Soluble carbon production by honeydew scale insects in a New Zealand beech forest

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Abstract: We estimated the annual production of honeydew per unit land area of beech (*Nothofagus* spp.) forest by measuring the amount of honeydew produced in 24 h by scale insects (*Ultracoelostoma* spp.) (Hemiptera: Margarodidae) every month for 2 years. We used exclosures to prevent animals (notably *Vespula* wasps) removing honeydew, and we compared the standing crop of honeydew inside permanently closed exclosures with that outside exclosures. Honeydew production and the number of honeydew droplets was highly variable between individual trees, tree type, position on tree, and, exclosure type, and within and between years. The amount of honeydew available outside exclosures was significantly reduced in year 2, predominantly by *Vespula* wasps, even though wasp density was relatively low. Sugar composition also varied between tree type and between years. Up to 5% of the sugar was glucose, with varying proportions of fructose, sucrose and oligosaccharides. The surface area of trees infested with scale insects was estimated using allometric regression relationships between tree diameter and total surface area of tree trunk and branch material. These estimates were combined with measurements of tree diameter in 10-m radius circular plots to give a production estimate of between 3500 and 4500 kg dry weight honeydew ha^{-1} $year^{-1}$. Using this data, combined with previously published estimates of carbon uptake, it was estimated that between 6 and 8% of net primary productivity was released as honeydew. Honeydew scale insects provide large amounts of biologically available carbon in the form of soluble sugar. It is a crucial resource for the above-ground system, and probably also for the below-ground system. We conclude that scale insects have the potential to function as keystone species in these forests.

Keywords: carbohydrate; ecosystem processes; *Nothofagus* spp.; nutrient cycling; sugar composition; *Vespula* spp.; *Ultracoelostoma* spp.

Introduction

Honeydew-producing scale insects (*Ultracoelostoma assimile* and *U. brittini* (Hemiptera: Margarodidae)) have been proposed to function as keystone species in some New Zealand beech (*Nothofagus* spp.) forests because of the strength of their effect on the beech forest community relative to their biomass (Beggs and Wardle, *in press*). Honeydew produced by beech scale insects provides a year-round sugar resource for a range of species at several trophic levels, including micro-organisms, invertebrates, reptiles and birds (Hughes, 1976; Gaze and Clout, 1983; Beggs and Wilson, 1991; Moller *et al.,* 1991; Didham, 1993; Markwell *et al.,* 1993; O'Donnell and Dilks, 1994; Wilson *et al.,* 1998; Beggs, 2001; Murphy and Kelly, 2003). For example, a sooty mould complex, sometimes involving as many as seven species (Trichopeltheca, Capnocybe and Capnodium spp.) (Hughes, 1976) grows on any surface that is coated with honeydew when it drips or is washed by rain onto the surrounding ground and vegetation.

Other microbes probably also consume the honeydew and this may affect nutrient cycling in these forests. In the Northern Hemisphere, honeydew produced by aphids has been shown to substantially affect populations of soil microorganisms (Dighton, 1978; Michalzik *et al*., 1999), which in turn can influence nutrient availability (e.g., Stadler and Michalzik, 1998; Stadler *et al*. 2001). Therefore it is possible, depending on the quantity of honeydew produced, that the beech scale insect also affects ecosystems processes in New Zealand forests (Beggs, 2001; Beggs and Wardle, *in press*).

In addition to its importance for native species, the availability of honeydew is a major factor in the high abundance of invasive social wasps (*Vespula germanica* and *V. vulgaris*, Hymenoptera: Vespidae) in these

forests (Beggs, 2001). Wasps, which are present in high numbers for about 4 months of the year, are a major consumer of honeydew during this period (Moller *et al.,* 1991). These invasive wasps are having a major impact on native animals through competition for honeydew and predation on invertebrates (e.g., Moller and Tilley, 1989; Beggs and Wilson, 1991; Beggs, 2001), so again, the quantity of honeydew produced is a key factor influencing important interactions in this community.

Honeydew is a waste product from the beech scale insect that accumulates at the end of a long, waxy anal filament (Morales *et al.*, 1988; Morales, 1991). It is produced by encapsulated second- and third-instar females and second-instar males which insert their mouthparts into beech phloem cells to feed on the sap. Excess sugar is excreted as drops of honeydew (a mixture of sucrose, fructose, oligosaccharides and small quantities of glucose (Grant and Beggs, 1989)).

Beech scale insects are found in generally high, but variable densities on red (*N. fusca*), black and mountain (*N. solandri*) and hard (*N. truncata*) beech trees (Wardle, 1984) in about 1 million ha of forest in northern South Island (Beggs, 2001). Estimates of scale insect population density range from about 1×10^5 scale insects ha^{-1} in Westland (Kelly, 1990) to about 2×10^7 ha^{-1} in Canterbury (Crozier, 1978). As well as site differences, the number of scale insects per tree is highly variable, and the honeydew standing crop varies seasonally (Moller and Tilley, 1989; Murphy and Kelly 2003), temporally (Gaze and Clout, 1983; Kelly *et al*., 1992), with prevailing weather (Moller and Tilley, 1989), and between canopy and ground level (Beggs and Wilson, 1991).

No measurements have been made of the annual production of honeydew, but based on a 24 h measurement at one site in August (Kelly *et al*., 1992) and the range of insect densities recorded, it has been estimated to be between 6 and 1200 litres of honeydew ha^{-1} $year^{-1}$ (Beggs, 2001). Belton (1978) estimated that 20-40% of all carbon fixed by beech trees may be lost to the tree through excretion of honeydew by scale insects, and Kelly *et al*. (1992) suggested it may be as high as 80%, although a more recent estimate was considerably lower (1.8%; Dungan and Kelly, 2003). These estimates are based on several untested assumptions and approximations. Given the widespread nature of the resource, and its likely importance in New Zealand's beech forest ecosystems, it is timely that more quantitative estimates of annual honeydew production are made.

This paper quantifies the amount and type of soluble carbon released to the ecosystem by the honeydew scale insect. We compare 24-h honeydew production with standing crop in *N. fusca* and *N. solandri* beech trees every month for two years. We also compare two different size classes of *N. fusca* beech, the amount of honeydew produced at two heights up the tree, i.e., approximately 1.3 m and 15.5 m above the ground, and standing crop in open and closed exclosures. The latter is used to estimate the impact of foraging animals (particularly *Vespula* wasps) on the standing crop of honeydew. We compare the sugar composition of honeydew from different tree types and between years.

Methods

This study was carried out near the Sabine hut on the southern edge of Lake Rotoroa, Nelson Lakes National Park (41°54'S, 172°41'E), South Island, New Zealand. The forest is dominated by *N. fusca*, *N. menziesii* and *N. solandri*, and is infested with honeydew-producing scale insects. The study site initially slopes gently from lake level (450 m a.s.l.), but then rises steeply to about 550 m a.s.l. The site is at the base of a mountain range, which rises to c. 2000 m a.s.l.. Mean annual temperature is about 10°C, and annual rainfall is about 1600 mm (J.R. Leathwick and R.T.T. Stephens, Landcare Research Ltd, Lincoln, N.Z., Unpubl.).

Five trees in each of three categories were selected for their ease of access into the canopy. Unlike many earlier studies, trees were not selected on the basis of honeydew density. These categories were: large *N. fusca* (0.80 m > diameter at breast height (d.b.h.) > 0.50 m), small *N. fusca* (0.20 m > d.b.h. < 0.50 m) and small *N. solandri* (0.20 m > d.b.h. < 0.50 m). *N. solandri* do not reach a d.b.h. > 0.50 m, so only one size category of that species was used. Six rectangular quadrats (10 × 25 cm) per tree were aligned with the long edge vertical to the trunk: three of the quadrats were located at chest height (1.3 m) and three equivalent quadrats in the subcanopy (15.5 m, s.e. ± 1.0). Quadrats were randomly located with respect to aspect and relative position on trunk. Some of the subcanopy quadrats were located on the branches and some on the trunk, depending on which were the most accessible. Each set of three quadrats consisted of one that was left open permanently (henceforth called "open quadrats"), a second one was covered permanently by a frame of shade cloth to exclude insects and birds ("closed quadrats"), and the third quadrat had a removable shade cloth frame so that we could open and close the quadrat ("closed 24-h quadrats").

The open quadrat was used to measure the standing crop of honeydew, while the closed quadrat measured standing crop in the absence of harvesting by invertebrates, birds and reptiles. Standing crop is defined as the amount of honeydew available on the trees at a given point in time.

Honeydew production was measured using the

closed 24-h quadrats. The closed 24-h quadrats had all honeydew removed c. 24 h prior to sampling. The exclosure for these quadrats was only in place for 24 h prior to sampling. We recorded the time between removal and sampling so that we could calculate how much honeydew was produced in exactly 24 h.

Approximately monthly from June 1999 to June 2001, the honeydew was sampled in each quadrat. All quadrats were sampled on the same day. Honeydew was measured using a simple gravimetric technique as described by Dungan *et al.* (2004). Honeydew was absorbed onto a small piece of filter paper; one piece of filter paper was used for each quadrat. The filter paper had been dried to constant weight, weighed and recorded prior to collecting honeydew. If the honeydew was too sticky to absorb onto the filter paper, then it was lightly sprayed with a mist of distilled water to dilute it. The filter papers were kept separated so that fluid did not move from one paper to another. The papers were then dried at 40°C to constant weight (about 24 h) and weighed. The difference in the mass of paper before and after honeydew collection was used as a measure of the dry weight of honeydew.

Calculation of honeydew production per m^2 forest

Eight circular plots (10 m radius) were positioned randomly, and the d.b.h. of each tree in each plot was measured. Allometric regression relationships previously developed for determining the relationship between tree d.b.h. values and total surface area of tree trunk and branch material (where branch material was defined as having a diameter over 0.5 cm) for *N. truncata* (Benecke and Evans, 1987; see also Hart *et al.,* 2003) were used for determining the total trunk and branch surface area for each tree. Values for individual trees were summed for each plot to give a measure of trunk and branch surface area per unit ground area. The total amount of honeydew produced per hectare was calculated separately for *N. solandri* trees, small *N. fusca* trees (d.b.h. < 50 cm) and large *N. fusca* trees (d.b.h. > 50 cm). This was done by multiplying the amount of honeydew produced per year per surface area of trunk or branch by the total trunk and branch surface area per hectare.

Honeydew sugar analysis

We analysed the sugars in the honeydew samples using a modification of the method of Picha (1985). Monthly samples for each year for each tree were combined so that there was sufficient material to analyse. Thus, comparisons can only be made between years for each treatment, and not within years.

Each filter paper was transferred into a 50-ml capped 'Falcon' centrifuge tube. A solution of 10 ml of 80% (v/v) ethanol was added to the tube, capped, and agitated gently for 24 h. The samples were then clarified by centrifugation (c. 5000 × *g*, 10 min), and the clear supernatant removed into a fresh centrifuge tube. The residue for the first extraction was then washed with an additional 5 ml of 80% ethanol and the suspension was clarified by centrifugation (c. 5000 × *g*, 10 min). The second extraction supernatant was combined with that from the first extraction and then mixed thoroughly. The extracts were stored at 4°C prior to HPLC analysis.

A Waters liquid chromatograph consisting of a model 2690 pump/controller/auto sampler and a model 410 refractive index detector was used. The detector signal (output at attenuation setting 64) was stored, integrated and manipulated using a personal computer running Waters Millennium software (version 3.2). Sugars were separated with a 220 × 4.6 mm Applied Biosystems "Brownlee" AMINO column fitted with a 18 × 4.6 mm Alltech "Allguard" AMINO guard column, maintained at 30°C using a Waters column heater. The mobile phase was degassed HPLC-grade acetonitrile: water (73:27, v/v). Solvent flow rate was 1.5 ml/min. Five "standard" samples of fructose, glucose and sucrose were used to cover the concentration range of interest (0.1 - 2.0 mg/ml for each sugar). Injection volume for both sugar standards and honeydew samples was 25 µl. Identification of each sugar was based on HPLC retention times, and quantification was based on peak area. Simple sugars other than fructose, glucose and sucrose were not detected. The detection limit for the method was c. 3 µg/ml for all of the simple sugars considered.

Statistical analysis

Analysis of variance was used to test variation in dependent variables, which included mass of honeydew produced, number of honeydew droplets produced and sugar composition. The effect of treatments (tree type, position on tree, exclosure type) on each variable was tested, as well as interactions. Values of the proportions of sugars in honeydew (glucose, fructose, sucrose and oligosaccharides) were arcsine-transformed to satisfy the requirement of normality.

Results

Honeydew standing crop and production

Tree type had a strong effect on honeydew standing crop and production and the number of honeydew droplets in both years (Tables 1, 2). In most months, there was significantly more honeydew per surface area of tree (mass and number of droplets) in small *N. fusca* and *N. solandri* trees than large *N. fusca* trees (Fig. 1a). Honeydew mass was highly variable, but tended to be low in winter (May-July) and in summer

Table 1. *F*-values (and corresponding *P*-values) for effects of treatments on the production of honeydew (mass (mg/quadrat/24 h) and number of droplets (number/quadrat/24 h)), derived from analysis of variance. All two-way interaction terms were tested in the ANOVA model, but none were found to be significant (data not shown).

Factor	Degrees of Freedom	Mass of honeydew produced		Number of honeydew droplets produced	
		Year 1	Year 2	Year 1	Year 2
Tree type[1] (A)	2	6.62 (0.002)	6.96 (0.002)	9.33 (<0.001)	15.13 (<0.001)
Position on tree[2] (B)	1	11.47 (0.001)	9.38 (0.003)	0.14 (0.714)	11.55 (0.002)
Exclosure treatment[3] (C)	2	0.81 (0.448)	3.16 (0.048)	0.28 (0.757)	1.95 (0.151)

[1]Tree types = large *N. fusca*, small *N. fusca* and small *N. solandri*
[2]Positions = chest-height (1.3 m), subcanopy (15.5 m)
[3]Exclosure treatments = open, closed for 24 h, closed

Table 2. Honeydew mass and numbers of droplets produced, averaged over all measurement dates for each of the first and second years of the study. Within each column, for each factor, numbers followed by the same letter do not differ significantly from each other at *P*=0.05 (Tukey's test following Analysis of Variance).

Factor	State of factor	Mass of honeydew produced (mg dry weight / quadrat / 24 h)		Number of honeydew droplets produced (number / quadrat / 24 h)	
		Year 1	Year 2	Year 1	Year 2
Tree type	Large *N. fusca*	1.41 b	1.79 b	2.01 b	1.83 b
	Small *N. fusca*	5.02 a	8.38 a	11.03 a	9.83 a
	Small *N. solandri*	6.88 a	9.80 a	11.04 a	13.44 a
Position on tree	Chest height (1.3 m)	2.33 b	3.79 b	7.66 a	5.37 b
	Subcanopy (15.5 m)	6.55 a	9.52 a	8.39 a	11.36 a
Exclosure	Open	5.03 a	8.87 a	7.05 a	8.30 a
	Closed for 24 h	3.22 a	3.40 b	8.19 a	6.26 a
	Closed	5.03 a	7.70 ab	8.83 a	10.53 a

Table 3. Percentage of total annual honeydew produced each month, for each of the exclosure treatments, and averaged over all years, types of trees, and positions on trees.

Month	Closed quadrats	24h closed quadrats	Open quadrats
January	4.5	3.1	2.3
February	3.6	3.9	1.4
March	15.1	8.9	10.2
April	10.2	12.8	15.8
May	4.5	4.1	3.2
June	2.2	2.3	1.6
July	8.0	9.0	10.0
August	13.0	19.6	12.0
September	9.0	7.8	9.2
October	6.7	10.3	11.7
November	17.1	13.6	19.8
December	6.1	4.6	2.8
TOTAL	100.0	100.0	100.0

(January/February) (Fig. 1a, Table 3), with peaks in production in spring (August-November) and in autumn (March/April) when the majority of the total annual honeydew production occurred (Table 3).

There was also a strong effect of quadrat position on both the mass of honeydew and number of droplets produced (Table 1). There was more honeydew per surface area of bark in the sub canopy than at chest-height on the trunk in most months (Figs. 1b, 2b). However, across the 15 trees the total production of honeydew (using data from the 24 h closed quadrats) for the subcanopy quadrats was not strongly related to the production for the quadrats at chest height (R^2 for years 1 and 2 were 0.322 (P = 0.027) and 0.153 (P = 0.153) respectively; all data log transformed). Honeydew production was negatively correlated with tree d.b.h., but this was only statistically significant for the subcanopy quadrats in year 2 (R^2 for year 1 = 0.095 (P = 0.261) and 0.013 (P = 0.692) for the subcanopy and chest-height exclosures respectively, and for year 2 = 0.262 (P = 0.061) and 0.361 (P = 0.023) for the subcanopy and chest-height exclosures respectively).

There was no detectable difference in honeydew mass collected in different exclosure treatments, except for year 2 when there was less honeydew in the 24-h

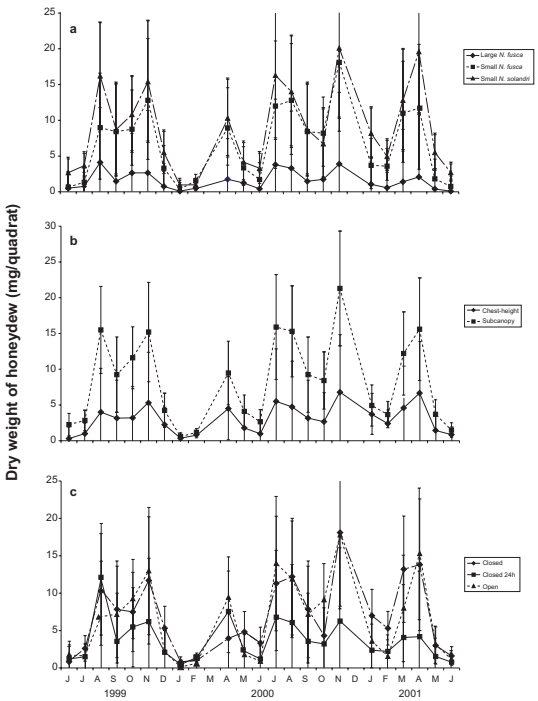

Figure 1. Comparison of dry weight of honeydew measured monthly over two years for a) tree type; b) position on tree; and c) exclosure treatment. Means are given with standard deviations. See Table 1 for statistical analyses.

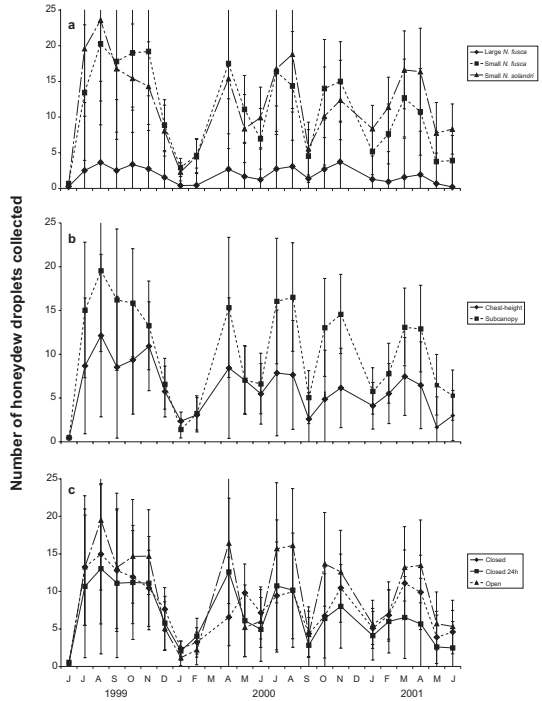

Figure 2. Comparison of number of droplets of honeydew collected for a) tree type; b) position on tree; and c) exclosure treatment. Means are given with standard deviations. See Table 1 for statistical analyses.

honeydew production exclosures than in the open standing crop exclosures (Fig. 1c, Table 1, 2). At the peak of the wasp season (March) in year 2, the standing crop was lower in the open exclosure than in the closed ones, but owing to a field accident, the March measurement was missed in year 1. There were no significant interactions between tree type, position on tree or exclosure treatment.

The production to standing crop ratio (ratio of data from the 24h closed quadrats to data from open quadrats) fluctuated considerably throughout the year but was lowest in the March-April and September-November periods (Table 4), indicating a lower turnover of honeydew in these periods. The ratio of standing crop in the closed to open quadrats was about twice as high for the December-February period than for the rest of the year (Table 4), indicating a greater removal of honeydew in the open quadrats during these months compared with the rest of the year.

Honeydew composition

The only treatment that affected sugar composition was tree type. Large *N. fusca* trees differed significantly

Table 4. Total honeydew production (data from 24h closed quadrats), ratio of production to standing crop (ratio of data from 24h closed quadrats to data from open quadrats), and ratio of closed to open standing crop (ratio of data from closed quadrats to data from open quadrats), averaged across all years, types of trees, and positions on trees.

Month	Production (mg/quadrat/24h)	Production to standing crop ratio	Closed to open quadrat ratio
January	1.42	0.763	2.097
February	1.81	1.675	2.935
March	4.07	0.508	1.647
April	5.87	0.474	0.717
May	1.90	0.769	1.587
June	1.06	0.855	1.581
July	4.15	0.530	0.889
August	8.99	0.958	1.210
September	3.57	0.496	1.090
October	4.71	0.512	0.642
November	6.24	0.405	0.967
December	2.11	0.981	2.474
AVERAGE	2.99	0.744	1.358

Table 5. *F*-values (and corresponding *P*-values) for effects of treatments on the proportion of glucose, fructose and sucrose in the total honeydew produced during each of the first and second years of the study, derived from analysis of variance. All data are Arcsine-transformed. All two-way interaction terms were tested in the ANOVA model, but none were found to be significant (data not shown).

Factor	Degrees of Freedom	Year 1			Year 2		
		Glucose	Fructose	Sucrose	Glucose	Fructose	Sucrose
Tree type[1] (A)	2	0.47 (0.068)	12.32 (<0.001)	19.40 (<0.001)	2.06 (0.137)	1.46 (0.242)	6.08 (0.004)
Position on tree[2] (B)	1	0.09 (0.912)	1.02 (0.282)	1.37 (0.247)	1.08 (0.304)	0.00 (0.959)	0.27 (0.604)
Exclosure treatment[3] (C)	2	2.16 (0.122)	0.35 (0.707)	0.25 (0.779)	1.75 (0.183)	0.11 (0.899)	0.26 (0.773)

[1]Tree type = large *N. fusca*, small *N. fusca* and small *N. solandri*
[2]Position = chest-height (1.3 m), subcanopy (15.5 m)
[3]Exclosure treatments = open, closed for 24 h, closed

Table 6. Total honeydew production per unit land area. Numbers in brackets are standard deviations.

Measurement variable	*N. solandri*	*N. fusca* (small)[a]	*N. fusca* (large)[a]	Total
Tree basal area (m^2/ha)	15.4 (13.5)	8.6 (4.9)	23.5 (21.4)	49.7 (18.0)[b]
Surface area of trunks + branches (m^2/ha) (S)	9270 (7642)	5247 (3238)	10379 (9080)	26501 (7512)[b]
Total honeydew production in Year 1 (kg dry weight/m^2 trunk or branch surface)[c] (P1)	0.25 (0.14)	0.18 (0.09)	0.05 (0.07)	
Total honeydew production in Year 2 (kg dry weight/m^2 trunk or branch surface)[c] (P2)	0.40 (0.18)	0.30 (0.16)	0.07 (0.13)	
Total honeydew production in Year 1 (kg dry weight/ha) (= S × P1)	2271	960	529	3760
Total honeydew production in Year 2 (kg dry weight/ha) (= S × P2)	3041	988	590	4619

[a]Small = < 50 cm d.b.h., large = >50 cm d.b.h.
[b]Values include *N. menziesii*, which does not produce honeydew.
[c]Values derived from Fig. 1 (closed 24 h exclosures).

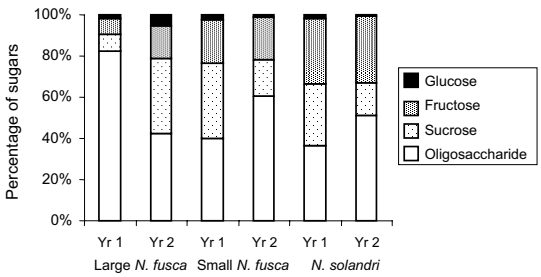

Figure 3. Comparison of sugar composition of honeydew for different tree types in two years. See Table 5 for statistical analyses.

from both small *N. fusca* and *N. solandri* trees (Table 5). Honeydew was composed of a small proportion of glucose, and larger (but varying) proportions of fructose, sucrose and unidentified oligosaccharides (Fig. 3). At least 30% of the sugars were oligosaccharides, and for large *N. fusca* in year 1, it was over 80%. The oligosaccharides were not identified, but were short-chain sugars. Sugar composition not only varied with tree type, but also between years (Fig. 3). In year 1, the ratio of fructose:sucrose was similar for each tree type, but in year 2 the ratios were variable.

Honeydew production per ha of forest

We estimate the total honeydew production per unit land area in this forest in year 1 (3800 kg dry weight ha^{-1}) was less than in year 2 (4600 kg dry weight ha^{-1}) (Table 6). *N. solandri* contributed about 60% of the total production, whereas large *N. fusca* only contributed about 10% despite having a larger biomass than *N. solandri* (Table 6).

Discussion

Honeydew scale insects can add a large amount of soluble carbon to New Zealand beech forest ecosystems in the form of soluble sugars. In this study 3800–4600 kg dry weight honeydew ha^{-1} $year^{-1}$ was produced. This is at least an order of magnitude greater than the amount of honeydew produced (400–700 kg fresh mass ha^{-1} $year^{-1}$) by high aphid densities in Northern Hemisphere Norway spruce (*Picea abies*) forests (Zwölfer, 1952; Zoebelein, 1954; Eckloff, 1972 (quoted in Stadler *et al*., 1998)), depending on the concentration of honeydew in the Northern Hemisphere studies.

Combining our annual honeydew production and sugar composition data (which estimates the carbon content of honeydew sugar is 42% by molecular mass) with published data on net primary productivity (NPP) gives an estimate of the carbon loss to beech trees via honeydew. Detailed measurements by Benecke and Evans (1987) found NPP in an ecologically similar forest of *N. truncata* to be 24.7 t ha^{-1} $year^{-1}$. Assuming our site has a similar NPP, and NPP does not vary between years, then between 6 and 8% of NPP was released as honeydew. This is biologically significant – consumption of this amount of NPP would usually be sufficient to reduce plant growth (Cebrian, 1999; Cyr and Pace, 1993).

Our estimate of the amount of carbon lost to the tree via honeydew is higher than the 1.8% of NPP estimated using production measurements over 4 days in late autumn at a higher altitude site (Dungan and Kelly, 2003). However, the estimates from studies published even earlier (23–40%, Belton, 1978; 80%, Kelly *et al*., 1992) were an order of magnitude higher than these recent estimates. All the estimates are based on a number of assumptions, but the estimate from this study is more robust because it is based on honeydew production data collected monthly for two years.

The earlier estimates of %NPP lost via honeydew were strongly influenced by the ratio of daily honeydew production: standing crop. Belton (1978) guessed that daily honeydew production was five times the standing crop, whereas Kelly *et al*. (1992) measured the ratio between production and standing crop on a single day as 1:11.5. Dungan and Kelly (2003) measured the average ratio as 1:6.61, but their study did not measure seasonal patterns in production. The ratios measured in this study were considerably lower (average across all trees and years = 0.74; Table 4) than the earlier estimates of the ratio and this largely explains why our estimate of the carbon contained in honeydew as a percentage of NPP was lower than the Belton (1978) and Kelly *et al*. (1992) estimates.

Additional differences between the studies are the estimates of NPP and the method of calculating tree surface area. The earlier studies used lower estimates of NPP than the 24.7 t ha^{-1} $year^{-1}$ estimated by Benecke and Evans (1987) used in our study. Using Belton's (1978) estimate of NPP for a similar altitude site would increase our estimate to between 14 and 17% of NPP released as honeydew. We also used a more complex model for calculating the surface area per tree (based on Benecke and Evans, 1987), whereas the earlier studies used an equation for simple cones.

Honeydew production is highly variable between individual trees, tree type, and, position on tree, and within and between years. Since honeydew production and number of droplets followed similar patterns in the 24-hr exclosures (Figs. 1, 2), and the number of droplets is largely a reflection of the number of active scale insects, this suggests the population density of scale insects was responsible for much of the variation. Other factors contributing to this variation are not well understood, but we suggest that climate may also be

important, particularly in variation between years.

Sugar composition of honeydew also varied between years, and again, this may be because of inter-year variation in climate affecting the population dynamics of the scale insects or wasps, changes in the physiology of the tree or some combination of these factors. Honeydew sugar composition could be influenced by change in instar stages of the scale insect if the age distribution of the insect populations varied between years. Costa *et al*. (1999) found that the nymphal stage of the honeydew-producing *Bemisia argentifolii* (Homoptera: Aleyrodidae) was a factor in influencing sugar composition, probably because of changes in the metabolic needs of nymphs, or changes in the abundance of endosymbiotic bacteria housed in the nymphs. Sugar composition of honeydew can also be influenced by the presence of other insects that remove the honeydew. This has been shown for ants attending *Tuberculatus quercicola* (Homoptera: Aphididae), possibly because the ant directly induced changes in aphid excretion behaviour and carbohydrate metabolism (Yao and Akimoto, 2001). Similarly, the population density of wasps in honeydew beech forests may affect the sugar composition of honeydew by increasing the flow rate through the scale insect, perhaps causing the scale insect to alter its behaviour or physiology. A further possibility is a change in physiology in the beech trees. In the first year of this study, c. 200 beech seeds m^{-2} of seed tray were collected at nearby Mt Misery, whereas in the second year of this study, c. 4900 beech seeds m^{-2} were collected in the same trays (Butler, 2003). Such a difference in seeding could have altered the sugar composition of phloem sap. Earlier work has shown that crop load of fruit trees can affect the non-structural carbohydrate composition of the plant (e.g., Grossman and De Jong, 1995; Nii, 1997; Klages *et al*., 2001).

The composition of honeydew sugars in this study was similar to that of Grant and Beggs (1989) i.e., small amounts of glucose, and larger proportions of fructose, sucrose and oligosaccharides. However, this longer-term study detected significant differences in honeydew composition between *N. fusca* and *N. solandri*, whereas Grant and Beggs (1989) found no difference. Grant and Beggs (1989) also found honeydew composition varied with weather–further support that climate has an important role in variation.

Earlier experiments with wasp exclosures demonstrated that wasps were the main consumers of honeydew for about four months of the year (Moller *et al.,* 1991). Wasps removed more than 90% of the honeydew over this period (Moller *et al.,* 1991), but those measurements were made when wasp density was similar to, or higher than, the peak measured in 1989 (Thomas *et al.,* 1990). Average wasp nest density was relatively low (c. 8 nests ha^{-1}) in the two years of our study compared to 1989 (c. 23 nests ha^{-1}) (Barlow *et al.,* 2002). Our experiment did demonstrate differences between exclosure types in year 2, which we largely attribute in some months (January – March 2001) to wasps consuming honeydew in the open exclosures. Further, by far the highest ratios for standing crop between the closed and open exclosures were for the December–March period (Table 4), which would reflect greater consumption of honeydew in the open exclosures at this time of the year, compared to other times of the year. However, the effect was less than measured by Moller *et al.* (1991), which is consistent with lower wasp densities.

Honeydew is a key food source in this habitat for some native birds such as kaka (*Nestor meridionalis*) (Beggs and Wilson, 1991), tui (*Prosthemadera novaeseelandiae*) (Moller *et al.*, 1996) and bellbird (*Anthornis melanura*) (Murphy and Kelly, 2003). However, native birds and insects currently remove only a small proportion of honeydew and, in the absence of wasps, the majority of it falls to the ground around the tree (Moller and Tilley, 1989). A much larger proportion of honeydew may have been consumed by birds in pre-human times than is the case now, since introduced mammalian predators have greatly reduced the abundance of birds in these forests (e.g. Wilson *et al.,* 1998; Murphy and Kelly, 2003).

Honeydew that reaches the ground may play an important role in ecosystem processes driven by soil organisms; such as decomposition, mineralisation of nutrients, and the supply from the soil of plant-available nutrients (Beggs and Wardle 2005). Soil micro-organisms and the soil fauna that consumes them are often limited by the availability of carbon (Burford and Bremner, 1975; Bradley *et al.,* 1992) and addition of even small amounts of soluble carbon to most soils results in rapid microbial growth and activity (e.g., Dighton, 1978; Anderson and Domsch, 1985), although exceptions exist (Wardle, 1992). The effect of large quantities of soluble sugar on the microbial biomass in honeydew beech forest is unknown.

In the only comparable work to date, studies in Norway spruce forests in Germany found that addition of honeydew from seasonal aphid outbreaks in the northern hemisphere produced higher concentrations of dissolved organic carbon in the throughfall beneath infested trees compared to uninfested trees, but lower concentrations of dissolved organic nitrogen, NH_4-N and NO_3-N (Stadler and Michalzik, 1998; Michalzik *et al.,* 1999; Stadler *et al.,* 2001). However, honeydew in spruce forests did not affect the concentration of dissolved organic carbon in the soil leachate, presumably because of complete and rapid metabolism by soil micro-organisms (Stadler and Michalzik, 1998; Michalzik *et al.,* 1999; Stadler *et al.,* 2001). Honeydew in spruce forests did significantly affect the nitrogen

mineralisation-immobilisation balance on the forest floor (Michalzik *et al.,* 1999), although time scale and degree of infestation can obscure effects (Stadler *et al.,* 2001).

Honeydew produced by the beech scale insect in New Zealand consists of low levels of nitrogen (Grant and Beggs, 1989), but large amounts of low molecular weight sugars that are easily consumed. While we do not know what influence this honeydew will have on forest floor solution chemistry, the amount of soluble carbon entering the system is far greater than that which has caused measurable changes in northern hemisphere forests. Therefore, the consequences of beech honeydew production for the functioning of the decomposer subsystem and nutrient cycling processes are likely to be considerable.

New Zealand honeydew beech forests are unique internationally in the quantity of soluble carbon produced per unit land area of forest. Such a large, biologically available carbon source is a crucial resource for the above-ground system, and probably also for the below-ground system. Therefore, scale insects, despite their relatively small biomass in the ecosystem, have the potential to exert important effects at both the community- and ecosystem-levels, and are therefore likely to function as keystone organisms in these forests.

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