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# HONEYDEW STANDING CROP AND PRODUCTION OVER 24 HOURS IN *NOTHOFAGUS SOLANDRI* FOREST IN CANTERBURY

**Summary:** The standing crop and daily production of honeydew by *Ultracoelostoma brittini* on *Nothofagus solandri* var *solandri* was measured on 28-29 August 1990 near Oxford, Canterbury. In 64 quadrats of 125 $cm^2$, all 740 active individual insects were mapped by their anal threads and honeydew production was recorded every three hours over 24 hours. Mean production of honeydew per insect over 24 hours was 0.169 $\mu$l, but ranged from zero (4% of all active insects) to 11.5 $\mu$l. Standing crop peaked just after dawn, and production was apparently higher at night. Removing drops every three hours and covering the quadrats to exclude animals had no significant effect on honeydew production. The greatest variation was between the 16 trees. *Ultracoelostoma* densities were higher on trees with higher daily honeydew production per insect. The honeydew production per unit area over 24 hours represented 3.2 to 23.0 times the standing crop, depending on what time of day the latter was measured; for the daylight samples, production was 11.5 times the mean standing crop.

**Keywords:** Honeydew; black beech; sooty beech scale; standing crop; production; *Ultracoelostoma brittini; Ultracoelostoma assimile; Nothofagus solandri* var *solandri*.

## Introduction

Throughout large areas of the eastern and northern South Island, beech forests *(Nothofagus* spp.) support large populations of *Ultracoelostoma* spp. (Hemiptera: Margarodidae), sooty beech scale insects, which produce a sugary exudate known as honeydew (Morales, Hill and Walker, 1988). The system is important economically (large quantities of honeydew honey are sold; Wardle, 1984), biologically (the honeydew is an important food source for insects and native birds like tui and kaka; Gaze and Clout, 1983; Moller and Tilley, 1989), recreationally (wasps feeding on the honeydew have spoiled many peoples' experience of the outdoors; Read, Donovan and Schroeder, 1990), and ecologically (Wardle, 1984; Kelly, 1990). Amazingly, there has been very little research on honeydew until recently.

One basic piece of information of use in all the above topics is the rate of production of honeydew. This is important both to estimate the effect on the tree of carbon loss, and to calculate the available food resource for the bees, wasps, birds etc. which utilize it. A number of studies (Crozier, 1978; Gaze and Clout, 1983; Boyd, 1987; Moller and Tilley, 1989) have measured the standing crop of honeydew (i.e., the amount present as drops on anal threads on the tree trunks at anyone instant). Some of these studies refer to their standing crop data as 'production' (Gaze and Clout, 1983; Moller and Tilley, 1989), but this is an unfortunate confusion of two different variables. The standing crop is affected by rates of production, but also by harvesting rates, rainfall, wind, evaporation and other factors. For example, standing crops are often very low in February when wasp harvesting is very intense, but this could be in spite of high rates of production *sensu stricto*. There seem to be absolutely no published data on the rate of production of honeydew, and how this relates to the standing crop.

We set out to fill that gap in the literature. We measured rates of production and the size of the standing crop at one site over 24 hours in winter, when few animals are harvesting honeydew.

## Methods

### Study site

The study area (map reference NZMS 260 L34 364713) was by Coopers Creek at the base of Mt Oxford in the foothills of Canterbury. The study was conducted in late August, when few insects such as bees and wasps are actively harvesting honeydew. An area of *Nothofagus solandri* var *solandri** (black beech) forest growing on a west-facing river terrace of 15° slope at 390 m altitude, and close to the Payton Lodge scout camp, was selected. Many of the trees carried heavy infestations of *Ultracoelostoma;* these are almost certainly *U. brittini* Morales (Morales, 1991), although they had previously been referred to *U. assimile*

* Nomenclature follows Allan (1961) and Edgar (1971).

(Maskell). The beech trees were up to 20 m tall, with manuka *(Leptospermum scoparium)* around the edges, and a sparse understory of beech seedlings, *Cyathodes juniperina,* and *Coprosma rhamnoides*. Occasional *Pseudopanax arboreus, Carpodetus serratus* and *Coprosma Lucida* were found on the edges of steeper banks nearby. Air temperature and relative humidity were recorded every 60 seconds and averaged every 15 minutes for the duration of the study with a Campbell CR21X datalogger near the forest edge.

## Sampling methods

Sixteen trees were selected along a 100 m section of the terrace to give a range of physical locations, trunk diameters, and degrees of exposure (from shaded to open). For each tree, the diameter at breast height (d.b.h.) and exposure of the trunk to sunlight on a subjective five-point scale were noted. The trees ranged from 18 cm d.b.h. to 44 cm (mean = 31 cm). The level of exposure of the trunks ranged from very shaded (surrounded by dense manuka shrubs with several large beech trees to the north) to very open (growing on the margin of a grassy area with little undergrowth around the tree). Trees were not selected on the basis of honeydew density.

On each tree, two sampling frames were nailed on opposite sides of the trunk at eye height (approx 1.6 m). On eight trees these were aligned east/west, and on the other eight, north/south. We could not sample all four aspects on each tree because some trunks were too small in diameter to fit on four frames. On each tree, one of the two frames was covered by a nylon mesh sheet to exclude foraging animals, and the other was left uncovered. These were arranged randomly among trees so that four of the frames on each aspect were covered and four uncovered. The mesh covers had I mm holes. Small insects may have been able to crawl under the edges of the covers, but few insects were seen foraging on honeydew during this study.

Each frame carried two "windows" or quadrats, each 25 cm by 5 cm. In each quadrat, all the anal threads and honeydew drops were mapped, but only anal threads which produced some honeydew were counted as connected to active insects. In one quadrat per frame all drops were mapped and removed and their volume measured at each census. In the other quadrat the size of the mapped drops was estimated by eye, but they were not removed (until the final census, when all drops were removed and measured). Removed drops were captured individually in microcapillary tubes of 2 ~I capacity and their volume (length in the tube) measured to an accuracy of 0.03 ~I. Constant use of the capillary tubes on removal quadrats kept the visual estimations on the non-removal quadrats accurate. A test using two observers who estimated and then measured the volumes of 30 drops showed a high level of accuracy (estimated vs measured, $R^2 = 0.983$, log-transformed).

To summarize, the experimental design was a full factorial with three factors: covered (yes/no), removed (yes/no), and aspect (north, south, east or west), each replicated four times, giving 64 quadrats in total on the 16 trees.

Sampling began shortly after noon on 28 August 1990, and was repeated every 3 hours until noon on 29 August 1990. The first census took 2.5 hours while all anal threads were initially mapped, but subsequent censuses were faster (1.5 hours). We did not measure the sugar concentration of the honeydew produced, because when time was available to collect samples for this purpose (in the middle of both days), the standing crop of honeydew was too low (<50$\mu$l m$^{-2}$; Fig. 1).

### Analysis

From the maps, the drops present at each census for each individual insect (anal thread) were shown. Where the drops were removed, this represents a direct measure of production of honeydew. Where the drops were not removed, production was estimated as the *increase* (if any) between censuses in the size of each drop present. In theory this would underestimate production, because it would not be detected if a drop was removed and then replaced with one the same size or smaller. However, the typical pattern observed was for a drop to form, and then disappear at the next census or the census after that; after several more censuses with no drop present, another would form. Therefore with a 3-hour census interval, the drop-by-drop data for the non-removed frames were frequent enough to be good estimates of total production. This was confirmed by the fact that there was no significant difference in production per quadrat between removed and non-removed quadrats (Table I). For the non-removed areas, we therefore had estimates of both the standing crop and production over each interval. Losses (Le., removal of drops by insects, gravity, wind etc.) could thus be estimated by adding production over the interval to the standing crop at the start, and subtracting the standing

Table 1: *Analysis of variance for total honeydew production per quadrat over* 24 *hours. Coopers Creek.* 28-29 *August 1990.*

| SOURCE | df | MS | F | *P* |
|---|---|---|---|---|
| Tree | 15 | 1.5877 | 2.75 | 0.004 |
| Aspect | 3 | 0.6209 | 1.08 | 0.369 |
| Cover | 1 | 0.0009 | 0.00 | 0.968 |
| Removed | 1 | 0.0003 | 0.00 | 0.981 |
| Error | 43 | 0.5772 | | |

crop at the end.

The effect of cover, removal, aspect and tree on the total production of honeydew per quadrat over the 24 hours was examined with a balanced 4-way ANOVA. Honeydew quantities, in 111, were log-transformed to correct for non-normality before analysis, so the back-transformed confidence intervals presented are asymmetrical. The total production of honeydew per quadrat over the 24 hours (summed for all insects in the quadrat) was compared to the standing crop present at each census for the 58 quadrats with non-zero total production. From these data we calculated the mean and confidence intervals of the ratio between standing crop and production over the day.

The temperature and relative humidity data were used to calculate the mean Vapour Pressure Deficit (VPD) for each IS-minute interval and average these over the 3-hour inter-census interval. The VPD measures the strength of the evaporative gradient from liquid water into the air, which may affect the size of honeydew drops.

To see if the large differences between trees in honeydew insect density were constant over time, the site was revisited early on 15 December 1990. The quadrats were relocated by the nails which were left in position. Warm weather before the second visit meant there were many drops present, but the drops were concentrated and too sticky to capture in the capillary tubes. Therefore, drop volumes and the standing crop could not be determined, but the number of anal threads carrying a drop was recorded for comparison with the August data.

# Results

**Total honeydew production per unit area**

Analysis of variance on the total honeydew production per quadrat showed no significant differences due to covering, removal or aspect (Table 1). The lack of effect from covering may have been because few animals were seen harvesting honeydew anywhere at the site. By day, occasional honey bees and flies were seen; there was no sign of wasps. Overnight, a number of invertebrates appeared on the tree trunks, including native cockroaches and moths, but these were not directly observed to be feeding on honeydew. Birds, principally silvereyes *(Zosterops lateralis* Latham) were active on the beech trunks in the morning of the second day.

Total honeydew production per quadrat varied widely between trees (Table 1). The range for the 16 trees studied was 6.32 - 446 111 m,2 day"', with an overall mean of 162 µl $m^{-2}$ $day^{-1}$ (95% C.I. 113 - 222). There was no significant relationship between honeydew production per quadrat and either trunk diameter (n = 64, F = 0.77, NS) or exposure of the tree to sunlight (F = 0.481, NS).

**Time course of production**

The standing crop in the non-removed quadrats increased from a minimum at 1200 hr on the first day (33 ml $m^{-2}$; Fig. 1) to peak at 0900 hr the following morning (118 ml $m^{-2}$) before dropping most of the way back again by 1200 hr (53 ml $m^{-2}$ ).

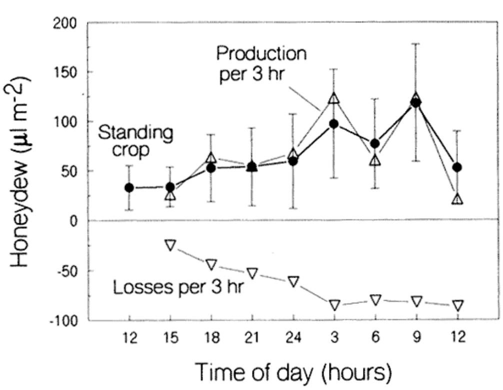


Figure 1: *Mean standing crop of honeydew (µl $m^{-2}$, with 95% confidence limits), and rates of production and loss (µl $m^{-2}$ over 3 hours) from 32 quadrats on 16* Nothofagus solandri *var* solandri *trees where drops were not removed, over 24 hours at Coopers Creek, 28-29 August 1990.*

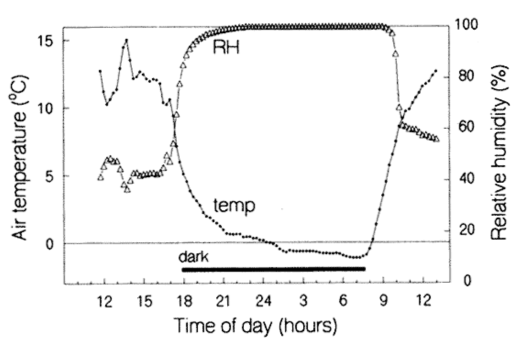


Figure 2: *Mean air temperature (temp) and relative humidity (RH) sampled every 60 seconds for* 15 *minute intervals at Coopers Creek during the study period. Night-time is indicated by a black bar.*

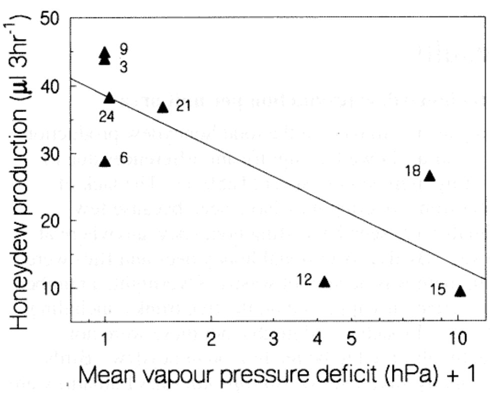


Figure 3: *Mean honeydew production (μl $m^{-2}$ over 3 hours) from non-removed quadrats in relation to mean Vapour Pressure Deficit over the interval, over 24 hours at Coopers Creek. 28-29 August 1990. Each point is labelled with the hour at the end of the interval. Production = 38.7 - 25.6(log VPD + 1); $R^2$ = 0.661, n = 8,* P = *0.014.*

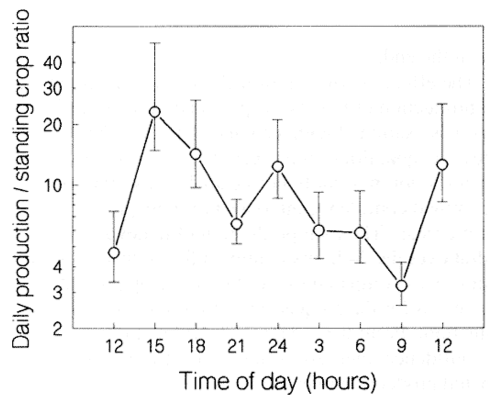


Figure 4: *Mean ratio (with 95% confidence intervals) between total production of honeydew over the 24 hours, and standing crop at different times, averaged over the 58 quadrats with non-zero total production. Coopers Creek, 28-29 August 1990.*

Production was apparently lowest at the first revisit (l500 hr) and the last (l200 hr; Fig. 1). This may have been partly caused by changes in evaporation rates of droplets as well as changes in exudation rates.

During both days the weather was sunny and cool (Fig. 2) with little wind. Relative humidity was much higher at night, suggesting that evaporation would have been reducing the size of droplets much faster in the daytime than at night. There was a significant relationship between estimated production and mean VPD over the interval (Fig. 3), with lower apparent production at high VPDs, However, even after allowing for this, production was lower from 0900 to 1200 hr, and also varied overnight while the VPD was essentially zero. Therefore some changes in real production rates must have been occurring, quite apart from any evaporative effects.

The losses to gravity, wind, insects, birds etc. were initially small but increased to a plateau of around 80 μl $m^{-2}$ per 3-hour interval after 2400 hr (Fig. 1). Variations in standing crop were due more to changes in production rates than to changes in losses; losses were constant from 2400 hr onwards, while production and standing crop varied widely over this time.

Since the standing crop varied with time, the ratio between total daily production of honeydew and standing crop also varied (Fig. 4). As expected, the ratios were lowest at 0900 hr when the standing crop was at a peak The ratios varied rapidly during daytime (1200 - 1800 hr and 0900 - 1200 hr) when standing crop would normally be measured. Overall, the total production was between 3.2 and 23.0 times the instantaneous standing crop, with an average for the daylight samples of 11.5.

**Insect density and production per insect**

In all, 740 insects had a drop on their anal thread in the 64 quadrats at some stage, producing 1900 recorded honeydew drops. The mean density over all trees was 574 insects m- (log-transformed; 95% C.I. 422 - 769 $m^{-2}$ However, there was wide variation in mean insect density between trees, from 39.6 insects m,2 for the lowest to 1770 insects m-2 for the highest. There was a significant correlation between the number of drop-producing insects in each quadrat in August and December (R = 0.612, n = 64, $P < 0.001$), showing that the differences between trees were stable over four months.

The mean production per insect over the 24 hours was 0.169μl (log-transformed; 95% C.I. 0.154 - 0.184). The range was from zero (30 insects had a drop at the start, which was removed, and thereafter nothing was produced) to the two highest totals of 5.8 and 11.5 μl. There were wide differences between the 16 trees in mean production per insect. The range was from 0.051 to 0.326 μl per insect over the 24 hours. There was a significant positive correlation between mean daily production per insect and density of insects per tree (R = 0.5153, n = 16, $P < 0.05$).

# Discussion

**Removing drops and covering quadrats**

The two methods of estimating production (removing drops every three hours, or simply mapping them) gave results that did not differ significantly. This was because drops were usually produced at quite long intervals on each individual thread, allowing the mapping to follow the fates of individual drops. If production was faster, such as at other times of year (Crozier, 1978; Gaze and Clout, 1983; Moller and Tilley, 1989), then mapping alone might not be sufficient to accurately measure production.

There was also no evidence that the covers, by preventing harvesting, were increasing the measured rates of production. However, the August sampling date was chosen because there is little harvesting going on at that time, so animals were apparently not the major determinant of losses from the ends of the threads. Therefore keeping animals off would be expected to have little effect. Moreover, it is difficult to design an experimental protocol on covering quadrats which would clearly show a difference due to harvesting. Even with a fine mesh, it is difficult to prevent insects from crawling under the edges of the mesh; and conversely larger animals, such as birds or even honey bees, might well be deterred by the presence of an uncovered frame on the trunk. (Our frames were made of white plastic; in hindsight, black would have been less conspicuous.) It would be very interesting to repeat this work in summer when many animals are harvesting the honeydew, but it might be difficult to keep wasps and bees from harvesting drops as soon as the covers were removed. Finally, any kind of cover will affect the air movement, relative humidity and rate of evaporation of drops under the covers relative to the controls.

Despite all the above, it is reassuring (for future sampling projects) that removing drops of honeydew every three hours does not seem to alter the total amounts of honeydew produced by individual insects. This extends the conclusions of Boyd (1987) who sampled at 24-hour intervals and found no effect on drop size or sugar concentration. Presumably the insect is exuding honeydew for its own purposes, and is not much affected by harvesting, except when highly evaporated drops block the ends of the anal tubes. However, Moller and Tilley (1989) showed that many insects form a new drop if the case within which the insect lives is tapped.

**Productivity estimates**

Production within the day was lowest at the first revisit (1500 hr) and the last (1200 hr). There may be some effect of humidity and evaporation in reducing apparent production in daytime. Since we did not record sugar concentration, we could not detect if the same total amount of sugar was being produced but in more concentrated drops. The night-time maximum of honeydew production is partly related to lower evaporation from drops at night. However even after allowing for VPD, there were large changes in the rates of honeydew production over the 24 hours. There seems to be no information on whether honeydew production is regulated by events within the plant or in the insect, or both (Moller and Tilley, 1989).

Standing crop is affected by both rates of production and rates of removal of honeydew drops. In this case, production had a larger effect on standing crop than removal (Fig. 1). This is presumably because there was little harvesting by animals in our quadrats. The loss rate was constant from midnight to noon, which would be consistent with most losses being due to gravity and/or wind, rather than animal harvesting (which should vary between night and day). Therefore, the sudden decline in standing crop between 0900 hr and 1200 hr was mainly due to the decrease in production over that time. In summer, when many animals are harvesting honeydew, it would be expected that removal rates would mainly determine the size of the standing crop.

The overall factors controlling the amount of honeydew are not well understood. In contrast to the findings of Crozier (1978) for summer measurements at a nearby site in Canterbury, but in common with data from Westland (Kelly, 1990), we did not find any significant effect of aspect at Coopers Creek. In this study individual trees varied 70-fold in their production of honeydew per square metre. Exposure of trunks to the sun did not explain a significant amount of the variation (c.f. Crozier, 1978, 1981). Tree diameter at breast height did not have any effect either, in contrast to the data of Kelly (1990), but that study had a much wider range of diameters (3 - 110 cm) than we did (18 - 44 cm). The differences between trees in insect density were relatively constant over a four month interval. There was a correlation between honeydew production per insect and insect density, suggesting that insects are more common (due to migration, better survival or higher fecundity) on the trees where each insect excretes phloem sap at a higher rate. Of course, none of the above indicates why insects are able to excrete sap at a higher rate on some trees than others. Another factor which is probably important (but operating in the other direction) is that the empty cases of earlier insects persist on the trunks; on some trees, these occupy a substantial proportion of the space (Morales *et al.,* 1988). Beyond these few generalizations, we are no closer to understanding why some trees yield much honeydew and others very little. In any future study it would be important to sample a large number of trees, using strict randomization for selecting them, since that is the level at which we found the greatest variation in honeydew production.

**Standing crop estimates**

Standing crop levels given here are similar to the few published studies. Boyd (1987) working in Nelson found 7.5 $\mu l\ m^{-2}$ in summer, 8.7 $\mu l\ m^{-2}$ in autumn and

37.0 $\mu$l m$^{-2}$ in July. Data in Moller and Tilley (1989) work out at 354 $\mu$l m$^{-2}$ on average over the year in the same province. The August levels at Coopers Creek of 33 to 118 $\mu$l m$^{-2}$ fall between these estimates.

Boyd (1987) also recorded changes in standing crop through the daylight hours in summer, autumn and winter. In May/June there was a rapid drop from 0800 hr onwards, as seen here; in July standing crop was uniformly high through the day; and in January/ February it was uniformly low from 0700 hr onwards.

### Estimating production from standing crop

The standing crop of honeydew varied 3.5-fold over the 24 hour study period. It also varied widely from day to day depending on weather and other factors. For example, during a reconnaissance at Coopers Creek in warm dry weather on 5 August 1990, the trunks were covered in many large; sticky, concentrated drops of honeydew. Several days of rain before the 28 August sampling presumably washed these off and reduced the standing crop to a low level. There were also many large, concentrated drops on 15 December. Of course, the rate of harvesting is also a major determinant of the level of standing crop (Moller and Tilley, 1989).

Standing crop is clearly not an ideal variable to use as an index of honeydew production (c.f. Gaze and Clout, 1983; Moller and Tilley, 1989), because of this variation from hour to hour and day to day. In particular, the variation in this study was great between 0900 hr and 1200 hr, during the period when field work is likely to be under way. However, despite its drawbacks, there are few easily measured alternatives. Production, even over only 24 hours, is too difficult to record routinely. When the data given here have been verified at other sites and other times of year, we may be able to use approximate conversion factors to relate standing crop to production, but more attention needs to be given to the effects of time of day and harvesting rate on the conversion factor.

The only previous consideration of the relationship between daily production and standing crop was by Belton (1978), who guessed daily production to be five times the standing crop for the purposes of some approximate calculations. From the data given here, it seems his guess was too low (at least for daytime winter samples shortly after the trunks have been washed clean by rain). Using his factor of five, Belton showed that as much as 23 - 40% *of* all carbon fixed by the beech trees may be lost through the anal tubes of *Ultracoelostoma*. If the correct factor is nearer our daytime average of 11.5, then beech trees may be losing more than 80% of their carbon to the insect. We urgently need better data on honeydew production at different times of year, and on the total annual carbon fixation of black beech in lowland Canterbury, to confirm or refute this amazing estimate.

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