterns between *Ph. ovata* and *P. robustus* strongly suggest interspecific variability in Al tolerance among different plant tissues and within the same tissue in different Al-accumulating mistletoes.

Despite high Al concentrations, seeds of *P. robustus* were viable. A fundamental difference between the two mistletoe species studied is that *P. robustus* has been reported to be a relatively specific parasite of Vochysiaceae (Monteiro *et al.* 1992), which is known to be a family of Al-accumulating species, but is also found in Melastomataceae hosts (another Al- accumulating taxon), as described here. *Ph. ovata*, on the other hand, seems to be a more generalist parasite, found on host plants belonging to many different families. In the study site, we found it parasitizing seven species from seven different families: *Styrax ferrugineus* (Styracaceae), *Dalbergia miscolobium* (Fabaceae), *Kielmeyera coriacea* (Clusiaceae), *Erythroxylum suberosum*, (Erythroxylaceae), *Qualea grandiflora* (Vochysiaceae), *Miconia albicans* (Melastomataceae) and *Byrsonima verbascifolia* (Malpighiaceae). The absence of Al in seeds of *P. ovata* growing on Al-accumulating host plants could be a strategy to guarantee the germination and survival of such seeds on non-Al-accumulating hosts, as well as on Al-accumulating hosts (personal communication, Bruna Locardi).

This study also shows, for the first time, that Al accumulation by the host could be involved in host selection by mistletoes. It is probable that *P. robustus*, like the previously investigated Al-accumulating host plant *M. albicans* (Haridasan 1988), could be dependent on this element for normal development. In this context, the exclusive preference for Vochysiaceae and Melastomataceae hosts might occur not only because of the habit of the disperser agent, as suggested in Monteiro *et al.* (1992), but also because *P. robustus* requires high concentrations of Al, which would be available through tapping the xylem of these Al-accumulating plants. In a recent study, Teodoro *et al.* (2010) found that 29.6% of the *Vochysia thyrsoidea* population (the main host in their study site) was infected with *P. robustus*. We suggest that Al may play an essential role for *P. robustus* and this can explain their preference for Al-accumulating Vochysiaceae and Melastomataceae hosts, whose species are known to be highly abundant and widespread within the cerrado region (Ratter *et al.* 2003; Haridasan 2008). From this perspective, we have enough evidence to consider *P. robustus* as an obligate Al-accumulating mistletoe, whereas *Ph. ovata* should be considered a facultative Al-accumulator. This is the first report of an obligate Al-accumulating hemiparasite in the Loranthaceae family.

It is usually accepted that mistletoes have higher leaf N concentrations than the host plants (Glatzel 1983; Lamont 1983; Ehleringer *et al.* 1985; El Sharkawy *et al.* 1986; Panvini & Eickmeier 1993). However, in this study we found no differences between hosts and mistletoes in N leaf concentration, and a number of other studies have reported leaf N concentrations of parasitic plants that were similar or even lower than their respective host (Lamont & Southall 1982; Küppers *et al.* 1992; Bannister *et al.* 2002; Bowie & Ward 2004; Burns *et al.* 2011). Higher leaf N concentrations than the host might make mistletoe leaves more attractive to herbivores (Marvier 1995; Kyto *et al.* 1996) and lead to a decrease in their fitness. Mistletoes could therefore benefit from down-regulating the amount of N in their leaves to avoid higher rates of herbivory. One suggestion is that they could exclude N by not recycling it *via* retranslocation from older leaves. This is supported in reports that mistletoes do not show evidence of pre-senescence retrieval of nutrients (Pate *et al.* 1991), and that they produced N-enriched litter (March & Watson 2007).

In contrast to N, there was a clear trend for higher leaf P in mistletoes growing on *M. albicans,* but not on *B. verbascifolia*. The lack of correlation between N and P in leaf tissues of both species of mistletoe on all hosts suggests an imbalance between these two nutrients (Garten 1976), while parasitized hosts were able to maintain the balance between N and P, as evidenced by the significant positive correlation between leaf N and P for host plants (Fig. 4). Because mistletoes are directly connected to the xylem of the host, integrated anatomical and physiological studies of the xylem connection in mistletoe–host pairs with contrasting leaf N and P concentrations, and of mistletoe N and P balance are necessary to better understand N and P relations of mistletoes and associated hosts.

There were no differences between mistletoes and their hosts for leaf Ca, Mg, Mn and Al. Bannister *et al.* (2002) also found no difference in Ca and Mg foliar concentrations among New Zealand mistletoes and their hosts. The significant correlation between mistletoes and hosts for leaf Ca concentrations is consistent with the fact that Ca is passively transported through the xylem and is mostly immobile in the phloem (Marschner 1974). If nutrient flux to the mistletoes is exclusively passively driven by transpiration, an immobile ion, like Ca, should be found in similar proportions in the mistletoes and in tissues of the hosts. In fact, many studies have shown that mistletoes have similar Ca levels to their hosts (Glatzel 1983; Goldstein *et al.* 1989; Pate *et al.* 1989), as found in the present study, even though mistletoes generally maintain higher transpiration rates than the associated host (Ullmann *et al.* 1985; Stewart & Press 1990; Pennings & Callaway 2002). The other nutrients that showed correlations between mistletoes and hosts, with the exception of Mg, are considered to have medium mobility (Mn, Cu and Al), which could explain the pattern being similar to that of Ca. On the other hand, Mg is related metabolically to Ca, which could explain this correlation despite the higher mobility of this ion in the phloem. This aspect is supported by the positive correlation between Ca and Mg for both mistletoes and hosts (Fig. 3).

On both hosts, mistletoes had higher leaf K concentrations than their hosts. It is common to find higher K concentrations in mistletoe leaves (Lamont & Southall 1982; Schulze *et al.* 1984; Glatzel & Geils 2008). This pattern is probably an inevitable consequence of the lack of connections between the phloem of the mistletoe and the host. In other words, this occurs because of the impossibility of mobile ions being retranslocated to the phloem of the host and, as a result, highly mobile ions tend to accumulate in leaf tissues of the mistletoe (Glatzel 1983; Glatzel & Geils 2008).

Although passive Al uptake occurred in both hemiparasites growing on Al-accumulating hosts, this element is probably immobilised in the leaf tissue in *Ph. ovata,* while it is retranslocated to different plant organs in *P. robustus.* The significant correlation between parasite and host in leaf concentrations of Ca, Mg, Mn, Cu and Al, but not N, P and K, suggests passive nutrient uptake from hosts by mistletoes for the former group of elements; more complex uptake mechanisms are more likely for the latter group. Leaf N and P were correlated in hosts but not in mistletoes, suggesting some nutritional imbalance of these two nutrients in hemiparasitic plants.

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