Effect of host-tree and environmental variables on honeydew production by scale insects (*Ultracoelostoma* sp.) in a high elevation *Nothofagus solandri* forest

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Abstract: Honeydew excreted by phloem-sap sucking scale insects (*Ultracoelostoma* sp.) living in the bark of beech (*Nothofagus solandri*) trees growing at a high elevation (900 m) site in the Craigieburn range of Canterbury, New Zealand, was measured over four days during 1–10 May 1996. Average standing crop of honeydew sugar was 3.1 mg m^{-2}, and ranged from 0.4 to 5.5 mg m^{-2}. Daily production of honeydew sugar ranged from 0.2 to 1.5 mg insect^{-1} 24 h^{-1}, and 4.1 to 45.9 mg m^{-2} 24 h^{-1}. Honeydew production varied significantly between trees, and trees with the highest mean individual rates of production (mg sugar insect^{-1} 24 h^{-1}) tended to be those with the highest numbers of insects per unit bark area. Air temperature averaged over the 24 hours preceding each production sample explained 65% of the variability in 3-hourly honeydew production, showing that honeydew production is controlled by environmental and host-tree variables. Using this data, together with previously published estimates of carbon uptake and seasonal variability in honeydew standing crop, it was estimated that carbon contained in honeydew is equivalent to 1.8% of net primary production of beech trees at Craigieburn. Determining the effects of environmental variables on tree and insect physiology will allow formulation of an environmentally-driven process-based model of honeydew production.

Keywords: environmental controls; herbivory; honeydew; *Nothofagus*; phloem feeding; primary production; sooty beech scale; *Ultracoelostoma*.

Introduction

A notable feature of the beech (*Nothofagus* spp.) forests of the northern South Island of New Zealand is the interaction between beech trees and sap-sucking sooty beech scale insects in the genus *Ultracoelostoma* (Margaridoideae). Second- and third-instar females and second-instar males of *Ultracoelostoma* construct and inhabit tests on the trunks and branches of beech trees (Morales *et al*., 1988). They insert their stylets into phloem cells and feed on the phloem sap, which is rich in photosynthetically derived-carbohydrates but contains only low concentrations of proteins (Grant and Beggs, 1989). The insects ingest more carbohydrate than they assimilate or utilize, and excrete excess sugar in solution through a waxy, filamentous, anal tube. The resulting sugar-rich solution, called honeydew, forms droplets at the end of the insects' anal tubes. Honeydew is a key component of beech ecosystem energy fluxes. It is an important food source for birds and insects, both native (Gaze and Clout, 1983; Beggs and Wilson, 1991) and introduced (Moller and Tilley, 1989; Moller *et al*., 1991; Beggs, 2001). Honeydew that drops from the tubes supports thick communities of sooty moulds on tree trunks, leaves, and in the forest floor litter layer, and honeydew may be important in regulating ecosystem nutrient turnover (Wardle, 1984). In the beech forests of the Craigieburn range in Canterbury honeydew is one of the few food resources available to birds year round (Murphy and Kelly, 2003).

Although there is a growing body of work that has investigated interactions among honeydew consumers, very little is known about what controls honeydew production by individual insects, or at the scale of individual beech trees. This study used four days of field data to investigate honeydew production dynamics at a high altitude (900 m) *Nothofagus solandri* forest. This expands on the only other published honeydew production data, collected over 24 hours from a lower altitude (390 m) site in the Canterbury foothills (Kelly *et al*., 1992). That study presented data in terms of volume of honeydew excreted by scale insects. While such data are relatively easy to collect, they are of limited use in investigating the importance of honeydew to beech forest ecosystem dynamics. Here, by combining honeydew volume and concentration data, a direct measure of host-tree carbohydrate losses via scale-insect sap feeding can be obtained.

The aims of this study were to quantify honeydew standing crop and production at a high altitude beech forest site, and to investigate tree and environmental factors associated with high honeydew production. Field-collected data, together with information from previously published investigations, were used to scale-up our insect-level production data to estimate the proportion of net annual beech tree growth increment accounted for by the sap extracted by the sooty beech scale insects.

Methods

Data were collected over four separate periods ("days") during the period May 1 to May 10 1996 in a *Nothofagus solandri* var. *cliffortioides* forest growing at Craigieburn (171°42'E, 43° 06'S). The site is at an altitude of 900m a.s.l., which is near the upper altitudinal limit of *Ultracoelostoma* (Morales, 1991). A temporary weather station was installed at the site to record 30 min average air temperature (T_a) and relative humidity. These data were used to calculate air saturation deficit (D). Irradiance (Q, 400–700 nm) data were obtained from a permanent weather station located 200 m from the field site.

On the first day, sample trees were selected randomly along a walking track. The trees were used for subsequent honeydew sampling only if anal threads were present; trees where tubes were absent were noted, but not used further. Fifty-seven trees were selected, of which 28 (49%) had anal threads and were used for subsequent honeydew sampling. A band of bark 50 cm high around the trunk of each sampling tree was defined from 1.1 to 1.6 m high for subsequent honeydew sampling, giving sampling areas of 0.15 to 0.57 m^2 per tree, depending on tree diameter. On each sampling day a quarter of the band was covered with fine nylon mesh to exclude foraging birds and insects. There was no difference in honeydew production from covered and uncovered parts of the sampling bands on any of the days (range of P values 0.17 to 0.95), so data from covered and uncovered areas were pooled. Each bark band was further divided into two 25-cm high bands, and the location of every anal thread within each of these bands was mapped. At each collecting day, either of the upper or lower bands was selected randomly for production data collection, and the other left uncollected. While this treatment was designed to reduce any potential effect of honeydew collection on production rate, it meant that honeydew was not collected from every mapped insect on every day. All drops of honeydew present on mapped threads within the bands selected for sampling at each day were collected every three hours in capillary tubes. Apart from on the third day, honeydew was not collected at 3 am because drops were too small to be collected.

The gravimetric concentration (g carbohydrate per 100 g solution) of sugar in honeydew collected from outside the defined bark bands was estimated at each three-hourly sampling with a hand-held refractometer (HSR500, Atago, Japan), and corrected for actual carbohydrate concentration by dividing by 1.145 (Grant and Beggs, 1989). Gravimetric concentrations (g sucrose 100 g solution^{-1}) were converted to volumetric concentrations using the equation

$$y = 0.81 + 0.92x + 0.0059x^2,$$

where y is the concentration per volume (g sucrose 100 ml solution^{-1}) and x is the concentration per mass (Moller *et al.*, 1996). A linear relationship between three-hourly honeydew sugar concentration (g 100 g^{-1}) and air saturation deficit (D; concentration = 115.5×D–3.9, R^2 = 0.64, P < 0.001) permitted estimation of sugar concentration at three sampling times when honeydew volumes were too low for collection in the capillary tubes (Day 1, 1500 h; Day 4, 2400 and 0600 h).

Data analysis

Honeydew volume and concentration data were combined to give an estimate of honeydew sugar production. This provides a useful measure of carbohydrate losses from host trees, and is able to be used in calculating ecosystem energy flows and in determining the effect of insect infestation on host-tree carbon dynamics.
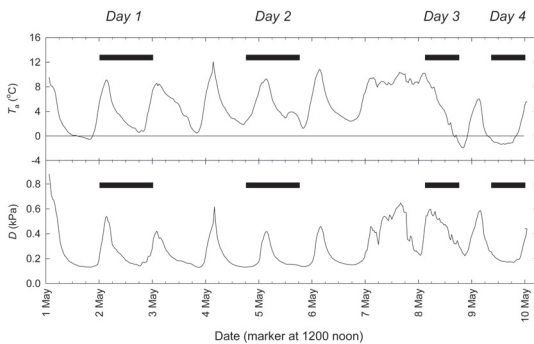
Four tree-level variables were measured or calculated; the number of productive insects per unit bark area (a productive insect was defined as one that excreted a measurable volume of honeydew on at least one of the measuring days), host tree diameter at 1.4 m (d.b.h.), the proportion of bark area covered by sooty mould, and the total quantity of honeydew sugar (mg m^{-2} bark) collected over the four days as a measure of tree-level honeydew production.

Variability in production by individual mapped insects between days, and between trees within days, was investigated with analysis of deviance statistics calculated with a generalized linear model with a gaussian error structure and identity link function. The effect of air temperature (T_a), air saturation deficit (D), and irradiance (Q) on 3-hourly honeydew production was investigated using a multiple regression model. At each 3-hourly sampling period, average T_a and D, and integrated Q, over the preceding 3, 12, and 24 hours were calculated from the weather station data. The predictive power of these nine variables was investigated with automated backward elimination, using the minimum Akaike Information Criterion as the selection statistic (Venables and Ripley, 1994).

Results

Weather conditions at the field site

Weather data were collected for 10 days, beginning May 1 (the day before honeydew sampling began), and ending with the final honeydew measurements on May 10 (Fig. 1). The first two honeydew sampling days coincided with mild late autumn conditions, with morning minimum $T_a > 0$°C on both days (Table 1). In contrast, Days 3 and 4 coincided with the progression of a cold frontal system across the South Island. Air temperature was around 10°C from midday on May 7 to midday May 8, associated with warm NW winds preceding the front. In the afternoon of May 8, during which the Day 3 honeydew data were collected, T_a steadily dropped as the front passed over the field site. Sampling was suspended during the day of May 9, because rain was washing honeydew from the trees, and resumed that evening as Day 4. Midday T_a was 5°C cooler on May 9 than it was on May 8. Freezing T_a was observed from the afternoon of May 9 until the morning of May 10; Day 4 data were collected during this time.
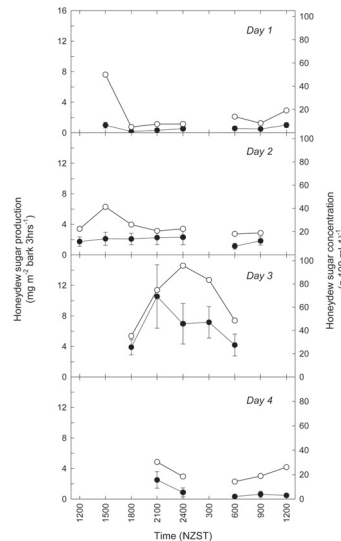
Honeydew standing crop and production

Honeydew production data were collected from 203 mapped insects. Data were collected from 26 of these insects on every day, 119 insects on two or three of the days, and 58 insects on only one of the days. Production of honeydew was highly variable at the tree level. Of the 28 sample trees that hosted productive insects, honeydew was excreted by insects on eight trees on every day, 15 trees on either two or three days, whereas insects on five of the trees excreted honeydew on only one of the days. Daily production varied significantly between days, both by individual insects ($F = 29.14$, $P < 0.001$) and on a bark-area basis ($F = 8.52$, $P < 0.001$; Table 1). The range of production values varied seven-fold on a per-insect basis, but eleven-fold on a bark-area basis because bark-area production is the product of per-insect production, as well as the number of productive insects per m^2 bark.

Daily patterns in honeydew production were inconsistent among days (Fig. 2). While honeydew production varied during the day on each collecting day, analysis of variance showed no evidence that

Figure 1. Daily course of 30 min average values of air temperature (T_a) and air saturation deficit (D) from midday 1 May 1996 to 1:00 pm 10 May 1996. Honeydew production data were collected over four sampling days, marked by black bars.

Figure 2. Three-hourly honeydew sugar production (●), averaged over the 28 sampling trees, and honeydew sugar concentration (○) for each sampling campaign. 0600 data on Days 1, 3, and 4 were measured over 6 hours. Error bars are ±1 standard error of the mean.

Table 1. Daily maximum and minimum air temperatures, and values for average honeydew excreted per scale insect and per quadrat over the four honeydew sampling days. Values in parentheses are one standard error of the mean.

	Air temperature (°C)		Standing crop	Average honeydew production	
	Max.	Min.	mg m^{-2}	mg insect^{-1} 24 h^{-1}	mg m^{-2} 24 h^{-1}
Day 1 (May 2/3)	8.9	0.6	0.42 (0.13)	0.22 (0.05)	4.08 (1.28)
Day 2 (May 5/6)	9.1	1.2	1.94 (0.54)	0.50 (0.07)	13.52 (4.23)
Day 3 (May 8/9)	10.7	2.7	5.54 (1.38)	1.54 (0.19)	45.87 (12.00)
Day 4 (May 9/10)	6.2	−1.5	4.54 (2.07)	0.25 (0.06)	6.75 (3.33)

variability between 3-hourly samples was greater than the variability between trees at each 3-hourly sample (range of P values; 0.09–0.97). Given this lack of significant diurnal pattern, and the fact that few animals were observed harvesting honeydew either by day or by night, it was assumed that the first honeydew sampling at each collecting day was a suitable approximation of the standing crop during the day. This allowed calculation of the daily standing-crop-to-production ratio, which ranged from 1:1.49 on Day 4, to 1:9.71 on day 1, and averaged 1:6.61 (Table 1).

Factors accounting for high honeydew production

Across all days there was a weak but significant relationship between the number of insects per unit bark area and individual per-insect production (Table 2; Fig. 3). This effect was positive, suggesting that some trees were able to support heavier infestations of scale insects, each of which tended to be more productive than insects on trees with lighter insect infestations. There was no evidence that individual insect production was related to tree diameter, or the proportion of bark area covered by sooty mould (Table 2).

Table 2. Analysis of deviance for individual insect honeydew sugar production (mg insect^{-1} 24 h^{-1}) across all sampling days, where per-tree production is the average honeydew production per tree (mg m^{-2}), insects m^{-2} is the number of productive insects m^{-2} of host-tree bark, tree diameter is diameter at 1.4 m, and % sooty mould is the proportion of bark area covered by sooty mould. All two-way interactions were tested, and none was found to be significant (data not shown).

Effect	d.f.	Deviance	F	p
Day	3	149.23	30.11	<0.001
Per-tree production	1	19.28	11.62	<0.001
Insects m^{-2}	1	6.69	4.03	0.05
Tree diameter	1	3.16	1.91	0.17
% sooty mould	1	0.22	0.13	0.72
Residual	479	961.79		

The backward elimination of environmental variables selected a model with average D and T_a over the preceding 24 hours as predictors of 3-hourly honeydew production. Over the ten-day period spanning honeydew sampling, the three environmental variables were generally all cross-correlated at each 3-hourly sampling, particularly when averaged or integrated over the previous 24 hours (24 hour T_a and D, $R^2 = 0.29$, $P = 0.006$; T_a and Q, $R^2 = 0.73$, $P < 0.001$; D and Q, $R^2 = 0.21$, $P = 0.02$). A single environmental variable, the average T_a over the preceding 24 hours was selected. This explained 65% of the variability in 3-hourly honeydew production (Fig. 4), showing that honeydew production was significantly related to environmental conditions in the time preceding sampling.

Discussion

Honeydew standing crop and production

The honeydew concentration values we observed at Craigieburn are among the highest so far reported, in part because the correction of Moller *et al.* (1996), used to correct gravimetric honeydew concentrations (i.e. g 100 g^{-1} as read from the refractometer scale) to volumetric concentrations (i.e. g 100 ml^{-1}), has a small effect at low honeydew concentrations but a relatively large effect at concentrations higher than *c*. 60 g 100 g^{-1} (Bolten *et al.*, 1979). Also, the maximum honeydew concentrations observed in this study seem high because previous concentration data have usually been collected early in the morning, before significant droplet evaporation has occurred [e.g. 9:00 am to 11:00 am (Gaze and Clout, 1983; Moller *et al.*, 1986; Moller and Tilley, 1989; Murphy and Kelly, 2003)]. It is not surprising, therefore, that the concentrations observed during a day with dry winds and relatively high air saturation deficit associated with NW föhn winds should be higher than previously reported.
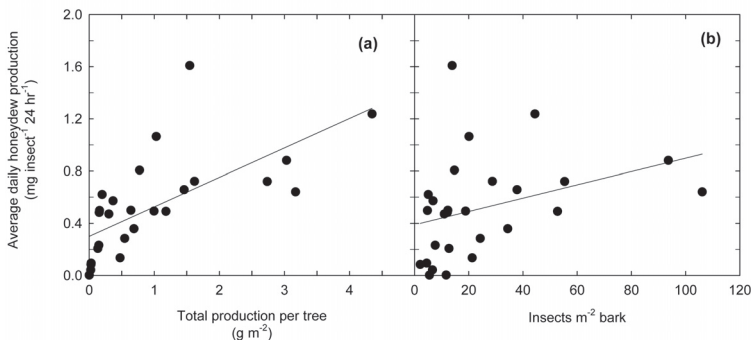
Figure 3. The relationship between overall average honeydew production per insect on each of the 28 sampling trees and the number of productive insects per square metre of bark sampled. Regression line: average production = 0.005 × insects m^{-2} + 0.39, $R^2 = 0.08$, $P = 0.07$. See Table 2 for analysis at the individual insect level.
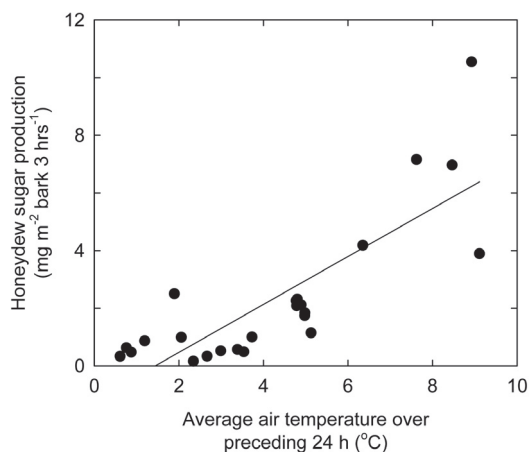
Figure 4. The relationship between 3-hourly honeydew production and average air temperature (T_a) in the 24 hours preceding honeydew sampling. Production $= 0.83 \times T_a - 1.20$, $R^2 = 0.65$, $F_{(1,22)} = P < 0.001$.

The estimate of average honeydew standing crop observed at Craigieburn is at the low end of the range of values previously reported, which have been recalculated in units of mg sugar m^{-2} bark and collated in Table 3. The estimate derived in this study is relatively low, due to seasonal, altitudinal, and methodological factors. Sampling was conducted in late autumn, and the maximum standing crop estimate observed here is similar to winter values from other seasonal studies [e.g. minimum values from Gaze and Clout (1983) and Moller *et al.* (1991)]. The comparatively low values may have been affected by sampling methodology. Some of the higher standing crop values collated in Table 3 [e.g. maximum values from Gaze and Clout (1983), Moller and Tilley (1989) and Moller *et al.* (1991)] were observed in studies where trees were not randomly selected and sampling was either definitely or probably skewed towards higher levels of scale insect infestation. Studies where sample trees were selected because they had a large standing crop (e.g. Gaze and Clout, 1983; Moller *et al.*, 1991) have standing crop estimates at least an order of magnitude greater than those where trees were randomly selected (e.g. Murphy and Kelly, 2003; this study).

The results collated in Table 3 hint at a location-dependent effect on honeydew production, with studies from the Nelson region reporting higher values than studies from Canterbury. Whilst some of this may be a result of methodological biases mentioned previously, some may also be due to host-tree species (i.e. *Nothofagus fusca* or *N. truncata* near Nelson, compared with *N. solandri* in Canterbury). Kelly (1990) reported a highly significant effect of host-tree species on scale insect infestation in a study near Greymouth, with *N. fusca* having more than ten times the number of insects m^{-2} of bark area than *N. solandri*. Some of the location-dependent variability may also be due to altitude. Kelly

Table 3. Range of published honeydew sugar standing crop data. Standing crop values re-calculated from data presented in each study, with assumptions regarding honeydew concentration and average drop size, are described in notes.

Source	Location	Standing crop mg sugar m^{-2} bark		Notes
		max.	min.	
Boyd (1987)	Nelson	85.8	1.9	Re-calculated from Table 1.1
Gaze and Clout (1983)	Winns Bush	306.0		Absolute seasonal range over 3 sites near Nelson.
	Grahams bush		14.3	Calculated from Figs. 3 and 4, assuming drop size = 0.5 µl, 20 trees chosen with "good quantities of honeydew".
Moller *et al.* (1991)	Trass, Nelson	305.4	28.8	10 heavily infested tree chosen in paired covered vs. uncovered design. Calculated from Figs. 4, 5, and 6.
Moller and Tilley (1989)	Trass, Nelson	607.8	0.8	10 trees chosen with a range of infestation. Calculated from Figs. 4, 5, and 6.
Moller *et al.* (1996)	Trass, Nelson	540.3	91.6	Range is from 1 hour (min.) to 1 day (max.) after cropping. From Figs. 2, 3, and 4.
Kelly *et al.* (1992)	Oxford	27.9	7.8	Range with one 24 hour period. Assumes average honeydew concentration of 25% w/w.
Murphy and Kelly (2003)	Craigieburn	6.4	0.1	Seasonal range, average over all bark on 20 randomly selected trees.
A.W. Robertson, *pers. com.*	Richmond	19.4	0.3	Trees randomly selected
This study	Craigieburn	138.0	2.5	Range over all trees with productive insects
		67.6	1.2	Range averaged over all trees

et al. (1992) observed much higher levels of honeydew infestation on *N. solandri* at a lower altitude (400 m) Canterbury site than were observed on the same species growing at 900 m in this study. This point is discussed further in relation to estimating production as a proportion of carbon uptake.

Factors associated with high honeydew production

There were strong tree and environmental effects on honeydew production at the Craigieburn site. Some of these effects may have been influenced by aspects of sampling methodology. Honeydew production was sampled over only four days. Although this is four times longer than the only other published honeydew production data (Kelly *et al.,* 1992), it limited the range of environmental conditions that the insects and trees were exposed to during the sampling period. However, the passing of a southerly front between sampling days 3 and 4 meant that a wide range of temperatures was observed over the four days (continually warm temperature over the 24 hours preceding day 3, then freezing conditions during day 4). Furthermore, because insects were individually mapped, the same insects were followed over the four days. This meant that if an insect produced a single drop of honeydew on day one, it was counted as being present and capable of producing drops on the other three days.

Honeydew production was sampled over a relatively small proportion of bark area, conveniently close to the ground. Scale insects can be found in bark in the upper reaches of beech trunks and branches (Morales *et al.,* 1988). We cannot be absolutely certain that insects are randomly distributed over the available bark area, or that there is not a tree-position effect on individual insect honeydew production. However, casual observation suggested that insects were evenly distributed within trees at Craigieburn, and that if any within-tree pattern in insect distribution was present, it was present equally over all the trees sampled. Furthermore, the area of bark sampled in this study is considerably larger than in previously published work [e.g. 0.0125 m^2 in Kelly *et al.* (1992), 0.04 m^2 in Moller *et al.* (1991), cf. 0.15 to 0.57 m^2 in this study] that has sampled bark at similar height on tree trunks.

There was no effect of tree diameter on insect infestation. This is in contrast to Kelly (1990), who observed a highly significant effect of host tree diameter on the number of productive threads per unit bark area. This difference may be partly due to the relatively small range of tree diameters that were sampled (10 to 36 cm d.b.h.) compared with the range of sizes in the Kelly (1990) study (2 to 100 cm d.b.h.), although re-analysis of the Kelly (1990) data did show a significant relationship between diameter and infestation over the 10 to 36 cm d.b.h. range (R^2 = 0.31, P < 0.01).

The results presented in Fig. 3 show a positive relationship between the number of scale insects m^{-2} bark and daily mean honeydew production per insect that has been observed previously (Kelly *et al.*, 1992). This points towards a strong effect of host-tree on honeydew production. It appears that some trees are able to support greater numbers of more productive insects. Carbohydrate availability has been shown to alter the success of gall-forming aphids (Inbar *et al.*, 1995), so this host-tree effect may be linked to tree photosynthesis or tree growth rate. Recent work has shown that the host-tree effect is not transient; the relative rank of trees, determined by honeydew standing crop, was remarkably consistent over 12 months of measurements (Murphy and Kelly, 2003). Future work might examine whether the relationship between the number of insects m^{-2} and per-insect production is due to higher survival or fecundity of scale insects on trees where average per-insect honeydew production is higher. Confirmation of a direct effect of host-tree net productivity on scale insect honeydew production will require direct measures of photosynthesis and phloem dynamics as well as rates of honeydew sugar production.

This study highlighted a strong environmental control on honeydew production. Some of this effect may be due to the effect of elevated air saturation deficit on honeydew sugar concentration. Xylem transport can be described as a simple mass flow driven by gradients of negative water potential from the leaves to the roots. In contrast, phloem transport is determined by gradients in positive hydrostatic pressure that are maintained by active transport of photosynthetically-derived carbohydrates into phloem cells. Water diffuses into phloem cells along gradients of osmotic potential, and the resulting increase in cell turgor pressure generates mass flow of solution along phloem pathways (van Bel, 2003). Environmental control can act on this process through regulation of photosynthesis and carbon uptake, transpiration, soil water uptake and whole plant water status. A summary of aphid feeding studies (Tjallingii, 1995) provides strong evidence in support of the view that phloem flows through an insect's stylet under positive hydrostatic pressure from phloem cells, whereas the rate of flow is under direct insect control. Bark temperature has been shown to be a strong determinant of the behaviour of bark-dwelling beetles (Schmid *et al.*, 1992), and it is possible that beech scale insects are similarly temperature regulated. The strong environmental control on honeydew production identified in this study is probably a combination of tree (i.e. photosynthesis and phloem transport) and insect factors that are likely to be regulated by the same environmental variables. Separating these factors will not be easy, but will be a key component of studies that determine to what degree honeydew production is controlled by individual insects, host trees, or

environmental variables. Understanding the factors that limit honeydew production will allow better evaluation of the evolutionary interactions between scale insects and their host trees, and better prediction of annual honeydew production totals.

Scaling-up: Honeydew as a proportion of canopy carbon uptake

It has been estimated that the energy loss to individual beech trees via honeydew production can account for between 30 and 80% of their net annual carbon uptake (Belton, 1978; Kelly et al., 1992). The data presented here can, in conjunction with values from other studies, be used to estimate the proportion of net annual carbon uptake accounted for by honeydew sugar losses at our field site. Net annual growth increment by beech forest at Craigieburn has been estimated to be 16.8 t C ha^{-1} yr^{-1} (Benecke and Nordmeyer, 1982). Using the data on honeydew composition in Grant and Beggs (1989), accepting their choice of tetrasaccharide as the probable mean chain length among the honeydew oligosaccharides, and data from standard chemical tables (Bruno and Svoronos, 1989), the carbon content of honeydew sugar can be estimated as 42.1% by molecular mass. Assuming that the estimate of average honeydew standing crop : production ratio (1:6.61) at Craigieburn remains approximately equal over the year, the ratio of production during May to total annual honeydew production can be estimated (= 0.47%) using the data of Murphy and Kelly (2003); this assumes that the single-day observations they report from each month are approximately equal to the average monthly value. If the same logic is applied to the data presented here, and assuming that the proportion of trees with and without productive insects described in the methods to this paper (= 49%) is approximately constant through the forest, annual honeydew production is estimated to be 24.9 g C m^{-2} bark year^{-1}. The area of bark suitable for scale insects at Craigieburn has been estimated to be around 8300 m^2 ha^{-1} (Murphy and Kelly 2003). Combining these values gives an estimate of the carbon in annual honeydew production of 207 kg C ha^{-1} yr^{-1}. This is equal to 1.8% of the annual growth increment of beech trees at Craigieburn.

This estimate is markedly lower than the two previously published estimates. Belton (1978) assumed that daily honeydew production was five times the instantaneous standing crop, and on this basis that 23–40% of annual tree carbon uptake was accounted for by honeydew production. Using similar reasoning, and a field measurement of the ratio of standing crop to daily production of 1:11.5, Kelly et al. (1992) estimated that honeydew sugar may account for up to 80% of tree carbon uptake. The estimate presented here is lower than previous estimates for two reasons. First, Kelly et al. (1992) and Belton (1978) used lower estimates of beech forest growth increment (between 11 t C ha^{-1} yr^{-1} at 450 m and 8.6 t C ha^{-1} yr^{-1} at 900 m) than the 16.8 t C ha^{-1} yr^{-1} estimated by Benecke and Nordmeyer (1982). While Benecke and Nordmeyer's estimate is based on measurements of photosynthesis and respiration, it may have overestimated net carbon uptake at the site (cf. values in Whitehead et al., 2001). Recalculating the carbon lost to honeydew at Craigieburn using Belton's estimate of growth increment at 900 m increases the estimated honeydew drain to 2.5% of carbon uptake. Second, the estimate presented here is lower mainly because the number of insects per unit bark area was much greater at the lower altitude sites of Belton (1978) and Kelly et al. (1992); an average of 23.9 insects m^{-2} was observed at the Craigieburn site, whereas Kelly et al. (1992) observed an average of 574 insects m^{-2} at their 390 m altitude study site.

In this study carbon losses were estimated as a proportion of whole-forest carbon uptake. Because not all trees support scale insects (49% of trees had no productive insects in this study), losses of carbon from honeydew-infested trees should be on average twice the 1.8% reported here, with even higher values for the heaviest honeydew producers. Trees that support large insect populations do not appear to be adversely affected at Craigieburn (D. Kelly, unpubl. data), or at lower elevation sites [Mt. Richardson, 400 m a.s.l. (Y. Chew, unpubl. data)]. This is unsurprising at Craigieburn, given the low estimated losses of carbon, but at lower elevation sites, carbon losses of the range estimated by Kelly et al. (1992) and Belton (1978) would be expected to adversely affect tree growth and competition (Dixon 1971; Llewellyn, 1974; Crawley, 1983; Cyr and Pace, 1993). Vranjic and Ash (1997) showed an effect of phloem feeding on seedling growth even at low levels of scale insect infestation. Clearly, further work on honeydew production at lower elevations would be worthwhile.

The dynamics of forest carbon uptake can be modeled with environmentally-driven process-based models (e.g. Leuning et al., 1995, Whitehead et al., 2002). The strong links we observed between environmental variables and honeydew production suggest that a mechanistic model of honeydew production could be formulated. It will be particularly useful to develop a model which couples tree photosynthesis and phloem transport, environmental factors, and per-insect honeydew production, in order to further elucidate what controls the production of honeydew — the energy supply which fuels many beech ecosystem processes.

Acknowledgements

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