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Parasites boost productivity: effects of mistletoe on litterfall dynamics in a temperate Australian forest

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Abstract The importance of litter in regulating ecosystem processes has long been recognised, with a growing appreciation of the differential contribution of various functional plant groups. Despite the ubiquity of mistletoes in terrestrial ecosystems and their prominence in ecological studies, they are one group that have been overlooked in litter research. This study evaluated the litter contribution from a hemiparasitic mistletoe, *Amyema miquelii* (Lehm. ex Miq.) Tiegh., in an open eucalypt forest (*Eucalyptus blakelyi*, *E. dwyeri* and *E. dealbata*), at three scales; the forest stand, single trees and individual mistletoes. Litter from mistletoes significantly increased overall litterfall by up to 189%, the amount of mistletoe litter being proportional to the mistletoe biomass in the canopy. The high litter input was due to a much higher rate of mistletoe leaf turnover than that of host trees; the host litterfall and rate of leaf turnover was not significantly affected by mistletoe presence. The additional litter from mistletoes also affected the spatial and temporal distribution of litterfall due to the patchy distribution of mistletoes and their prolonged period of high litterfall. Associated with these changes in litterfall was an increase in ground litter mass and plant productivity, which reflects similar findings with root-parasitic plants. These findings represent novel mechanisms underlying the role of mistletoes as keystone resources and provide further evidence of the importance of parasites in affecting trophic dynamics.

Keywords Leaf litter · Leaf lifespan · Productivity · Eucalyptus forests · Hemiparasite

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Introduction

Litterfall dynamics determine a number of ecosystem processes that shape the structure of plant and animal communities in most terrestrial ecosystems. Litter is a key component in nutrient cycling (Ashton 1975; Attiwill et al. 1978; Polglase et al. 1992), determining the availability of essential nutrients which, in turn, affect the productivity, diversity, dynamics and interactions of plant, animal and microbial populations (Vitousek 2004). The physical presence of litter also has significant effects, modifying the microclimate, providing a habitat and influencing plant growth (Facelli and Pickett 1991). Consequently, changes in litterfall can have far-reaching effects on many ecosystem processes.

Although there is an extensive litterfall literature (e.g., reviews in Bray and Gorham 1964; Facelli and Pickett 1991), one aspect that has been largely ignored has been the contribution from parasitic plants. This is despite their ubiquity in forest and woodland systems worldwide (Pennings and Callaway 2002; Press and Phoenix 2005), and their status as keystone resources (Watson 2001; Press and Phoenix 2005). The significance of the litter input from parasitic plants has been demonstrated in recent studies, which have found that litter from sub-arctic root hemiparasites can affect rates of nutrient cycling and plant growth (Quested et al. 2002, 2003). However, the generality of these principles to other parasitic plants, or to other environments has not been demonstrated. Therefore, it is uncertain whether other hemiparasites such as mistletoes, which are aerial stem hemiparasites, would have similar effects.

The aim of the study was to investigate how mistletoes affect litterfall dynamics and understorey plant biomass. Specifically, this study determined the extent to which mistletoe presence changed the litterfall biomass, structure, spatial and temporal distribution, as well as relationships between litterfall and understorey plant biomass. This study focused on litter from the box mistletoe, *Amyema miquelii* (Loranthaceae) and eucalypt hosts belonging to members of the "red gum" group, *Eucalyptus blakelyi*, *E. dwyeri* and *E. dealbata* (Myrtaceae). Our primary focus was on individual trees with and without mistletoe. We also examined forest stands with a range of mistletoe densities, as the majority of litter studies take place at this scale. To gain greater insight into the dynamics of mistletoe litterfall, we also incorporated a study of individual mistletoes, including leaf lifespan. Adopting this three-tiered design enabled us to compare findings across multiple scales and examine interactions between stands, single trees and individual mistletoes, thereby improving our ability to evaluate the overall role of mistletoe litterfall in this system.

Materials and methods

Study area

The study was carried out at Morgan's Ridge, a privately owned remnant of open forest and woodland 10 km north-east of Holbrook, in the south-west slopes of New South Wales, Australia (35°42.4′S, 147°24.0′E). Tree densities ranged between 10 and 1,400 stems ha^{-1} and the dominant species were red gums (*Eucalyptus blakelyi*, *E. dwyeri* and *E. dealbata*), long leaf box *E. goniocalyx*, red box *E. polyanthemos* and red stringybark *E. macrorrhycha*. The understorey was open and grassy, dominated by native and introduced grasses and shrubs [see Cooney and Watson (2005) for a more detailed description]. *Amyema miquelii* is an endemic Australian loranthaceous mistletoe that commonly parasitises eucalypts (Downey 1998) and is widely distributed across the continent. It has a patchy distribution, with densities ranging from 20 to over 500 plants ha^{-1} at the study site. As *A. miquelii* was the only mistletoe examined, all references to mistletoes hereafter refer to this species.

The mean maximum daily temperature over the 12 month study period ranged from 12.5°C in July to 30.3°C in January and the total rainfall was 687.6 mm at Holbrook which is approaching the annual mean. The previous 2002–2003 season had been declared one of the driest on record, with rainfall averaging 348 mm.

Sampling protocol

Litter was collected at three scales, the forest stand, the tree, and individual mistletoe. Trees were the focus of this study, primarily because the litterfall and understorey could be directly related to mistletoe occurrence in the associated canopy. All trees were red gums (*Eucalyptus blakelyi*, *E. dwyeri* or *E. dealbata*, or their hybrids), randomly selected until 20 trees with a range of mistletoe densities (hosts) and 15 trees with no mistletoe (non-hosts) were chosen (Table 1). To minimise the confounding effect of tree size on litterfall, size was restricted to a diameter at breast height-over bark (DBH-OB) of 0.25–1.60 m. Tree DBH-OB measurements were taken at 1.3 m and calculated as the sum of the diameter of all stems originating from the same base. Canopy height and width were also measured. To minimise litter input from neighbouring trees, there was a minimum of 1 m with a mean of 7.3 m between canopies, and trees near exceptionally large trees were avoided. The foliage density of each eucalypt host was estimated using a scale of 1–5, where one was a dead tree and five was a healthy tree with a full canopy (after Heatwole and Lowman 1987).

Total leaf biomass of each tree was estimated with the non-destructive "Adelaide technique" (after Andrew et al. 1979). This technique used a reference eucalypt branch to

Table 1 Descriptive data for trees used in the study

	Hosts	Non-hosts	*t*	*P*
Number of trees	20	15		
Mistletoe number	7 ± 1 (1–24)	0		
Mistletoe leaf biomass (kg)	8.0 ± 2.2	0		
Tree foliage density scale (1–5)	4.7 ± 0.13	4.6 ± 0.13	0.537	0.595
Eucalypt leaf biomass (kg)	26.6 ± 1.9	20.2 ± 1.2	2.589	0.014
DBH-OB (mm)	66 ± 8	40 ± 4	2.545	0.016
Height (m)	9.2 ± 0.4	7.7 ± 0.4	2.395	0.022

Means (±1 SE), with range in parentheses. *t* tests with 1, 33 *df* score the number of equivalent branches contained within the tree canopy, multiplied by the branch leaf biomass to gain the total canopy biomass. The branch leaf biomass was calculated as the mean biomass of eight branches of equivalent size to the reference branch. The canopy leaf biomass was strongly correlated with DBH-OB (Pearson's $r = 0.781$, $P < 0.01$), confirming that this technique accurately estimated relative differences in canopy size which was sufficient for the comparative purposes of this study.

If there were mistletoes on the tree, the width, breadth and vertical depth of each mistletoe was measured and the leaf density rated using a scale of 1–5. Specifically, 1 = less than 10% of the maximum foliage density, 2 = 10–30%, 3 = 30–60%, 4 = 60–90% and 5 = in excess of 90% maximum foliage density. An estimate of mistletoe leaf biomass was made by determining the relationship between the mistletoe dimensions and leaf biomass. Twenty mistletoes were randomly selected and the same measurements taken as for the mistletoes on the trees. All the leaves were removed from the plant, oven-dried at 70°C for 48 h and weighed to determine the mistletoe leaf biomass. The mistletoe measurements were used to calculate a "leaf volume index" (Eq. 1). This equation was adapted from the equation of an ellipsoid as used by Miller et al. (2003), with an added correction for leaf density which improved estimates.

$$\text{leaf volume index} = \frac{1}{6} \times \pi \times a \times b \times c \times \text{ leaf density} \qquad (1)$$

Where a, b and c were width, breadth and vertical depth of the mistletoe plant, respectively, measured in metres. Leaf density has no units as it is a scale of 1–5, and as such nor does the leaf volume index. There was a strong relationship between the mistletoe leaf biomass and leaf volume index ($y^{0.25} = 2.996 \times {}^{0.25} + 0.754$, $r^2 = 0.909$, $n = 20$, $F_{1,18}$ 180.1, $P < 0.001$). Consequently, the leaf biomass of each mistletoe in the study was estimated using this regression equation, where x = leaf volume index.

Litter collection

The same litter trap design was not used at all scales, but structured such that the litter traps were appropriate to the system being sampled. For the tree-scale, 16 litter traps were placed in a grid pattern beneath each tree crown. The traps used were plastic buckets, 270 mm in diameter and 250 mm high, with a 2-mm polyethylene mesh layer inserted 60 mm from the base. These were secured to the ground and any overhanging understorey trimmed away from the trap. The litter traps at the mistletoe-scale were constructed from the same 2-mm mesh, secured to four 1-m wooden stakes, forming a pocket beneath the mistletoe of approximately the same width as the mistletoe plant and a rock was placed in the bottom of each. Netting of 20 mm diameter was draped over the mistletoe and attached to the top of the mesh pocket, completely enclosing the mistletoe to minimise litter loss. Litter was collected from the forest in six 0.1 ha rectangular plots with a range of mistletoe densities. The number of mistletoes in each plot, tree species and DBH-OB of all trees above 40 mm were recorded (Table 3). Eight litter traps were placed randomly in each plot. Traps were constructed of the same 2-mm mesh, sewn into a pocket and attached to a 0.90 m diameter circular frame. They were suspended 1 m from the ground by four wooden stakes and a rock placed in the bottom of each.

Litter was collected and processed from all traps at the same time and in the same manner, commencing in May 2004 and repeated every month for 12 months (litter collection from forest plots was delayed 1 month due to equipment failure). Litter from the 16 litter traps under each tree and the eight traps per plot were pooled, to gain an overall rate of litterfall per tree and per plot. Litter was oven-dried at 70°C for a minimum of 48 h and sorted into mistletoe leaves, mistletoe reproductive components (fruit and flowers), eucalypt leaves, eucalypt reproductive components (fruit and flowers), bark, and large and small twigs (<50 mm long and 2 mm in diameter).

Leaf lifespan

Leaf loss was monitored every 3 months for 12 months commencing May 2004, on 20 of the trees (10 host and 10 non-host) used in the litter collection and ten mistletoe plants randomly selected from each of the ten host trees (after Southwood et al. 1986; Wright and Cannon 2001). Six leaves on each of eight twigs were randomly selected and labelled from the full 360° radius of the canopy and below a height of 2 m, to facilitate leaf inspection. A permanent ink mark was placed on each of the six leaves so that existing leaves could be distinguished from newly emerged leaves at each census.

Collection of understorey litter and plant biomass

Litter on the forest floor was collected in April 2004 from within 0.25 m^2 quadrats randomly located beneath each of the 35 study trees. Leaves were separated from the litter, dried at 70°C and weighed. Live plant biomass was harvested in November 2005 from within four 0.25 m^2 quadrats located beneath the same ten host trees used in the leaf lifespan study. Four quadrats were placed beneath each tree, one half way between the two the outer litter traps in each quarter. All plant matter was cut at the soil surface and placed in a bag, dried at 70°C and weighed.

Data analysis

Statistical analyses were carried out using SPSS (Version 12.0.1). Student's *t* tests were used to compare annual litterfall from host ($n = 20$) and non-host ($n = 15$) trees. Data normality were checked graphically and with the Kolmogorov–Smirnov statistic with a Lilliefors significance level, and homogeneity checked with the Levene's test. Data were transformed (fourth square root) to meet statistical assumptions. Pearson's product–moment correlations were used to evaluate the strength of relationships between the forest characteristics and litter, and regressions to describe linear models. One-way, repeated measure ANOVAs were used to compare litterfall from host and non-host trees in monthly collections. The Friedman test was used for the forest plots as the sample size was low. Where the assumption of sphericity was not met, significance values followed the Greenhouse-Geisser correction (Field 2000). When a significant interaction was detected, values were compared separately for each month with Student's *t* tests. Annual litterfall from the plots was calculated by estimating the litterfall of the missing month as the mean of the following 2 months, as was the trend with litterfall from isolated trees.

Leaf turnover was the mean proportion of leaves marked at the start of the monitoring that were lost after 12 months. Leaf lifespan was calculated as the inverse of the rate of leaf turnover (after Southwood et al. 1986; Wright and Cannon 2001) on data pooled over 1 year (after Wright and Cannon 2001).

Results

Litterfall from trees

The number of mistletoe plants per tree varied widely and, consequently, the amount of mistletoe leaf biomass in the canopy (Table 1). Hosts were larger (Table 1) but there was no correlation between tree size (DBH-OB) and eucalypt litterfall per unit area (Pearson's $r = 0.287$, $P > 0.05$). Consequently, tree size was not included as a factor that could confound litterfall rates.

Leaf litter was the major litter component, being 42 ± 5% (mean ± 1 SE) of the litter from non-hosts. Bark represented 33 ± 4% of non-host litter, large twigs 8 ± 1% and small twigs 4 ± 1%. Host trees had similar proportions of eucalypt litter to non-hosts (Fig. 1) but the additional mistletoe litter led to leaves becoming more dominant, as well as adding the mistletoe reproductive components (i.e. fruits and flowers). The extra litter from mistletoes increased the amount of litterfall by 6–189%, the variability reflecting the amount of mistletoe in the canopy. Mistletoe leaves were 72 ± 2% of the mistletoe litter and 24 ± 3% of the total litter biomass (i.e. mistletoe + eucalypt litter), and the reproductive material 10 ± 2%. There was a significant effect of mistletoe presence on total litterfall, total leaf litter and small twig input (Fig. 1). There were no differences in the amount of bark, large twigs, and eucalypt leaf and reproductive litter between host and non-host trees.

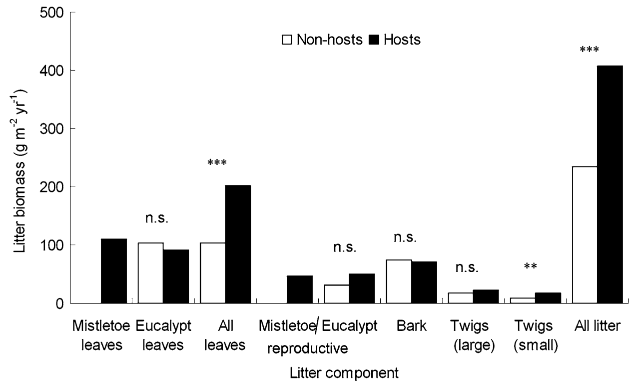

Fig. 1 Mean (± 1SE) annual litterfall biomass from host ($n = 20$) and non-host ($n = 15$) trees. *t* tests with 1, 33 *df*. ** $P < 0.01$, *** $P < 0.001$, n.s. = non significant

Temporal distribution of litterfall

Total leaf litterfall from host trees was significantly greater than non-hosts in a repeated measures ANOVA ($F = 33.72$, $P < 0.001$), with post hoc *t*-tests showing significant differences in all months except January, February and April (Table 2; Fig. 2). The mass of all litter components differed significantly between months (Table 2); leaf litterfall increasing from a low in winter (June–August) to a high in summer (January and February; Fig. 2). Leaf fall from host trees reached a level approaching the highest non-host leaf fall 2 months earlier, then maintained the higher litterfall for a further 2 months.

Mistletoe leaf fall was lowest in June and highest in November but dropped in summer (December–February), before rising in March (Fig. 2). The reproductive component of mistletoe litter was highest in December and lowest in June and February. Twigs showed a significant effect of mistletoe presence, with post hoc tests revealing they were significantly higher from host trees in January and September (Table 2).

Litter from hosts

There was a significant positive linear relationship between mistletoe leaf biomass in the canopy and total litterfall

Table 2 Repeated measures ANOVA of litter components over 12 months from non-host (n = 15), and host trees (n = 20)

	Effect of month			Effect of Mistletoe	Post hoc t tests (months deviating from norm shown)		
	df	*F*	Interaction F	F (*df* = 1, 33)	*t*	Month	*P*
Mistletoe leaves[a]	11, 209	16.87***		–			
Mistletoe reproductive[a]	11, 209	7.356***		–			
Eucalypt leaves	11, 363	75.51***	0.85	0.23			
Total leaf litter	11, 363	23.04***	5.87***	86.44***	0.23, 2.0, 1.96	Ja, Fe, Ap	>0.05
Eucalypt reproductive	11, 363	46.584***	0.86	4			
Bark	11, 363	67.68***	0.99	3.15			
Twigs	11, 363	28.18***	1.42	7.09*	3.16, 2.74	Ja, Se	<0.05
Total litter	11, 363	103.37***	3.86**	33.72***	0.61, 1.3	Ja, Fe	>0.05

Post hoc t test with 1, 33 *df*. Month is represented by the first two letters

[a] Mistletoe components were examined from hosts only

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

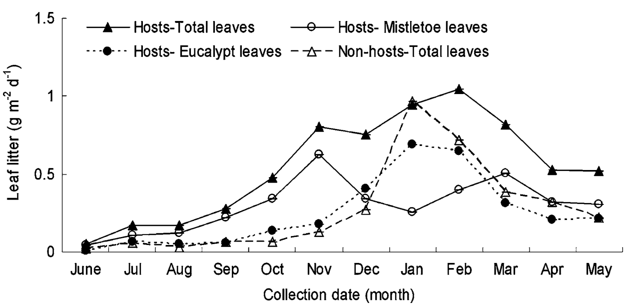

Fig. 2 Mean (± 1 SE) monthly leaf litterfall from host (n = 20) and non-host (n = 15) trees, with eucalypt and mistletoe leaf litter from hosts also shown separately. Lines are drawn between months to show seasonal trends

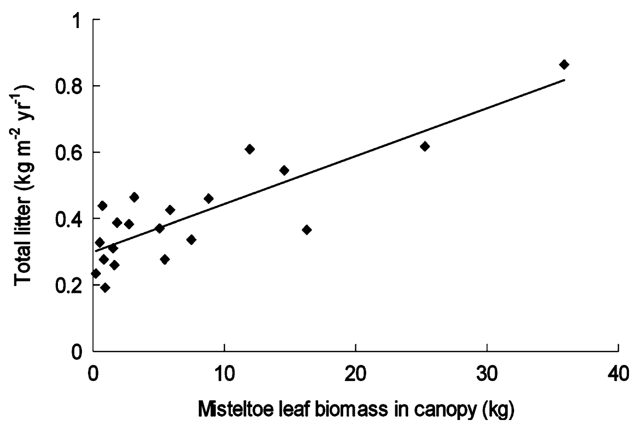

Fig. 3 Relationship between the amount of litterfall and the mistletoe leaf biomass estimate in the canopy of host trees, n = 20. Equation; $y = 0.014x + 299.34$, $r^2 = 0.723$, $F_{1,18} = 47.0$, $P < 0.001$

(Fig. 3), with a stronger relationship between mistletoe leaf biomass in the canopy and mistletoe litter ($r^2 = 0.802$, $F_{1,18} = 72.72$, $P < 0.001$, $n = 20$). Mistletoes produced more leaf litter per unit of live leaf biomass in the canopy than their hosts. In 1 year, 0.81 ± 0.08 g of mistletoe leaf litter was produced per gram of mistletoe leaf biomass in the canopy, compared with 0.13 ± 0.01 g of eucalypt leaf litter per gram of eucalypt leaf biomass. The high leaf litter production was evident in the high proportion of mistletoe leaves in the litter compared to the canopy; e.g. when 16% of canopy leaf biomass was mistletoe, 74% of the litter was mistletoe leaves, with 80% being the maximum (Fig. 4).

One of the mechanisms underlying litterfall, leaf turnover (proportion of live leaves lost annually) was significantly greater in mistletoes (0.65 ± 0.04) than hosts ($F_{2,27} = 23.95$, $P < 0.001$, $n = 10$). However, post hoc tests found no difference in eucalypt leaf turnover between host (0.22 ± 0.05) and non-host (0.25 ± 0.05). Mistletoe leaf lifespan was therefore 1.50, hosts 4.47 and non-hosts 3.97 years.

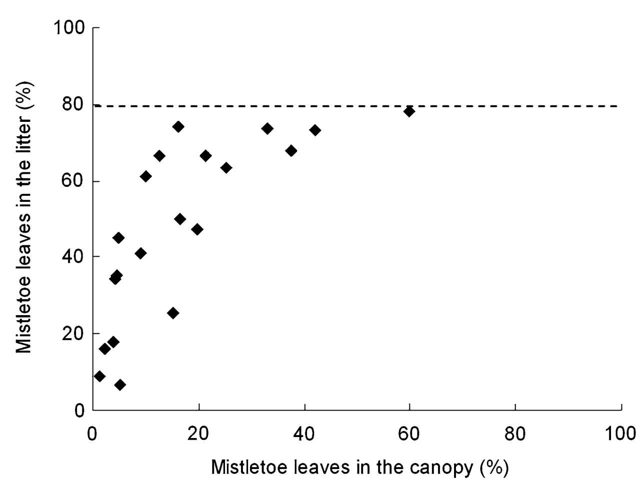

Fig. 4 Relationship between the percentage of the canopy that is mistletoe leaves and the percentage of leaf litter that is mistletoe leaves

Individual mistletoes

The mean monthly distribution of mistletoe leaf litterfall from individual mistletoes was similar to mistletoe litter from host trees but leaf litter fell more consistently throughout the year, with no significant effect of month ($F = 3.6$, $P = 0.07$; $n = 10$; Fig. 5). When leaf litter from each of the ten mistletoes was examined separately, there was little congruence in timing of maximum or minimum leaf fall between individual plants. The annual reproductive litter input was 16% of the total litter and was generally greatest from November to December but this also varied between mistletoe plants. Small twigs accounted for 3–8% of the mistletoe litter.

Forest plots

Plot 1 had the greatest number of mistletoes, followed by plots 2 and 3, whilst the remaining plots had low densities (Table 3). The highest amount of litterfall, particularly twigs and eucalypt reproductive litter, was recorded in plot 4, which also had the largest trees (Table 3). Mistletoes increased the litterfall by up to 16% above eucalypt litterfall (Table 3) with a significant negative relationship between mistletoe number and eucalypt leaf litterfall (Pearson's $r = -0.835$, $P < 0.05$). There was a significant linear relationship between the number of mistletoes and mistletoe leaf litterfall ($r^2 = 0.855$, $F_{1,4} = 23.537$, $P = 0.008$). The distribution of mistletoe leaf litter varied significantly between months (Friedman test; $\chi^2 = 22.72$, $P < 0.05$), with similar seasonal trends to the individual trees and mistletoes but the peak in litterfall was April–May (Fig. 5).

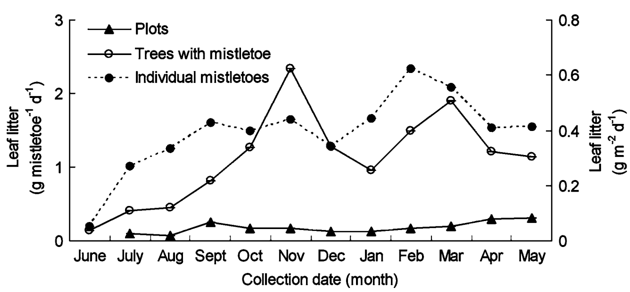

Fig. 5 Mean (± 1SE) monthly mistletoe leaf litterfall from host trees (g m^{-2} d^{-1}, $n = 20$), plots with high mistletoe litterfall (g m^{-2} d^{-1}, $n = 3$) and individual mistletoes (g mistetoe^{-1} d^{-1}, $n = 10$). *Lines* are drawn between months to show seasonal trends

Comparison of litterfall over the three scales

Mistletoe litterfall from isolated trees was higher than that found in the forest, as was the density of mistletoes (Table 4; Fig. 5). Similar quantities of mistletoe leaf litter fell from mistletoes at each scale, ranging from 123 to 162 g leaf litter per m^3 of mistletoe biomass or 544–648 g of leaf litter per mistletoe plant. This equated to between 66 and 80% of the mistletoe leaf biomass falling as leaf litter each year.

Relationship between litter and the understorey

There was significantly more leaf litter beneath host trees than that found beneath non-hosts (Table 5). The leaf litter on the forest floor beneath non-host trees was of the "mor" type, as there was a clear disjunct between the soil and litter (Attiwill and Leeper 1997). However, where mistletoe litter was present, particularly where there were high densities, the litter was of the "mull" form as there was no clear separation between the litter and soil. Here, there was a dense litter layer where litter fragments gradually reduced in size with depth until small litter fragments mixed with the soil surface. Trees with greater mistletoe biomass in the canopy also had greater plant biomass in the understorey, as indicated by their significant positive relationship (Fig. 6).

Table 3 Number of mistletoes and eucalypt trees in each plot with dimensions shown (dimensions did not include trees <40 mm DBH-OB). Litterfall and percentage contribution of mistletoe litter in each plot shown

	Plot					
	1	2	3	4	5	6
Mistletoe number (ha^{-1})	480	360	20	50	90	280
Eucalypts (stems ha^{-1})	620	860	1100	630	1090	1360
Mean DBH-OB (mm)	165 ± 12	124 ± 14	154 ± 23	192 ± 27	114 ± 9	82 ± 5
Eucalypt litterfall (g m^{-2} year^{-1})	223.9	121.5	313.7	401.7	217.7	89.9
Mistletoe litterfall (g m^{-2} year^{-1})	36.2	18.5	4.5	2.1	1.2	11.6
Total litterfall (g m^{-2} year^{-1})	260.1	140	318.2	403.8	218.9	101.5
Increase in litterfall with mistletoe litter	16%	15%	1%	1%	1%	13%

Table 4 Summary of annual mistletoe leaf litter characteristics at three spatial scales

	Trees	Mistletoes	Plots
Number of mistletoes (plants m^{-2})	0.17 ± 0.03	1	0.021 ± 0.008
Mistletoe live leaf biomass (g $mistletoe^{-1}$)	984.2 ± 120.8	678.4 ± 190.1	
Mistletoe leaf litterfall (g m^{-2})	109.8 ± 22.7		9.64 ± 4.4
Range in mistletoe leaf litterfall (g m^{-2})	9–386		1–28
Mistletoe leaf litter/live leaf volume (g m^{-3})[a]	123 ± 16	162 ± 28	
Mistletoe leaf litter/mistletoe (g $mistletoe^{-1}$)[b]	648 ± 93	544 ± 125	544 ± 262

Means are ± 1 SE. Trees n = 20, mistletoe n = 10, plots n = 6

[a] Mistletoe leaf volume calculated using the equation for an ellipsoid (Miller et al. 2003)

[b] Mistletoe leaf litter per mistletoe is the total litterfall per tree or plot divided by the number of mistletoes on the tree or in the plot

Table 5 Leaf litter mass beneath non-host (n = 15) and host trees (n = 20)

	Means		ANOVA	
	Non-host	Host	F	P
Mistletoe leaf litter	0	215.0 ± 60.8		
Eucalypt leaf litter	191.3 ± 21.6	238.0 ± 27.1	0.957	0.335
Total leaf litter layer	191.3 ± 21.6	453.1 ± 75.3	11.28	0.002

Means ± 1 SE (g m^{-2}). One-way ANOVA with 1, 33 df

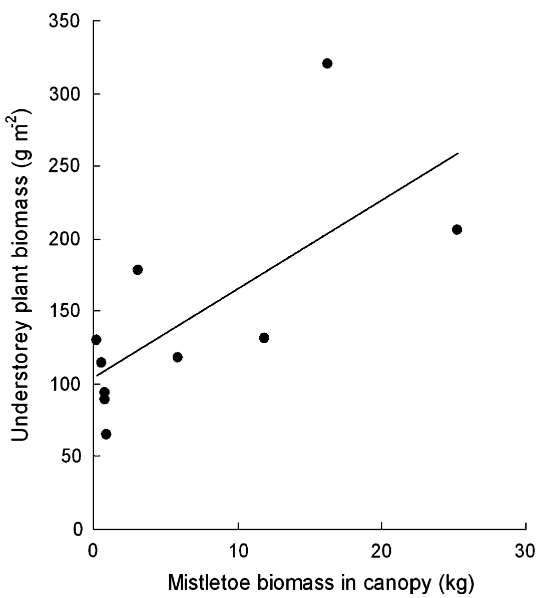

Fig. 6 Regression between mistletoe leaf biomass in the canopy of host trees and their understorey plant biomass. Equation: $y = 0.006x + 104.34$, $r^2 = 0.49$, $F_{1,8} = 7.704$, P = 024, n = 10

Discussion

This study has been the first to examine the contribution mistletoes make to forest litter inputs. Through choosing the novel approach of examining litterfall at three spatial scales this study demonstrated that mistletoe (*Amyema miquelii*) presence significantly affected litterfall dynamics, in terms of quantity, periodicity and structure. Furthermore, it was demonstrated that the increase in mistletoe litterfall was associated with a change in the depth and structure of ground litter as well as greater plant biomass.

Annual leaf litterfall per mistletoe was comparable at all three scales studied, to the extent that the plots and individual mistletoes both produced 544 g of leaf litter per mistletoe annually. Mistletoes produced leaf litter at a greater rate than their eucalypt hosts, evident in their higher rate of leaf litter production per gram of live leaf biomass and rate of leaf turnover. This translated to approximately 80% of their live leaf biomass lost as litter each year, leading to a disproportionate amount of leaf litter compared to their canopy biomass–mistletoe leaf densities of 20% of the canopy produced litter comprising up to 80% mistletoe leaves. This 80% level appeared to be a maximum, as no matter how much more mistletoe biomass there was in the canopy, mistletoe leaves did not exceed 80% of the leaf litter.

The high mistletoe litter production resulted in a significant increase in the total amount of litterfall from trees. The leaf litterfall was closely related to both the number of mistletoes and the estimated mistletoe leaf biomass in the canopy; relationships evident at both the forest and tree scale. Mistletoes had a particularly dramatic effect on litterfall when densities were high, reaching a maximum increase in total litterfall of 189%. Mistletoes were not as abundant in the forest plots and consequently litterfall increased by up to 16% above the eucalypt litterfall. The increase in litterfall associated with mistletoes was entirely due to the additional mistletoe litter, as the host litterfall was not affected by mistletoe presence. The lack of an effect of mistletoes upon host leaf loss was confirmed in the rate of leaf turnover, which did not differ between host and non-host. However, negative effects of this mistletoe species on host growth have been detected previously (Reid et al. 1994) and in such cases effects on litterfall dynamics may differ from those found in this study.

There are no data available for mistletoe litterfall with which to make comparisons, as this was the first study to evaluate mistletoe litterfall in any system. Recorded eucalypt litterfall rates (234 ± 18 g m^{-2} from trees) were similar to eucalypt litterfall in similar climatic regions (Hutson 1985; Grigg and Mulligan 1999; McIvor 2001). However, the additional mistletoe litter increased litterfall rates (408 ± 35, maximum of 864 g m^{-2}) to levels that are more commonly seen in climates with higher rainfalls (Ashton 1975; Polglase et al. 1992; Pook et al. 1997). Consequently, mistletoes were disrupting the association that commonly occurs between climate and litterfall.

The estimated lifespan of mistletoe leaves was 1.5 years—approximately one-third of host leaves. This leaf lifespan is comparable with another mistletoe in the *Amyema* genus, where lifespan was 1.3 years (calculated from published leaf mortality data, Pate et al. 1991). Typical leaf lifespans of eucalypts range from 1 to 4 years or more (Attiwill et al. 1996; Pook et al. 1997; Wright and Westoby 2002). The eucalypts in this study therefore have comparatively long leaf lifespans; however, the previous season was particularly dry and leaf mortality can be affected by climatic conditions (Pook et al. 1997). Like the rate of litterfall, the short leaf lifespan is another characteristic of mistletoes that is more typical in higher rainfall areas (Wright and Westoby 2002) but as lifespan and litterfall are directly linked this relationship is not unexpected.

Mistletoes also increased the spatial and temporal complexity of litterfall. Eucalypt litterfall was not affected by mistletoe presence, which had a winter low and summer high, typical of temperate eucalypt systems (Ashton 1975; Attiwill et al. 1978; Pook et al. 1997; McIvor 2001). However, mistletoe litterfall differed from this, being highest in late spring and decreasing in summer, thus displaying complementarity with host litterfall. Consequently, the period of high litterfall was extended by several months either side of the annual eucalypt litterfall peak. Further temporal variation in litterfall was evident at the scale of individual mistletoe plants, which were asynchronous in their peak litterfall; a feature also found in flowering and fruiting times within other *Amyema* sp. mistletoes (Reid 1986) and mistletoes generally (Watson 2001).

Mistletoes increased the spatial complexity through distributing the litter in patches of varying size and density across the landscape. Mistletoe litterfall varied between 9 and 386 g m^{-2} from isolated trees, to a more diffuse distribution and lower densities in the forest of 1–28 g m^{-2}. This created a mosaic of patches of mistletoe litter of varying density across the landscape. Litter from host trees also had different structural qualities to that of non-host trees. The change in structure was not due to any alteration in the proportion of eucalypt litter components but to the addition of mistletoe litter, which was primarily leaves. Leaves are typically the main component in many eucalypt systems (Crockford and Richardson 1998; Grigg and Mulligan 1999); however, mistletoes increased the dominance of leaves in the litter. Changes to the litter structure and mass can affect the physical environment on the forest floor and this was evident in the increase in litter depth, as well as the change in the litter environment from a mor to a mull type.

Changes in the litterfall and litter environment on the forest floor have the potential to affect communities inhabiting this environment. Among these are the plant communities and this study found a positive relationship between mistletoe presence and understorey plant biomass. Similar results have also been found with northern hemisphere root hemiparasites, which have been associated with increases in plant productivity in grassland communities (Joshi et al. 2000), and sub-arctic plants (Quested et al. 2003). This association between increased litterfall and greater productivity is also consistent with expectations based on experience from previous litterfall studies (Bray and Gorham 1964; Attiwill et al. 1996). This effect of hemiparasites releasing nutrients that were previously bound and therefore unavailable within the biomass of long-lived hosts has been proposed for root hemiparasites (Press 1998). However, this research provides evidence that it is also occurring in a system in the southern hemisphere and with aerial hemiparasites, and consequently may be more widely applicable to hemiparasites on a global scale.

A further common trait of hemiparasites is they tend to occur in less productive areas, where vegetation is sparse (Sterba et al. 1993; Ward 2005) or where soils are nutrient-poor (Quested et al. 2003). Mistletoe densities were higher where eucalypt leaf litterfall was lower in this study, suggesting that these mistletoes were also more abundant where the eucalypt canopy cover was sparse. Furthermore, mistletoes are often abundant in Australia where soils are nutrient-poor (Pate et al. 1991; Miller et al. 2003; Ward 2005). An implication of this common link between hemiparasites and their environment, as well as their effect on nutrient dynamics is that they may be raising the productivity of less fertile areas.

This study therefore establishes that mistletoes can significantly change litterfall dynamics in forests they occupy. Their disproportionate litter contribution increases litterfall rates to levels more commonly seen in climates with higher rainfall and they also alter the spatial, temporal and structural qualities of the litterfall. The demonstrated effects these changes have on the understorey establish that the patterns reported previously in northern hemisphere root hemiparasites are not idiosyncratic to one habitat type or species. Furthermore, in addition to supporting the keystone status of mistletoes, our findings also highlight the need to incorporate parasitic plants into litterfall studies. Current estimates of litterfall for many habitats may need to be revisited, with mistletoes and other parasitic plants potentially modifying both temporal and spatial variability in litterfall and, thereby, altering other aspects of ecosystem functioning.

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