

SHORT COMMUNICATION

Preliminary evidence suggests that beech scale insect honeydew has a negative effect on terrestrial litter decomposition rates in *Nothofagus* forests of New Zealand

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Abstract: Honeydew production by New Zealand beech scale insects (*Ultracoelostoma* spp., Hemiptera: Margarodidae) is widely considered to have a positive influence on native animal abundance and ecosystem functioning. As a first assessment of whether there is a positive relationship between honeydew throughfall and litter decomposition rates, we placed experimental litter bags in each of 10 high and 10 low honeydew plots in mixed southern beech (*Nothofagus*) forest at each of two sites, Lakehead and Rotoiti, in the Nelson Lakes National Park. High and low honeydew plots were selected using sooty mould biomass on the forest floor as a surrogate for honeydew throughfall, as sooty mould biomass was shown to be strongly correlated ($r = 0.906$) with scale insect population size at the Rotoiti site. Contrary to our expectation, terrestrial litter decomposition was significantly lower in high honeydew plots than in low honeydew plots, at both Lakehead and Rotoiti. The presence of introduced wasps (*Vespula* spp., Hymenoptera: Vespidae) at the Lakehead site did not appear to have any significant effect on litter decomposition rates, despite the fact that wasps are thought to intercept much of the honeydew produced in this forest. Variance in litter decomposition rates between high and low honeydew treatments was predominantly determined by a direct relationship between sooty mould biomass and litter decomposition rate at the scale of individual litter bags. However, the mechanistic explanation for the observed relationship is unclear. Future studies should be directed towards quantifying the functional relationship between honeydew throughfall and growth rates of sooty mould, and their subsequent effects on abiotic conditions, microarthropod community dynamics and microbial activity rates in litter.

Keywords: beech scale insect; decomposition; honeydew; litter bags; *Nothofagus*; sooty mould fungi; *Ultracoelostoma* spp.

Introduction

The feeding activities and excretion rates of insect herbivores have a substantial impact on energy and nutrient fluxes to the soil, which in turn influence populations of microorganisms and nutrient cycling in forest ecosystems (Michalzik *et al.*, 1999; Stadler *et al.*, 1998, 2001). For example Dighton (1978) showed that the application of synthetic honeydew to a woodland soil resulted in a 30% increase in fungal population levels and a 300% increase in bacterial numbers. Owen and Wiegert (1976) hypothesized that hemipteran honeydew promotes the growth of free-living nitrogen-fixing bacteria in the soil beneath host plants, increasing nitrogen uptake to the host plant and its associated herbivores. However, direct evidence for this positive feedback loop has been limited (Petelle,

1980; Choudhury, 1984, 1985; Foster, 1984; Belsky, 1986).

In New Zealand, the most ecologically important honeydew-producing insects are the beech scale insects (*Ultracoelostoma assimile* and *U. brittini*, Hemiptera: Margarodidae) (Morales *et al.*, 1988). Beech scale insects infest the trunks and branches of southern beech trees (*Nothofagus* spp., Fagaceae) across one million hectares of the northern South Island, producing copious amounts of carbohydrate-rich honeydew (Beggs, 2001). It has been speculated that the patchy distribution of beech scale insects affects nutrient cycling processes (Beggs, 2001) by creating patchiness in energy input to soil communities. However, since there has been no explicit test of this relationship the inference has typically been that beech scale insects are likely to have a positive impact on ecosystem

process rates in New Zealand beech forests (Beggs, 2001).

The effect of scale insect honeydew on decomposition was tested by mapping the spatial distribution of naturally-occurring patches of high and low honeydew throughfall. Experimental litter bags were used to give a standardized comparative measure of litter decomposition rates under differing levels of estimated honeydew throughfall. The relationship between honeydew throughfall and litter decomposition was tested at two sites differing in conservation management practices, with one at the Rotoiti Nature Recovery Area, Nelson Lakes National Park, where successful control of introduced wasps (*Vespula germanica* and *V. vulgaris*, Hymenoptera: Vespidae) has been undertaken since 1999 (Harris and Etheridge, 2001; Saunders and Norton, 2001) and the other at a wasp-infested site at Lakehead. It has been speculated that introduced wasps may affect nutrient cycling processes by reducing honeydew throughfall to the soil, causing a reduction in the biomass and activity rates of microorganisms involved in decomposition processes (Beggs, 2001).

Methods

The study was conducted in the Lake Rotoiti Nature Recovery Area (41°49'S 172°51'E; 650 m a.s.l.) where wasps are controlled through the application of poison bait (Harris and Etheridge, 2001; Saunders and Norton 2001), and at a wasp-infested site at Lakehead c. 2.5 km south, in Nelson Lakes National Park, New Zealand. All sampling was carried out in one 0.96 ha plot (divided into 96 10×10 m subplots) at each site. Both sites are within continuous beech forest on gentle west-facing slopes over 100 m from the forest edge, dominated by red (*Nothofagus fusca*) and silver (*N. menziesii*) beech, with a few mountain (*N. solandri*) beech in some areas. There are no other large-scale wasp removal treatments of this type in New Zealand, so it was not possible to replicate sites with and without wasps.

Honeydew treatments

Artificial litter bag experiments were conducted in naturally occurring high and low honeydew patches, rather than through the addition of measured amounts of synthetic honeydew, as we were primarily interested in the natural range of variation in honeydew throughfall under ambient environmental conditions. However, in order to detect the maximum possible effect size (in the absence of any prior knowledge of likely treatment effects) we attempted to select extremely high and extremely low areas of natural honeydew throughfall. Unfortunately, honeydew throughfall rates could not

be measured directly in the limited time available. Instead, to select honeydew treatments we initially mapped the densities of scale insects at breast height (1.4 m) on all trees greater than 5 cm DBH (Wardhaugh, 2004). However, we found that there was no relationship between density at breast height and total population size of scale insects on trees (Wardhaugh *et al.*, in press), so measurements low on the trunk are unlikely to reflect total honeydew throughfall in a forest. Instead, sooty mould biomass on the ground was found to be an accurate predictor of scale insect population size (Wardhaugh *et al.*, in press).

Ground cover of sooty mould (%) was visually estimated as a rapid method to identify areas of high and low honeydew throughfall at each site. We assumed that a 10×10-m subplot that was widely covered in sooty mould also had a large amount of honeydew throughfall from a relatively large population of scale insects over a wide area. The ten subplots with the highest and ten with the lowest cover of sooty mould were then selected at each study site for the measurement of litter decomposition rates. These subplots were randomly intermingled within a mosaic of other high and low honeydew patches.

Establishing a relationship between sooty mould biomass and scale insect abundance

Relative ground cover estimates of sooty mould fungus were useful for selecting sites, but for the purposes of analysis we directly quantified dry weight biomass of sooty mould in the immediate vicinity of each litter bag. In an earlier study we established that there was a strong relationship between sooty mould biomass on the ground and total population size of beech scale insects on red beech trees at the Rotoiti site (Wardhaugh *et al.*, in press). In that study, sooty mould biomass was collected in eight cylindrical core samples (10 cm diameter to a depth of 10 cm) taken beneath each of 14 trees, approximately halfway between the center and the outer edge of the crown projection of the canopy (in order to account for leaning trees in which the crown was not centred above the trunk). Core samples were dried at 70°C for 96 hours, then hand-sorted to remove leaf material and detritus before measuring the dry weight biomass of sooty mould (g m⁻²). A total census of scale insects infesting each of the 14 red beech trees was conducted by climbing each tree using single rope climbing techniques and measuring the density of insects up the trunk and along the branches. The relationship between total scale insect population size and sooty mould biomass was highly significant (correlation coefficient, $r = 0.906$, $P < 0.001$) (Fig. 1) (Wardhaugh *et al.*, 2006). Although we recognize that the form of this relationship may differ at Lakehead, due to differences in honeydew production rates per insect between trees at different sites, or due to wasp

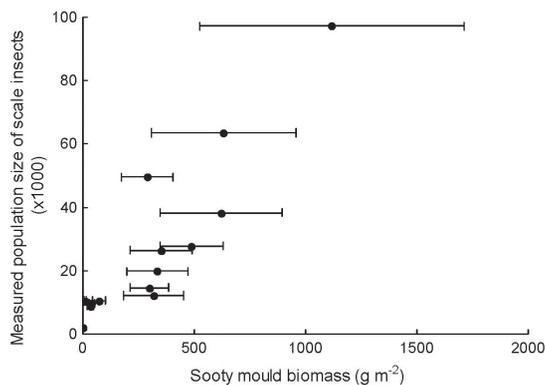


Figure 1. The relationship between the total measured population size of scale insects in a tree and the mean dry biomass (g m^{-2}) (± 1 SE) of sooty mould fungi growing on the ground beneath the tree, for each of the 14 red beech trees surveyed ($r = 0.906$, $n = 14$, $P < 0.001$). The equation of the fitted line is: total population size = $76.684 \times$ sooty mould biomass + 2746.5. Redrawn from Wardhaugh *et al.* (2006).

foraging, our purpose was simply to establish that a direct link does exist between the total number of honeydew-producing scale insects on beech trees and the growth of sooty mould biomass on the ground. Given the strong correlation observed, we assume that sooty mould biomass is a good surrogate for the relative amount of honeydew throughfall that hits the ground.

Measuring litter decomposition

Five litter bags (10×15 cm, c. 1-mm mesh), each containing between 2.02 and 2.09 g (dry mass) of fresh leaves from seven cultivated plum trees *Prunus domestica* (Rosaceae), were randomly placed on the litter surface within each of the ten high and ten low honeydew subplots, at both the wasp-infested Lakehead site and the wasp-controlled Rotoiti site (200 bags in total). Leaves were dried at 80°C for 24 hours and thoroughly mixed before placement in litter bags. *Prunus*, rather than *Nothofagus*, leaves were selected as a standardized experimental substrate because they are not present in New Zealand beech forests. Hypothetically, it is possible that high or low honeydew patches may have corresponded with the presence or dominance of a particular *Nothofagus* species, and that this may have introduced systematic bias into treatment effects if there were differences in the composition, preference or activity rates of the decomposer fauna on different *Nothofagus* leaf species at different sites.

Litter bags were randomly placed in the subplots from 20–26 March 2003 and retrieved on 10 March 2004 (c. 350 days). After retrieval, litter bags were placed in individual paper bags and dried at 70°C for

48 hours. Each litter bag was then carefully cleaned of all external leaf, twig, fungus and soil debris before being weighed to determine litter mass lost (initial dry leaf mass minus final dry leaf mass, after subtracting the mass of the mesh bag).

Measuring sooty mould biomass

At the end of the litter bag experiment in 2004, three cylindrical core samples (10 cm diameter to a depth of 10 cm) were taken at arbitrary points within 0.5 m around each litter bag. Core samples were dried at 70°C for 96 hours before the sooty mould was carefully hand sorted from leaves and other detritus and weighed. The average of the three core samples was used for subsequent analyses, expressed as dry mass of sooty mould in g m^{-2} adjacent to each litter bag.

Data analysis

Sooty mould biomass

A Type-I mixed-model Generalised Linear Model (GLM) was used to test the level of treatment effect imposed by the selection of naturally occurring patches of high and low honeydew based on the percent cover of sooty mould within subplots. The dependent variable, dry mass of sooty mould, was tested against the fixed treatment effects of site (wasp-infested Lakehead versus wasp-controlled Rotoiti) and honeydew throughfall (high versus low), and the random effect of variation among 10×10 -m subplots. A square root transformation ($(x + 0.5)^{0.5}$) of sooty mould biomass was used to normalize residuals.

Litter decomposition rates

A Type-I mixed-model GLM was used to test differences in the proportion of litter mass lost in relation to the fixed covariate effect of dry weight biomass of sooty mould immediately adjacent to each litter bag, the fixed treatment effects of site (Lakehead versus Rotoiti) and honeydew throughfall (high versus low), and the random effect of variation among 10×10 -m subplots. Following the analysis of sooty mould biomass above, the covariate factor was square root transformed prior to analysis. An arcsine square-root transformation of the proportion of litter mass lost was used to normalize residuals of the dependent variable.

In both analyses, we used a mixed effects model under the GLM module in Statistica v.7 (StatSoft, 2003). Type-I sums of squares were used because of the hierarchical design of the experiment in which there was dependence among litter bags within subplots, subplots within honeydew treatments, and honeydew treatments within sites. Individual litter bags within subplots were not treated as independent replicates when testing treatment effects. In mixed-effects GLMs

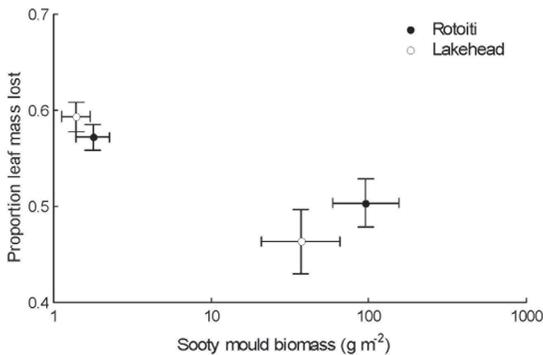


Figure 2. The relationship between litter decomposition rate and biomass of sooty mould fungus, as a surrogate of honeydew throughfall rate. Back-transformed mean (\pm 95% confidence interval) proportion of leaf mass lost from experimental litter bags c.350 days after stratified random placement in areas of high and low honeydew throughfall, at a wasp-controlled site at Rotoiti and a wasp-infested site at Lakehead, Nelson Lakes National Park. There was no significant covariate effect of sooty mould biomass on litter mass loss in an analysis of covariance, so sooty mould biomass is presented as mean (\pm 95% confidence interval) within site by honeydew treatment combinations.

the error degrees of freedom in F -ratio tests involving random treatment effects are calculated using the Satterthwaite (1946) method of denominator synthesis which can yield non-integer values.

Results

Sooty mould biomass

Sooty mould biomass in the immediate vicinity of litter bags varied from 1.48 g m⁻² (range 0.00 – 26.14) across all low honeydew subplots to 186.08 g m⁻² (range 0.00 – 1533.79) across all high honeydew subplots (honeydew treatment effect: $F_{1,35.06} = 128.00$, $R^2 = 0.397$, $P < 0.0001$; Table 1a, Fig. 2), indicating that selection of low and high honeydew subplots based on percent ground cover of sooty mould did impose an effective treatment difference in biomass of sooty mould. However, sooty mould biomass was marginally, but significantly, lower at the wasp-infested Lakehead site than at the wasp-controlled Rotoiti site (site effect: $F_{1,34.92} = 7.79$, $R^2 = 0.024$, $P = 0.008$; Fig. 2) and the degree of difference in sooty mould biomass between low and high honeydew treatments was marginally greater at Rotoiti (interaction effect: $F_{1,35.06} = 4.73$, $R^2 = 0.015$, $P = 0.036$; Fig. 2).

Litter decomposition rates

Of the 200 litter bags placed in the forest in March

2003, 184 were recovered for analysis. The proportion of dry mass lost across all subplots varied from 0.146 to 0.710 within c. 350 days. Litter bags in low honeydew subplots lost significantly more dry mass (mean = 0.583) than those in high honeydew subplots (mean = 0.485), with the covariate effect of sooty mould biomass in the immediate vicinity of litter bags explaining 17.6% of the variance in litter decomposition rates ($F_{1,79.38} = 41.65$, $P < 0.0001$; equation of covariate relationship in back-transformed units: proportion litter mass lost = $0.565 - 0.0002 \times$ sooty mould biomass) and the honeydew treatment effect explaining an additional 11.4% of the variance ($F_{1,62.48} = 26.17$, $P < 0.0001$; Fig. 2) (Table 1b). Despite the significant difference in sooty mould biomass between sites, there was no significant effect of site on litter decomposition rates ($F_{1,35.66} = 1.90$, $P = 0.177$; Table 1b, Fig. 2). However, there was a weak but significant interaction effect between site and honeydew throughfall ($F_{1,35.92} = 6.79$, $R^2 = 0.033$, $P = 0.013$), suggesting that the magnitude of the effect of honeydew throughfall on leaf litter decomposition rates was significantly greater at wasp-infested Lakehead than at wasp-controlled Rotoiti (Fig. 2).

Discussion

Contrary to our expectation, these preliminary data suggest that leaf litter decomposition rates were significantly lower in areas with high ground cover of sooty mould fungus resulting from the high throughfall of scale insect honeydew to the forest floor. These findings contradict one important component of the hypothesis that hemipteran honeydew promotes the growth of microorganisms, and increases decomposition rates and nitrogen fixation to the benefit of the host plant (Owen and Wiegert, 1976). Instead, the data are consistent with a number of other studies that have identified negative impacts of carbohydrate-rich hemipteran honeydew on soil nutrient cycling processes (e.g., Turner, 1977; Grier and Vogt, 1990; Michalzik *et al.*, 1999). This suggests that sap-sucking insects, such as beech scale insects, may have a larger detrimental effect on their host than the simple removal of large quantities of phloem sap. Increased honeydew throughfall reduces litter decomposition rates in the soil beneath heavily infested host trees, which should reduce nutrient turnover and decrease nitrogen availability to the host plant. Therefore, our data do not support the widely held assumption that beech scale insect honeydew has wholly positive effects on ecosystem processes in New Zealand beech forests (Beggs, 2001).

The covariate effect of sooty mould biomass in the immediate vicinity of individual litter bags had the

Table 1. Mixed-model Generalised Linear Model analysis of variation in (a) sooty mould biomass and (b) litter decomposition rates between sites (wasp-infested Lakehead versus wasp-controlled Rotoiti) and honeydew throughfall treatments (high versus low). Five randomly located mould and litter decomposition measurements were taken from each of 10 randomly selected 10×10-m subplots within each of the four site by honeydew treatment combinations. Sooty mould biomass was square-root transformed prior to analysis to normalize residuals. Proportion of litter mass lost was arcsine square-root transformed prior to analysis of litter decomposition rates, and transformed sooty mould biomass was entered into the model as a covariate effect. In this analysis, Type-I sums of squares (SS) are used because of the hierarchical design of the treatments. Error degrees of freedom (d.f.) and error mean squares (MS) in *F*-ratio tests involving random treatment effects are calculated using the Satterthwaite (1946) method of denominator synthesis, which yields non-integer values.

(a) Sooty mould biomass

Sources of variation	Effect	SS	d.f. effect	MS effect	d.f. error	MS error	<i>F</i>	<i>P</i>
Site	Fixed	258.84	1	258.84	34.92	33.24	7.79	0.008
Honeydew throughfall	Fixed	4255.15	1	4255.15	35.06	33.24	128.00	<0.0001
Site×Honeydew interaction	Fixed	157.29	1	157.29	35.06	33.24	4.73	0.036
10×10-m subplots	Random	1196.89	36	33.25	144.00	33.59	0.99	0.494
Error		4836.68	144	33.59				
Total		10704.85	183					

(b) Litter decomposition rate

Sources of variation	Effect	SS	d.f. effect	MS effect	d.f. error	MS error	<i>F</i>	<i>P</i>
Sooty mould biomass	Fixed covariate	0.2775	1	0.2775	79.38	0.0067	41.65	<0.0001
Site	Fixed	0.0144	1	0.0144	35.66	0.0076	1.90	0.177
Honeydew throughfall	Fixed	0.1804	1	0.1804	62.48	0.0069	26.17	<0.0001
Site×Honeydew interaction	Fixed	0.0514	1	0.0514	35.92	0.0076	6.79	0.013
10×10-m subplots	Random	0.2721	36	0.0076	141.00	0.0055	1.38	0.094
Site×Mould biomass	Fixed	0.0031	1	0.0031	141.00	0.0055	0.57	0.452
Honeydew×Mould biomass	Fixed	0.0094	1	0.0094	141.00	0.0055	1.73	0.191
Error		0.7702	141	0.0055				
Total		1.5785	183					

single greatest effect on litter decomposition rates. However, there was a substantial additional proportion of variance in litter decomposition rates explained by differences between high and low honeydew treatment subplots. This may be due to an additive effect of the biomass or patchiness of sooty mould fungus on litter decomposition at a spatial scale greater than individual litter bags (for example, through the effects of sooty mould cover on soil moisture retention, or on the abundance and species composition of litter decomposer organisms over the scale of metres or tens of metres), or it may indicate that the effect of honeydew throughfall on litter decomposition is mediated by factors other than sooty mould biomass.

We found a significant, but only relatively weak signal of reduced sooty mould biomass at the wasp-infested Lakehead site compared to the wasp-controlled Rotoiti site, despite the fact that introduced wasps are thought to harvest a large proportion of honeydew standing crop (Moller *et al.*, 1991). If this effect is directly related to wasp foraging and not simply random

intrinsic variation between the two sites, then the significant interaction term in the analysis suggests that the 'wasp effect' results from decreased mould biomass in the high honeydew subplots, but little change in mould biomass in the low honeydew subplots. This is consistent with wasps preferentially harvesting honeydew from the areas of highest honeydew density.

Despite a significant difference in sooty mould biomass between sites, there was no apparent difference in litter decomposition rates at Lakehead versus Rotoiti that could be attributed to the effect of introduced wasps. Furthermore, the magnitude of the effect of honeydew throughfall on decomposition rates was actually greater at Lakehead than at Rotoiti, which is not consistent with the reduced range of mould biomass observed among subplots at Lakehead. Wasps evidently do not intercept enough honeydew over a long enough time period to have an important effect on litter decomposition processes, at least not at the time scale of this study.

The lack of direct measures of honeydew production and throughfall to the ground limit the conclusions that can be drawn from these preliminary data. Future studies should be directed towards quantifying the functional relationship between honeydew throughfall and growth rates of sooty mould, and the subsequent biotic and abiotic effects of sooty mould on soil decomposer communities and nutrient cycling rates. The most important question is whether a positive feedback loop exists in which high honeydew throughfall causes low litter decomposition rates and reduces nitrogen uptake into the phloem sap of the host tree, which could subsequently increase the feeding rate of scale insects (if they are nitrogen limited, e.g. Wardhaugh and Didham, 2005), resulting in even higher honeydew production.

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