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The contribution of mistletoes to nutrient returns: Evidence for a critical role in nutrient cycling

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Abstract Both nutrient cycling and nutrient relationships between mistletoe and host have been widely studied; yet it is unclear whether high nutrient concentrations commonly found in mistletoes affect rates of nutrient cycling. To address this question, we assessed 13 elements in the litter of a temperate eucalypt forest in southern New South Wales, comparing concentrations from trees (*Eucalyptus blakelyi*, *E. dwyeri*, and *E. dealbata*) with and without the hemiparasitic mistletoe *Amyema miquelii*. Results were in accord with previous research on fresh leaves showing that concentrations of many elements were higher in the mistletoe than the host. This was not the case for all elements; most notably for N, where concentrations were significantly lower in the mistletoe. However, the return of all elements increased with mistletoe infection because of the combined effect of enrichment in mistletoe tissues and high rates of mistletoe litterfall. Annual returns of N and P in leaf litter increased by a factor of 1.65 and 3 respectively, with the greatest increase being for K by a factor of 43 in spring. These increased element returns were not significantly influenced by any changes in host leaf litter quality, as mistletoe infection was not found to affect host element concentrations. Mistletoe infection also altered the spatial and temporal distribution of element returns because of the patchy occurrence of mistletoes and extended period of mistletoe litterfall compared with the host. These findings provide a mechanistic explanation for the role of mistletoes as a keystone resource and, together with comparable results from root-parasitic plants in boreal tundra and cool-temperate grasslands, suggest that enhancing nutrient return rates may be a generalized property of parasitic plants.

Key words: ecosystem, hemiparasite, keystone species, leaf litter, nitrogen, phosphorus.

INTRODUCTION

Given their diversity, cosmopolitan distribution, aerial habit and popularity as a food resource, mistletoes have long attracted researchers and, consequently, represent some of the best studied parasitic plants. The anatomical and physiological basis of parasitism has been particularly well studied, quantifying nutrient transfer from host to parasite (e.g. Glatzel 1983; Lamont 1985; Bannister *et al.* 2002). What happens next, however, remains unexplored. Where do these nutrients go and what are the consequences of nutrient acquisition by mistletoes for interactions with other organisms and overall ecosystem function?

Nutrient acquisition by parasitic plants has been suggested to have a wider influence on nutrient dynamics beyond simple host-parasite interactions, potentially increasing rates of nutrient cycling, particularly in low-nutrient ecosystems (Press 1998; Press & Phoenix 2005). The pathway underlying this process involves the enrichment of tissues, where a range of elements obtained from the host concentrate in the parasite (e.g. Lamont 1985; Marshall *et al.* 1994). This previous research has primarily focused on living tissues but there is also evidence that the litter of parasitic plants remains enriched, with minimal withdrawal of elements occurring prior to abscission (Pate *et al.* 1991; Quested *et al.* 2002).

Effects on nutrient cycling associated with the deposition of hemiparasite litter have only been examined in one species – the holarctic root hemiparasite, *Bartsia alpina* (Orobanchaceae, ex Scrophulariaceae; Quested *et al.* 2002, 2003a,b), with dramatic increases in the return of nutrients reported and ascribed to the enriched leaf litter. In previous work, we demonstrated much higher rates of leaf turnover in mistletoes than hosts (March & Watson 2007), therefore the resultant increased volumes of litter may also be a contributing factor to higher nutrient returns in this system. Furthermore, the *Bartsia* study only examined N and P returns in the litter (Quested *et al.* 2002, 2003b), yet many other elements are frequently enriched in hemiparasites (Lamont & Southall 1982; Glatzel 1983; Lamont 1985). Another open question relates to the effect of parasitism on host litter quality. Trees infected

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with mistletoe have been found to have reduced element concentrations, particularly in the branch to which the mistletoe is attached (Lamont & Southall 1982; Kuppers 1992). If nutrient concentrations in the litter of infected hosts are substantially less than that of non-infected hosts, this could offset any increase in nutrient returns because of mistletoe litter.

To clarify the influence of parasitic plants on nutrient cycling, we assessed the extent to which mistletoes affected the return of 13 elements via litterfall. This was achieved by comparing infected trees (hosts) with uninfected trees (non-hosts), within an Australian eucalypt woodland infected with the mistletoe *Amyema miquelii*. Leaf litter was the main component examined as this is the chief pathway for element returns in eucalypt litterfall (Adams & Attiwill 1986), as well as being the principal component of mistletoe litter for this species (March & Watson 2007). Specifically, we addressed four questions:

- Did nutrient enrichment occur for the 13 elements tested in the mistletoe leaf litter and, if so, to what extent?
- Did mistletoes affect host leaf litter quality?
- Were element returns from hosts (*Eucalyptus blakelyi*, *E. dwyeri* and *E. dealbata*) with mistletoes (*A. miquelii*) greater than from non-hosts?
- How did mistletoe infection affect the seasonal distribution of element returns?

METHODS

Study area

The study was carried out from May 2005 to May 2006 on the edge of a 42-ha remnant of eucalypt forest and woodland in the south-west slopes region of New South Wales, Australia (35°42.4′S, 147°24.0′E). The host species (*E. blakelyi* (M.), *E. dwyeri* (M. and B.) and *E. dealbata* (A. Cunn. ex Schauer)) all belong to the subgenus *Symphyomyrtus* section *Exsertaria* (i.e. red gums). As these species are so closely related that they readily hybridize in this region and trees could not be reliably differentiated morphologically (K. Hill 28 September 2005, pers. comm.), they were considered as one group for the purposes of this study (see March 2007 for further detail). The mistletoe, *A. miquelii* (Lehm. ex Miq.) Tiegh., is an endemic Australian loranthaceous mistletoe that commonly parasitizes eucalypts (Downey 1998) and is widely distributed across the continent. As *A. miquelii* was the only mistletoe examined, all references to mistletoes hereafter refer to this species. Both mistletoe and hosts were the dominant species within their taxon at the site and are evergreen, with leaves shed primarily in the dry summer season (March 2007). The soil type was sandy loam with a pH 4–4.5. The mean maximum daily temperature over the study period ranged from 12.5°C in July to 30.3°C in January and the total rainfall was 687.6 mm which is approaching the long-term annual mean of 737 mm (Australian Bureau of Meteorology 2005). A more detailed description of the climate, vegetation and soil type is contained in March (2007).

Sampling protocol

Study trees were randomly selected from approximately a 1-km stretch of forest edge, where host trees were randomly dispersed among non-hosts. Litter was collected from 16 litter traps beneath each of 35 eucalypt trees – 20 hosts and 15 non-hosts. Traps were plastic buckets, 270 mm in diameter and 250 mm high, with a 2-mm polyethylene mesh layer inserted 60 mm from the base. Litter from the 16 traps under each tree was pooled to gain an overall measure of litterfall per tree. Litter was collected monthly but pooled into seasonal groups of 3 months each. Each seasonal group commenced on the following dates and was defined by the season it approximated: winter (4 May 2004), spring (9 August), summer (10 November) and autumn (10 February to 10 May 2005), yielding seasonal periods of 90–95 days. Further details of the litter collection procedure are described in March and Watson (2007) and March (2007).

Litter was oven-dried at 70°C for a minimum of 48 h, then sorted and the mistletoe and eucalypt leaf components separated visually. This yielded 20 mistletoe and 20 eucalypt leaf litter samples from hosts, and 15 eucalypt leaf litter samples from non-hosts. The mistletoe reproductive component (flowers and fruit) was assessed in less detail as it represented a smaller fraction of the mistletoe litter (approximating 16%, March & Watson 2007). A single sample of mistletoe reproductive litter in each season was obtained by pooling reproductive components from 10 host trees per season.

Leaf litter analysis

Dried leaf litter was brushed free of dirt and other debris, ground and then stored in plastic vials until analysis. Plant material (0.5 g) was analysed for total carbon (C) and total nitrogen (N) using high temperature combustion in a LECO analyser (CNS 2000). The remaining elements – P, Ca, K, Mg, Na, S, Al, B, Cu, Fe and Zn – were analysed using the ICPOES (Inductively Coupled Plasma Optical Emission Spectrometry) procedure and the plant material (0.5 g) was prepared for analysis using nitric acid digestion (Zarcinas *et al.* 1987). Element concentrations were expressed as % of dry weight or mg kg^{-1}.

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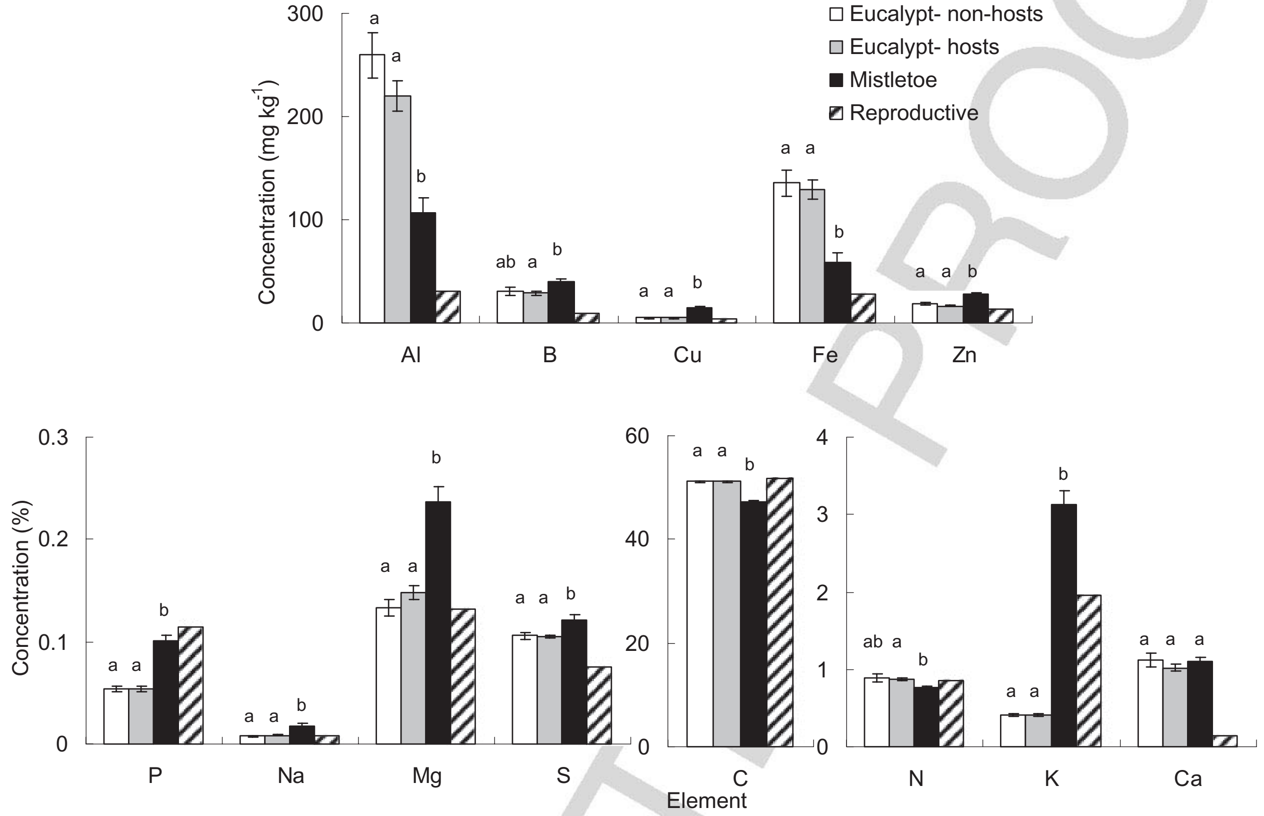

Fig. 1. Mean element concentrations (±1 SE) of non-host leaf ($n = 15$), host leaf ($n = 20$), mistletoe leaf ($n = 20$) and mistletoe reproductive ($n = 1$) litter. The same letters are not significantly different at $P = 0.05$ in separate t-tests between host and mistletoe (paired 9 d.f.), and host and non-host (independent 33 d.f.).

Data analysis

The return of each element was expressed in g ha^{-1} day^{-1} in each season by multiplying the element concentration of the leaf litter for that season by the mean daily mass of leaf litter in equivalent units. The annual element return to the forest floor was represented as kg ha^{-1} year^{-1}, by multiplying the mean concentration of each element by the seasonal litterfall, then summing these to obtain an annual input. As additional elements associated with the reproductive litter component were approximated from pooled data, they were not included in analyses comparing element returns from hosts and non-hosts.

Statistical analyses were carried out using SPSS (Version 15.0). Data normality was checked graphically and with the Kolmogorov–Smirnov statistic at a Lilliefors-corrected significance level and homogeneity checked with the Levene's test. Data were transformed (fourth square root or Arcsine if a percentage) prior to analysis to meet the assumption of normality. Student's t-tests were used to compare annual mean concentration differences between mistletoe and host (paired), as well as host and non-host (independent) and ANOVAs for annual element returns. Oneway, repeated measures ANOVAs were used to compare seasonal element concentrations and element returns; with season and litter type as within subject factors when comparing mistletoe and host; and season a within subjects factor and litter a between subjects factor when comparing eucalypt leaf litter concentrations and element returns from host and non-host. Where the assumption of sphericity was not met, significance values followed the Greenhouse–Geisser correction (Field 2005). Element concentrations and returns are presented in Appendices SI and SII, respectively. Spearman's rho correlations were used to evaluate relationships between variables.

RESULTS

Leaf litter element concentrations

Comparison of annual means of leaf litter concentrations demonstrated that mistletoe leaf litter was significantly enriched relative to the host for eight of the 13 elements tested (Fig. 1). Enrichment ranged from concentrations that were only slightly higher than the

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Table 1. Repeated measures ANOVAs of seasonal element concentrations of host (H, $n = 20$) and mistletoe (M, $n = 20$) leaf litter (element concentrations in Appendix SI of Supplementary Material). Ratios given are of the annual mean 'Mistletoe : host' element concentrations

	ANOVA (within subjects effects)			
	Season (d.f. 3, 57) *F*	Leaf litter type (d.f. 1, 19) *F*	Interaction (d.f. 3, 57) *F*	Mistletoe : host
C	4.82**	210.67***	4.32**	0.92
N	94.25***	8.94**	12.53***	0.90
P	11.76***	108.06***	15.03***	1.94
S	3.28*	12.67**	9.85***	1.17
Ca	1.79	1.59	3.33*	1.09
Mg	16.39***	56.89***	2.16	1.61
K	12.61***	394.87***	4.43*	7.98
Na	12.68***	31.84***	2.48	2.20
B	48.20***	73.93***	13.07***	1.43
Al	17.51***	68.68***	5.34**	0.50
Cu	4.09*	799.19***	9.03***	3.17
Fe	14.45***	71.53***	4.24**	0.47
Zn	7.48***	45.82***	14.12***	1.79

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

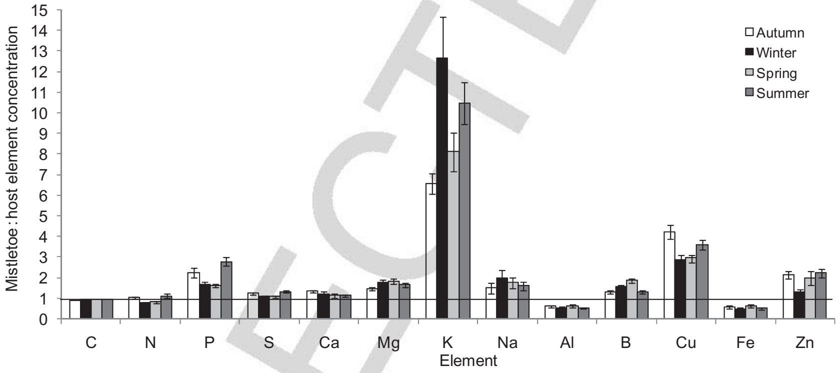

Fig. 2. Mean mistletoe : host ratios (±1 SE) of element concentrations in leaf litter, over four seasons. Horizontal line delineates the 1:1 ratio.

host (e.g. Ca), to up to eight times higher for K (mistletoe : host nutrient concentration ratio (M : H) in Table 1). Elements with significantly higher concentrations in mistletoe leaf litter were K, Cu, Na, P, Zn, Mg, B and S, listed in descending order of concentration difference between mistletoe and host (Fig. 1). In contrast, Al, Fe, C and N had significantly lower concentrations in the mistletoe leaf litter than the host. Mistletoe reproductive litter was generally not as enriched as the mistletoe leaf litter, with the majority of elements being lower in concentration and Ca being the lowest at approximately 10% of the mistletoe leaf litter concentration (Fig. 1). The only elements with higher concentrations in the reproductive litter than the mistletoe leaf litter were C, N and P but these differences were small.

Examination of the seasonal variation in element concentration differences between mistletoe and host leaf litter showed that differences were not consistent over the seasons. This was demonstrated by significant interactions for within-subject effects in all instances except for Mg and Na in repeated measures ANOVAs (Table 1). The extent of the difference in element concentration between mistletoe and host over the four seasons is represented by seasonal mistletoe : host element concentration ratios (Fig. 2). Those elements that had higher concentrations in the mistletoe leaf litter than the host in all seasons were P, S, Mg, K, Na, B, Cu and Zn (Fig. 2, Appendix SI). Nitrogen concentrations were similar to the host in summer and autumn but lower in winter and spring (Fig. 2, Appendix SI).

Table 2. Repeated measures ANOVAs of seasonal element concentrations of non-host (NH, $n = 15$) and host (H, $n = 20$) leaf litter (element concentrations in Appendix SI of Supplementary Material). Ratios given are of the annual mean 'Mistletoe : host' element concentrations

	ANOVA		
	Within subjects effects (d.f. 3, 99)		Between subjects effects leaf litter type (d.f. 1, 33)
	Season F	Interaction F	F
C	5.81**	4.73**	0.11
N	45.1***	5.72**	0.14
P	24.33***	1.05	0.02
S	9.55***	1.47	0.12
Ca	5.55**	3.48*	0.86
Mg	33.44***	1.02	2.26
K	29.32***	1.22	0.002
Na	16.64***	0.57	0.06
B	86.99***	1.64	0.006
Al	36.40***	4.03*	1.48
Cu	5.68**	0.91	0.17
Fe	36.75***	4.49*	0.01
Zn	41.45***	0.47	2.86

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Element concentrations of the eucalypt leaf litter did not differ significantly between host and non-host in comparisons of annual means (Fig. 1), as well as within seasons for all elements (Table 2, Appendix SI). Further evidence indicative of little effect of mistletoe infection on host element concentrations was demonstrated by a lack of any significant correlations (Spearman's rho) between the amount of mistletoe biomass on the tree (as estimated in March and Watson (2007)) and the annual mean concentration of each element in the host eucalypt leaf litter. That is, an increasing amount of mistletoe biomass in the canopy did not decrease host element concentrations in the leaf litter.

Element return to the forest floor

Mistletoe infection significantly increased annual element returns in leaf litter from host trees, by a factor ranging from 1.65 for N up to 8.5 for K, with P returns increasing by a factor of 3.0 (Table 3, Fig. 3). If mistletoe reproductive litter was included in the calculation of element returns from host trees, element returns increased further by a mean of 15% (Table 4, Fig. 3), ranging from 3% to 9% for Ca, B, Al, Cu and Fe, to 25% for N and 32% for P. However, if individual trees were considered rather than mean returns, the increase reached as high as 74% for K from a tree that was heavily infected with mistletoe. The increase in element returns from host trees was not influenced by any change in returns in eucalypt leaf litter, as there was no significant difference in returns from this litter between hosts and non-hosts (Fig. 3).

When element returns were examined seasonally, increases with mistletoe infection were even greater, with K returns exhibiting the greatest increase, by a factor of 43 in spring – explained by K having the highest degree of enrichment in the mistletoe leaf litter (Mistletoe : Host in Table 1, Appendices SI and SII). Statistical comparisons of element returns in each season found significant between-subject effects between hosts and non-hosts but significant interactions indicated the extent of the difference varied seasonally for all elements except Fe and Al (Table 3). The difference in element returns between host and non-host over the four seasons is represented by seasonal host : non-host element return ratios (Fig. 4). The only element returns that were not higher from host trees in all seasons were those of C and N, which were lower in autumn. Summer was the time of least difference in returns between host and non-host for all elements except C and N, which occurred in autumn. The greatest difference in element returns between host and non-host occurred in spring for all elements.

Mistletoe infection altered the seasonal distribution of element returns from eucalypt trees (Fig. 4, Appendix SII). Returns in the eucalypt leaf litter had a seasonal low in winter (June to August) and a high in summer (December to February) but the addition of mistletoe leaf litter extended the period of higher returns. Specifically, levels from hosts were comparable or greater than non-host returns one season earlier for most elements and maximum returns of Cu and K were also extended by one season (Fig. 4, Appendix SII).

An approximate value of the additional nutrient return in forests infected with mistletoe can be obtained through estimating the annual element return per mistletoe plant and multiplying this number by the mistletoe density in the forest (Table 3). For example, it was estimated 4.9 g of N and 0.7 g of P were returned in the leaf litter of an average-sized mistletoe each year. Therefore, as the mistletoe density at the study site ranged from 20 to 500 plants ha^{-1} (March 2007), additional N and P returns in the forest approximated 0.1–2.5 kg ha^{-1} year^{-1} of N and 0.01–0.3 kg ha^{-1} year^{-1} of P. However, these figures do not reflect the heterogeneity in nutrient returns associated with mistletoe infection, as patches of much higher nutrient returns occurred directly beneath infected trees. For example, at the study site, the mean additional N return in mistletoe leaf litter beneath trees was 8.3 ± 1.8 kg ha^{-1} year^{-1}, with an additional 3.8 kg ha^{-1} year^{-1} in the reproductive litter – equivalent to a doubling of N returns in the eucalypt leaf litter (Table 3). The mean return of other elements beneath study trees increased to an even greater extent, with a fourfold increase in P returns and a maximum 10-fold

Table 3. Repeated measures ANOVAs of seasonal element returns in leaf litter from hosts ($n = 20$) and non-hosts ($n = 15$) (element returns in Appendix SII). Ratio shown of total 'Host : non-host' element returns in leaf litter, where host leaf litter = mistletoe + eucalypt leaf litter

	ANOVA			
	Season (within subjects) (d.f. 3, 99)		Mistletoe infection (between subjects) (d.f. 1, 33)	
	F	Interaction *F*	*F*	Host : non-host
C	121.60***	17.86***	15.07***	1.6
N	74.71***	7.8***	15.14***	1.65
P	99.72***	7.79**	37.03***	3.0
S	145.8***	7.72***	24.04***	2.1
Ca	114.62***	4.71**	21.54***	2.1
Mg	161.64***	11.09***	36.25***	2.6
K	100.79***	8.22**	50.56***	8.5
Na	118.33***	11.36***	33.57***	3.4
B	150.2***	9.52***	13.88**	1.6
Al	73.39***	2.23	11.41**	1.6
Cu	106.01***	8.53***	35.01***	4.0
Fe	56.35***	1.63	12.8**	1.9
Zn	94.46***	8.23***	22.08***	2.6

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

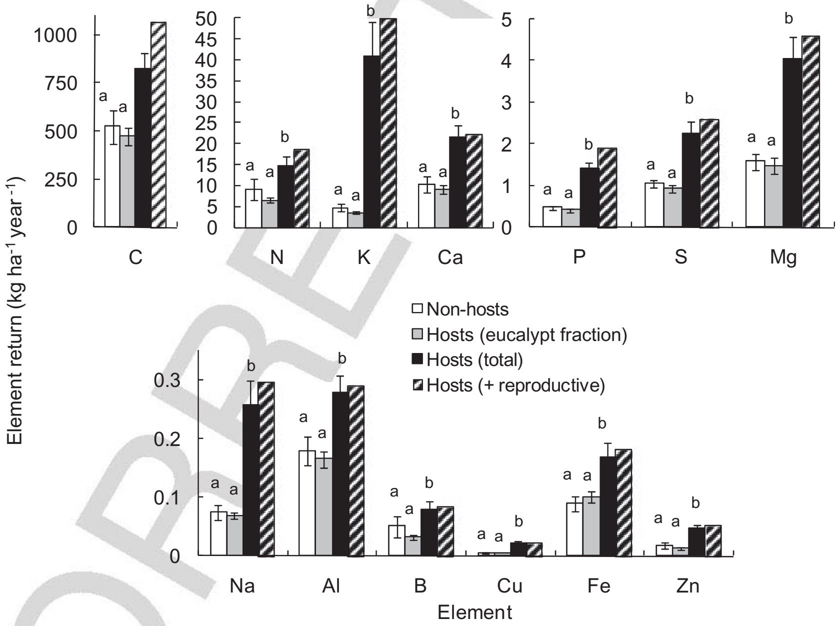

Fig. 3. Mean annual element return to the forest floor (±1 SE), from non-hosts ($n = 15$), hosts (eucalypt fraction) ($n = 20$), hosts (total) i.e. mistletoe + eucalypt leaf litter ($n = 20$), and hosts (+reproductive) i.e. total + mistletoe reproductive litter (not included in ANOVA) ($n = 20$). ANOVAs with 2, 52 d.f. The same letters are not significantly different at $P = 0.05$ in pairwise comparisons.

increase in K returns (Table 3). The most extreme increase in N returns with mistletoe infection from a tree with the greatest mistletoe density (i.e. 24 plants) was 42 kg ha^{-1} year^{-1}, which was over five times that returned in the eucalypt leaf litter.

DISCUSSION

As the first study to quantify the contribution mistletoes make to nutrient cycling, we have established that mistletoes can significantly increase the return of

Table 4. Mean (±1 SE) element return in mistletoe leaf litter ($n = 20$) (per unit area and per mistletoe; given a mean leaf litterfall of 648 g mistletoe^{-1} year^{-1} (March & Watson 2007) and in mistletoe reproductive litter ($n = 20$). Total element return from host trees = eucalypt leaf litter + mistletoe leaf and reproductive litter. Ratio shown of total host element return in the previous column: non-host returns in the leaf litter

	Element returns in mistletoe leaf litter		Mistletoe reproductive litter	Total	
	(kg ha^{-1} year^{-1})	(g mistletoe^{-1} year^{-1})	(kg ha^{-1} year^{-1})	(kg ha^{-1} year^{-1})	Host : non-host
C	353.4 ± 72.6	306.2	239	1063	2.0
N	8.3 ± 1.8	4.9	3.8	18.7	2.1
P	1.0 ± 0.2	0.7	0.5	1.9	4.1
S	1.3 ± 0.3	0.8	0.3	2.6	2.5
Ca	12.4 ± 2.7	7.1	0.6	22.2	2.1
Mg	2.6 ± 0.5	1.5	0.6	4.6	2.9
K	37.1 ± 8.5	20.3	9.1	49.8	10.4
Na	0.19 ± 0.04	0.1	0.039	0.295	3.9
B	0.05 ± 0.01	0.03	0.004	0.083	1.7
Al	0.11 ± 0.02	0.07	0.013	0.290	1.6
Cu	0.02 ± 0.004	0.01	0.002	0.023	4.6
Fe	0.07 ± 0.02	0.04	0.012	0.181	2.1
Zn	0.03 ± 0.01	0.02	0.006	0.052	2.9

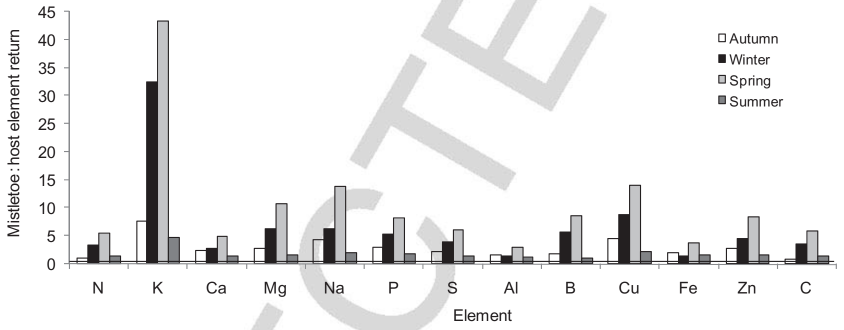

Fig. 4. Host : non-host ratios of mean annual element returns, over four seasons. Horizontal line delineates the 1:1 ratio.

nutrients in leaf litter; effectively doubling N return rates and quadrupling those of P, as well as having measurable effects on the entire group of 13 elements measured. The enhancement in nutrient cycling by mistletoes was primarily due to high litter returns for those elements with no enrichment in the mistletoe litter (N, C, Ca, Al and Fe). For those elements that were significantly enriched in the mistletoe litter (B, Cu, Zn, P, Na, Mg, S and K), it was both the enrichment and the high rates of litterfall that led to significant increases in element returns from infected eucalypt trees (i.e. host trees). The eucalypt leaf litter did not contribute to the increase in element returns, as there was neither a change in element concentration of the eucalypt leaf litter, nor quantity of eucalypt leaf litterfall (March & Watson 2007) associated with mistletoe infection.

Element concentrations of the mistletoe leaf litter in this study were comparable with those of live leaves (Lamont 1985; Ehleringer *et al.* 1986; Pate *et al.* 1991; Kuppers 1992) and leaf litter (Pate *et al.* 1991) of mistletoes within the *Amyema* genus in other areas of Australia. However, host and mistletoe element concentrations in leaf litter were considerably lower than values derived from northern hemisphere species (Glatzel 1983; Panvini & Eickmeier 1993). Another characteristic of this species and Australian mistletoes in general (Ehleringer *et al.* 1986), that is notably different to northern hemisphere hemiparasites, was lower N concentrations than the host; a feature possibly related to low N and water availability in the environment (Kuppers 1992).

It has been proposed that mistletoes may selectively parasitize nutrient rich hosts (Dean *et al.* 1994; Watson 2009) or alternatively, mistletoe infection may lead to lower host element concentrations (Lamont & Southall 1982; Kuppers 1992). This study did not provide evidence for either scenario, as element concentrations of eucalypt leaf litter did not differ between host and non-host. It is possible that both processes may have been operating in unison, effectively offsetting one another but, if this were the case, it would still

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be expected that greater mistletoe densities in the canopy would lead to a greater concentration deficit in the host – which did not occur. Thus, the argument for no detectable effect of mistletoe infection on host element concentrations appears stronger in this instance. There is, however, the necessity to explore this effect on live plant tissue, as leaf litter concentrations do not necessarily reflect those of live leaves (Killingbeck 1996).

Returns in eucalypt leaves were within the range of those recorded in leaf litter from other eucalypt forests in similar climatic regions (Lee & Correll 1978; Adams & Attiwill 1986; McIvor 2001). This is despite litterfall in this study being from isolated trees rather than from a continuous forest canopy. Where mistletoes were present, element returns increased to levels characteristic of higher rainfall areas (Attiwill & Leeper 1987; Adams 1996; McIvor 2001). It is also of note that increases in element returns with mistletoe infection may be greater than figures reported here because they did not include other returns to the soil that mistletoe could affect, such as leached nutrients in throughfall and stemflow.

Mistletoe infection increased N returns by 65% (i.e. a factor of 1.65), a figure greater than the 42% increase reported with root hemiparasite infection (Quested *et al.* 2003b) and comparable with that associated with N fixation by *Acacia* spp. (May & Attiwill 2003). The high N returns with root hemiparasite infection were attributed to higher N concentrations than their host (Quested *et al.* 2003b), while in the current study it was the high rate of leaf litterfall that was primarily responsible. Phosphorus and K, unlike N, were enriched in the mistletoe litter, and had returns that increased to an even greater extent than N returns with mistletoe infection – being a 197% and 750% increase, respectively.

This study raises many questions related to the wider consequence of mistletoe infection on ecosystem functioning. Imbalances in the nutrient cycle, where outputs exceed inputs from the ecosystem are commonly caused by disturbances, such as fire and herbivory (Attiwill & Leeper 1987; Adams 1996). However, the high nutrient transfers reported in this research suggest mistletoe infection, particularly when in high densities, may also disrupt this balance. Parasitic plants are considered to have less influence on nutrient cycling than herbivores (Pennings & Callaway 2002) and, certainly, when pulses in herbivory occur (Norgrove & Hauser 2000) this may be the case. However, the sustained effect of mistletoe infection on nutrient cycling suggests effects may be at least as significant as herbivory over extended periods of time and thus prompt further inquiry comparing the two processes.

Species diversity and productivity can be affected by changes in nutrient returns (Bray & Gorham 1964; Attiwill 1979), the timing of these returns (Goldberg & Novoplansky 1997) and environmental heterogeneity (Tilman 1982) – all factors that mistletoe infection has been shown to affect in this study. Specifically, as N is the main nutrient limiting plant growth in temperate environments (Vitousek 2004) and P can also be limiting, particularly in Australian sclerophyllous habitats (Attiwill & Leeper 1987; McLaughlin 1996), the large increase in N and P returns may entrain pervasive changes to community structure. This effect is further compounded by changes in the timing of element returns with mistletoe infection, from the typical winter low and summer high of eucalypt forests (Attiwill *et al.* 1978; McIvor 2001) to an extended period of high returns stretching from spring to autumn. Furthermore, the characteristically patchy distribution of mistletoes (Aukema 2003); March (2007) would alter the spatial distribution of nutrient returns and subsequently increase environmental heterogeneity. The effect of these changes on the availability of nutrients to plant communities will, however, be dependent upon many other interacting factors, such as the decomposition process once the litter is on the forest floor. Thus, much more work is required to examine the effect mistletoes are having on the spectrum of ecosystem processes in further detail.

In conclusion, these studies have been the first to explore the effect mistletoes are having on aspects of nutrient cycling. The consistency and magnitude of increased elemental returns associated directly with mistletoe infection provides a mechanistic basis for the hypothesis that mistletoes function as keystone resources (Watson 2001). This finding, together with comparable results from root-parasitic plants (Quested *et al.* 2003b), also suggests that enhanced nutrient return rates may be a generalized property of parasitic plants. Given the global distribution of mistletoes and described patterns of abundance in many systems, including forests of commercial significance, these findings have broad relevance and underscore the necessity to quantify effects in other systems. In addition to highlighting the ecosystem-wide influence of these plants, we suggest that their omission from nutrient cycling studies has led to systematic underestimates of nutrient return rates, prompting re-evaluation of previous data and prioritizing future investigations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix SI. Seasonal mean (±1 SE) element concentrations (C to Na in %, B to Zn in mg kg^{-1}) of non-host (NH, $n = 15$), host (H, $n = 20$) and mistletoe (M, $n = 20$) leaf litter. Reproductive litter = mean annual element concentrations in mistletoe reproductive components ($n = 1$, pooled across 10 trees).

Appendix SII. Seasonal mean (±1 SE) element returns (g ha^{-1} day^{-1}) in leaf litter from hosts (H, $n = 20$) and non-hosts (NH, $n = 15$).

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