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Review article

Nectar sugar content: estimating standing crop and secretion rate in the field

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Abstract – Field techniques for sampling and measuring the standing crop and secretion rate of nectar are described, in order to clarify some discrepancies and omissions in existing reviews of nectar measuring techniques. Slender microcapillary tubes (a fresh one for each sample) are recommended for withdrawing nectar, and a hand held sucrose refractometer, capable of operating with very small fluid volumes, is used for measuring concentration. Potential errors due to the presence of solutes other than sucrose, or to temperatures other than the calibration temperature, are discussed. I consider how measurements of secretion rate are affected by reabsorption and by the nature of the bags used to exclude nectarivores.

standing crop / nectar concentration / secretion rate / microcap / refractometer / sucrose / glucose / fructose / amino acids / nectarivore

1. INTRODUCTION

Floral nectar consists largely of sugars (chiefly sucrose, glucose and fructose) and water. Insects, birds and mammals take nectar, and its sugars provide energy that fuels activity or provisions the larvae. Although the water content of nectar can be important to plants (Galen et al., 1999) and to nectarivores (Willmer, 1986; Lotz and Nicolson, 1999), it is the sugar content of nectar that is usually of primary interest, because energy is the currency usually considered by, for instance, zoologists exploring the extent to which foragers maximise the net rate of energy gain (or efficiency, the ratio of energetic gain to energetic cost (Schmid-Hempel et al., 1985)), or botanists examining the costs and benefits of allocation of resources to pollinator attraction. Zimmerman (1988) and Kearns and Inouye (1993) review the ecological and evolutionary context in which measurements of the quantity and dynamics of nectar secretion are useful.

In the field, the sugar content of nectar can be estimated from measurements of nectar volume and solute concentration, measured with a sucrose refractometer. Publications that deal with techniques for exploring and quantifying nectar solutes include Beutler (1953), Cruden and Hermann (1983), Dafni (1992) and Kearns and Inouye (1993). Some omissions and discrepancies in these reviews make it difficult for a neophyte to assemble suitable equipment and bring the techniques into operation without preliminary trials. Bee-pollinated flowers often contain very small quantities of nectar, for which micropipette diameter and refractometer capacity are critically important, but these reviews do not mention micropipette diameter and the refractometer type recommended in some of them is no longer in production (see below). Sucrose refractometers

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are variously said to give percentage readings in weight of sugar per unit volume of solution (Kearns and Inouye, 1993, p. 170, presumably a misprint) or weight of sugar per unit weight of water (Cruden and Hermann, 1983, p. 235), whereas in fact the usual units are g sucrose per 100 g solution (Bolten et al., 1979; Dafni, 1992).

In this paper I consider micropipette diameter and refractometer capacity and recommend suitable instruments, and try to resolve discrepancies about the units of measurement by refractometers. I focus in more detail on field methods for estimating standing crop and secretion rate, and highlight some hints and problems arising from experience over a 25-year period.

The quantity of nectar sugar in a flower fluctuates through time as nectar is supplied by secretion or depleted by foraging animals or by reabsorption. These are the only avenues of transport for sugar; but water has additional routes. It can be supplied by condensation from humid air, or by precipitation; and it can be lost by evaporation.

To interpret the foraging behaviour of nectarivores, we need to know both the standing crop and the secretion rate of nectar. The standing crop, the quantity of nectar in a flower at a given time, is usually expressed in terms of mass of sugar per flower. It depends on the quantity secreted, less the quantity reabsorbed or removed, since secretion began. The standing crop increases when the secretion rate exceeds the rate of reabsorption or removal (as often happens in the early morning before most insect nectarivores are active) and it falls when rates of reabsorption and removal exceed secretion rate (as often happens at times when foragers are numerous). Hence the standing crop shows variation from hour to hour and from day to day, as well as variation associated with weather- and flower-age-related changes in rates of secretion and reabsorption. It also varies from flower to flower; rates of secretion may show intrinsic plant-to-plant and flower-to-flower variation (e.g. Gilbert et al., 1991; Feinsinger, 1978), and may vary with the microclimate surrounding individual flowers; and rates of removal will depend on the frequency of foraging visits, which may depend in part on position (e.g. sun or shade; centre or margin of a bush; within or outside the defended territory of certain species of bee or bird).

2. SAMPLING NECTAR AND MEASURING VOLUME

The sugar content of nectar is calculated from the volume and the solute concentration of the nectar sample from each flower. If nectar is withdrawn from the flower into a tube of uniform bore, such as a microcapillary pipette (a microcap), the volume can be measured (as the length of the column of liquid) before the nectar is deposited on a refractometer prism for measurement of solute concentration. If the nectar sample is too viscous or too small to be sampled in a microcapillary, sugar content must be quantified in some other way (see below), and water content may not be quantifiable at all.

After initial exploration of the structure of the flower to locate the nectar, preferably under a stereomicroscope, the microcap is touched gently against the nectar surface until repeated probing yields no further nectar. Nectar uptake can sometimes be speeded up by tilting the flower so that the nectar flows downwards into the microcap. At least initially it is wise to tear open the drained flower after sampling to check that all nectar has been removed, because any clogging of the microcap due to pollen, thrips, damaged floral tissues or air bubbles may prevent capillary flow. It is for this reason that unforced capillary flow is preferable to aspiration, because application of suction can draw bubbles into the capillary (Pleasants, 1983). For this reason, too, a new microcap should be used for every sample, because a microcap that has contained nectar is likely to contain a liquid meniscus that will impede capillary flow. If it is necessary for economic reasons to re-use microcaps, they should be deposited in a screw-top tube of absolute ethanol or acetone immediately after use, and later drained, dried and checked visually before re-use. Used microcaps rinsed with water alone often retain a meniscus that blocks capillary flow (Cruden and Hermann, 1983).

The size of the microcap must be appropriate for the flower. If the external diameter is too great it may be impossible to achieve contact between the end of the lumen and the

nectar surface, and the microcap may be too thick to reach the nectar without distorting the corolla. Drummond Microcaps® (Drummond Scientific Co., Broomall, Pa., USA; http://www.dru-mmondsci.com) are slender (0.2 microlitre microcaps have an external diameter of 0.5 mm, 1 microlitre microcaps 0.64 mm, 5 microlitre microcaps 0.92 mm), but many graduated micropipettes are thicker-walled and have a much greater external diameter.

The volumetric capacity of the microcap should also be appropriate. If the microcap holds less nectar than a flower, repeated fillings may be necessary for a single sample, with the risk that a meniscus will block the lumen. If the microcap is too large, its greater diameter will make nectar extraction difficult and measurement of the column length inaccurate. Drummond microcaps are available in a range of volumes from 0.1 microlitres upwards. The holder supplied with microcaps can be used to discharge the contents onto the centre of a refractometer prism by blocking the pinhole with a finger and squeezing the rubber bulb or, for better control, by blowing via a length of flexible tubing.

If the corolla tube is very slender even the smallest microcap may fail to drain the nectar. Nectar can be removed from the very slender corolla tubes of some Asteraceae by pulling the corolla tube off the ovary and gently squeezing so that the nectar emerges at the base as a droplet. This can be deposited directly onto a refractometer prism or first taken up into a microcap for volume measurement. Such nectar may be contaminated with tissue fluids.

Alternatively, a microcap can be drawn out into a fine hair-like point by melting the centre in a flame and pulling the two ends apart. The resulting tapered microcap is broken off at a suitable diameter and used to take up nectar. Its broken end will be sharp, and the probing should be gentle to avoid piercing the floral tissue and clogging the lumen. Volume measurement in these tapered tubes is not straightforward. Working under a stereoscopic microscope, set up in the field if necessary, it is possible to insert the tapered tip, and discharge the nectar, into the lumen of a slightly larger intact microcap, in which the length of the column of nectar can be measured before the droplet is deposited on the refractometer prism. Alternatively, the drop of nectar might be discharged into a dish of liquid paraffin, where its diameter can be measured under a stereoscopic microscope. If the drop is discharged onto filter paper, the diameter of the wet area can be measured as an index of volume (Dafni, 1992; Kearns and Inouye, 1993, p. 173), but laboratory procedures (reviewed by Dafni (1992) and Kearns and Inouye (1993)) are then required for the estimation of sugar content.

A hydrophilic surface, such as clean glass, is necessary for the capillary uptake of nectar. Equally hydrophilic fine plastic or polythene capillary tubing might have advantages over glass for nectar sampling. It would be less fragile and more easily handled, and could be cut to lengths appropriate to each sample. It would be softer, and so less likely to cause floral tissue damage, and its flexibility would make it easier to probe curved corolla tubes and to implant tubing to monitor secretion rate (see below). Portex autoclavable nylon tubing with an internal diameter of 0.5 mm is suitable for some purposes (Búrquez and Corbet, 1991).

Sometimes the consistency of the nectar or the shape of the nectar-bearing surface preclude the use of microcaps. If measurements of volume and concentration are not needed, nectar can be blotted up onto small triangles of filter paper. These can be organised in the field by pinning them to a sampling scheme outlined on a sheet of ruled paper clipped to a block of plastic foam (McKenna and Thomson, 1988). They are stored dry, and the nectar is later redissolved in distilled water for sugar analysis. Alternatively, nectar can be extracted by centrifuging groups of flowers (Dafni, 1992; Kearns and Inouye, 1993). Nectar that is intractably viscous or crystalline can be rinsed out of flowers into a known volume of distilled water (e.g. Mallick, 2000). Either the flowers are shaken in stoppered tubes of water (e.g. Käpylä, 1978), or known volumes of water are discharged onto the nectary, if necessary left until the sugar has gone into solution, and then withdrawn (Corbet et al., 1979a). Successive rinses yield progressively less sugar, and it is not clear how much of this would have been available to insect visitors. In *Crataegus laevigata*, for example, the quantity of sugar in solution rises at a diminishing rate over a period of about 30 min (Corbet et al., 1979a). The extent to which flies and other insects

mimic this technique, perhaps by spitting saliva onto the nectary and then reclaiming it, remains unknown.

3. MEASURING SOLUTE CONCENTRATION

The solute concentration in a flower changes with time as a result of (a) equilibration with the ambient humidity (Corbet et al., 1979b), (b) selective reabsorption of solutes or water (Nicolson, 1995), and perhaps (c) changes in the concentration at which nectar is secreted. Generally, in day-flowering species the concentration of accumulated nectar is low at night (when the relative humidity is high), and increases during the morning to reach high values when active depletion leaves very small standing crops and relative humidity is low around midday (Corbet et al., 1979a; Corbet and Delfosse, 1984; Corbet et al., 1995). At a given relative humidity, the rate at which evaporation elevates the solute concentration is inversely related to the size of the drop. A small droplet of nectar has a relatively large surface area and is quickly concentrated by evaporation. A large volume of nectar, as in the tubular corolla of a hummingbird flower, has a smaller surface volume ratio, and evaporation changes the concentration of the mass of nectar slowly, if at all. The degree of microclimatic protection offered by the corolla affects the rate of evaporative water loss (Corbet et al., 1979b; Plowright, 1987). In relatively open flowers exposed to low relative humidities evaporative concentration causes rapid changes of concentration through the day, and variation from flower to flower is exaggerated because the traces of nectar in recently-visited flowers become concentrated much faster than the larger volumes in unvisited flowers. It may sometimes be reasonable to assume that concentration is constant, and to track standing crop by measuring volume alone, in deep flowers with abundant nectar; but in more open flowers containing the smaller volumes of nectar characteristic of insect pollination, concentration can fluctuate rapidly and studies of sugar content must be based on measurements of concentration, as well as volume, in individual flowers.

Solute concentration is measured with a hand held refractometer. The droplet of nectar is discharged from the microcap onto the centre of the prism of the refractometer, and the reading is taken immediately, to minimise evaporation of the drop.

The refractometer measures the refractive index of the solution, which depends on the nature of the solute, concentration and temperature. For a sucrose solution at 20 ^{o}C, the concentration (g solute per 100 g solution) corresponding to a given refractive index can be read from tables (Weast, 1986; Reiser et al., 1995) but this is not necessary because the sucrose refractometers usually used by pollination ecologists are calibrated directly in g sucrose per 100 g solution (previously known as % Brix among food technologists). For the calculation of sugar content, these mass/total mass measurements are converted to mass/volume directly or by multiplying by the density of a sucrose solution at the observed concentration (Bolten et al., 1979) using tables (Weast, 1986; Dafni, 1992; Kearns and Inouye, 1993), an equation (Prys-Jones and Corbet, 1991; Dafni, 1992) or the web (Association Andrew van Hook for the Advancement of the Knowledge on Sugar, 2002, http://www.univ-reims.fr/Externes/AVH/MementoSugar/001.htm).

Sucrose is often the main solute in nectar, but other sugars, notably the hexose sugars glucose and fructose, are often present or even predominant. Fortunately, the presence of hexose sugars scarcely affects the relationship between solute concentration and refractometer reading (Weast, 1986). The refraction, r, of a solution is 10^4 times the difference between the refractive index of the solution and that of pure solvent (here, water) at the same temperature. The refraction per unit percent solute is known as the refractivity, r/P, where P is the percent solute by weight. Marov and Dowling (1990) and Lescure (1995) give equations that relate the reading on a sucrose refractometer to total dissolved solids for solutions containing various proportions of hexose sugars (glucose and fructose), but the ecologist rarely knows what proportion of the sugars in the solution are hexose sugars. Although broadly characteristic of species or higher taxonomic groups (Baker and Baker, 1983), this proportion can change with time in some species (Nepi et al.,

2001), if not in others (Bernardello et al., 1994; Davis, 1997). Fortunately, the corrections to the refractometer reading required to allow for the presence of hexose sugars are trivial in relation to the variance in concentration usually found in nature. Even for a concentrated solution whose solutes consist entirely of glucose and fructose, a refractometer calibrated in % sucrose gives readings that are too low by not more than 2% as sucrose w/w.

The hexose sugars glucose and fructose are similar to sucrose in the relation between density and concentration weight/weight and in the energy content per gram, so that the error in energy calculations introduced by assuming all solutes are sucrose, when in fact they are largely glucose and/or fructose, is only equivalent to about 3–4% as sucrose w/w (Weast, 1986; Kearns and Inouye, 1993).

Among other nectar solutes that can interfere are amino acids (Baker and Baker, 1986), some of which have refractivities very different from that of sucrose. Whereas the refractivities of sucrose, glucose and fructose are all given as 14 in Wolf (1966), those of common amino acids range from 4.3 to 29.4 (Jones (1975) or Swiss Institute for Bioinformatics (2002) http://www.expasy.ch/tools/pscale/Refractivity.html). Amino acids usually comprise a small proportion of the total solutes, and the estimated error due to all non-sugar components is unlikely to exceed 3.6% as sucrose w/w and is usually much less (Inouye et al., 1980). If all refracting solutes are treated as sucrose, the overestimation of energy content is likely to be less than the overestimation of sugar content, because some amino acids and other non-sugar components can be metabolised.

Hand held refractometers are not generally temperature compensated, but tables (supplied with the instrument, or in Reiser et al. (1995, Tab. 8.12, p. 207) or Weast (1986)) show that within the usual working temperature range of, say, 15–30 ^{o}C, the maximum temperature correction for sucrose at 20 ^{o}C is less than 1% as sucrose w/w.

The calibration of the refractometer scale is necessarily a compromise between range and accuracy. The low volume hand held sucrose refractometers from Bellingham & Stanley Ltd, Tunbridge Wells, UK (http://www.bs-ltd.com; e-mail sales@bs-ltd.com (UK) or sales@bs-rfm-inc.com (North America)) cover the range 0–50% and 45–80% as sucrose w/w, so for routine work in temperate climates two instruments are needed. When a small droplet of nectar is exposed to the air evaporation quickly changes its concentration, so if a small sample proves to be outside the range of one instrument it cannot be retrieved and tested with the other. Anyone who doubts the speed of evaporation should place a tiny droplet (say, less than 0.5 μL) of nectar or water under a stereoscopic microscope and simply watch as it shrinks by evaporation. When concentrations on the borderline between the two instruments are frequent, and samples are large enough, it may be possible to retain a little of each sample in the microcap in case a different range instrument needs to be used.

Bellingham and Stanley no longer make the metal-and-glass sucrose refractometers that they could modify individually for very small volumes of nectar as described by Dafni (1992) and Kearns and Inouye (1993). These have been replaced by Bellingham and Stanley Eclipse hand held sucrose refractometers, which are available in a low volume version manufactured to accept small volumes of fluid (code 45–81 for the range 0–50% and code 45–82 for 45–80% as sucrose). Although their nominal minimum volume is 1 μl, the instrument I tested gave a faint but legible reading with 0.2 μl, and sometimes with even less. This modification makes it possible to measure volume and concentration on small samples from individual flowers, which is desirable because pooling samples from different flowers is less informative, and potentially misleading. The overall sugar concentration based on pooled samples can differ by a few % as sucrose w/w from both the mean and the modal values based on measurements of individual flowers. More importantly, the calculation is based on the assumption that the entire standing crop of nectar is withdrawn from every flower, but that is unlikely to be achieved – clogging of the pipette with tissue or air bubbles becomes increasingly likely as successive flowers are probed with the same microcapillary, and the more concentrated, viscous nectar of the emptier flowers is likely to be incompletely sampled or incompletely mixed in the micro-pipette.

If only a low-range refractometer is available, it is tempting to dilute the sample in the microcap by adding a known volume of water. Again, it is not clear that adequate mixing can be achieved in the microcap, so this procedure should be tested carefully before use. If a layer of concentrated sugar solution adheres to the walls of the microcap, the concentration of the original solution will be underestimated.

4. STANDING CROP

The distribution of standing crop (the quantity of nectar in a flower at a given time) within a population of flowers may show some spatial patterning ('hot spots' and 'cold spots' of Pleasants and Zimmerman (1979); Kearns and Inouye (1993)). Statistically it often departs from a Poisson distribution (Brink, 1982). The accumulated standing crop in some (unvisited) flowers may be much larger than that in other (recently-visited or poorly-secreting) flowers. This distribution is the 'bonanza-blank' reward schedule of Brink (1982) and Feinsinger (1978), who coined the term for hummingbird flowers showing strong differences in reward due to flower-to-flower differences in 24-h sugar values (see below). There is evidence that foragers selectively visit the fuller flowers (e.g. Corbet et al., 1984). Under such circumstances, the standing crop encountered by bees foraging systematically (the encountered crop) is likely to exceed the mean standing crop measured by an unselective ecologist (Possingham, 1989), and a high frequency of forager visits is expected to result eventually in a much more evenly distributed, low standing crop. That situation is often found around midday (Corbet et al., 1995).

Although the secretion rate of a population of flowers in given microclimatic conditions may be more or less characteristic of a given plant species, the standing crop, because of its high variability through time and space, is better regarded as a feature of the recent and current interaction between a population of flowers and a population of foragers.

5. SECRETION RATE

To measure secretion rate, it is necessary to eliminate other routes of gain or loss of water and solutes, and then to measure the amount by which the standing crop increases over a known period of time. Usually, exchange of water with the atmosphere is eliminated by expressing rates in terms of mass of solutes, and depletion by foraging animals is eliminated by protecting flowers in a bag or cage that excludes all but the smallest insects.

Bags used to protect flowers from insect visits should be chosen with care to avoid effects on the contained microclimate and therefore on the concentration and production of nectar (Corbet, 1990; Búrquez and Corbet, 1998). Wyatt et al. (1992) compared unbagged flowers with flowers bagged in clear plastic (polyethylene), brown paper, pellon (a soft, white fabric of irregular mesh) and bridal veil (nylon netting of mesh size 10 × 10 threads/cm). Plastic bags caused marked elevation of humidity and temperature, lowered the nectar solute concentration and increased rates of sugar secretion. Paper and pellon had lesser effects, and bridal veil had very little effect, either on the microclimate in the bag or on the production and composition of nectar. Bridal veil is recommended as the preferred material for insect exclusion bags in studies of nectar secretion.

Reabsorption is more difficult to eliminate. It is usual to measure 'apparent secretion rate', the rate of change of solute content of nectar in an undisturbed, unvisited flower. In the many species that show no evidence for reabsorption, this probably represents the true secretion rate. But in many other species there is strong evidence, direct (Búrquez and Corbet, 1991; Nicolson, 1995) or indirect (Búrquez and Corbet, 1991), that reabsorption of nectar proceeds in conjunction with secretion, and sometimes continues after secretion has ended. The effects of reabsorption can be minimised by sampling a flower repeatedly at short intervals, minimising the quantity of nectar available in the flower for reabsorption. The cumulative increase in solute content of such repeatedly-sampled flowers, the 'gross secretion rate', often exceeds the apparent secretion rate measured in undisturbed flowers over the same total period of, say, 24 h. The difference is the 'apparent reabsorption rate'. Studies of this kind sometimes reveal marked diel patterning in the rates of both secretion and reabsorption (Búrquez and Corbet, 1991). The

'twenty-four hour sugar value' of Beutler (1953; Petanidou and Smets, 1995), the mass of sugar accumulating in an undisturbed bagged flower over 24 h, reflects the apparent secretion rate. The gross secretion rate may be much higher, and is probably a better (but less easily measured) index of the quantity of sugar supplied by a flower when forager visits are frequent, and thus of its value as a honey source. Further, if the balance between secretion rate and reabsorption rate changes with time, the 24-h sugar value will depend on the time of day at which the sample is taken.

Sometimes the cumulative mass of sugar secreted by repeatedly-sampled flowers is *less* than the apparent secretion rate. Some authors have attributed this to sampling damage to the nectary (Búrquez and Corbet, 1991), but others regard it as an adaptive feature: curtailed secretion and a shortened flower lifetime after a pollinator visit may reduce plant costs and help promote xenogamy (Freitas and Sazima, 2001).

Some species begin to secrete nectar before the flowers open (e.g. Pleasants, 1983). To measure apparent secretion rate, it is common practice to empty flowers of nectar, and then to bag the emptied flowers and resample them after a selected period. The initial nectar removal must be done gently, as damage to the flower may suppress secretion. Some authors therefore use filter paper wicks for this initial emptying. Preliminary sampling is necessary in order to decide the interval over which secretion is to be measured. To measure a secretion rate that approaches the gross secretion rate one should select an interval that is long enough for measurable amounts of nectar to accumulate, but not so long that reabsorption becomes important.

If repeated resampling is expected to damage the flowers, an alternative (but not statistically equivalent) procedure is to use a different set of ten (or more) flowers at each sampling time. The selected flowers are emptied, bagged, and then resampled for secretion rate after a known interval. This procedure is repeated at regular intervals from dawn until dusk or, for nocturnal flowers, through the night. A hand held refractometer can be operated in the dark by looking through it at a torch.

To monitor patterns of secretion and standing crop through the life of a flower, ten or more fresh flowers are selected at each sampling time from a cohort of even-aged flowers that were marked the previous evening, before sampling began. (Coloured plastic drinking straws, slit longitudinally and cut into short lengths, make useful rings for marking the stalks of small flowers.) If a pre-marked age cohort is not used, recruitment of newly-opened flowers during the day may cause an apparent increase in mean standing crop at times when secretion rate measurements are not necessarily high. Cohorts opening at different times of day may show different patterns of secretion depending on the interaction between flower age, weather and any circadian periodicity of secretion and reabsorption.

On the other hand, if the aim is to monitor patterns of secretion and standing crop in a population, such as would be encountered by a notional forager that is wholly unselective with respect to flower age, a random sample of flowers is taken at each sampling time.

Lengths of slender, flexible tubing can be inserted into a flower, left in contact with the nectary, and allowed to take up nectar as it is secreted over a period of time; periodic marking of the meniscus position allows the secretion rate to be monitored. Bertsch (1983) used graduated microcapillary pipettes for this purpose. If the tubing or pipette is slender enough to withdraw nectar as soon as it is secreted, reabsorption may be prevented and this method may measure gross secretion rate. If the nectar is protected from evaporation from the moment of secretion, the method can also be used to examine the concentration at which nectar is secreted (Bertsch, 1983).

6. CONCLUSIONS

Measurements of the standing crop and secretion rate of nectar are often a valuable or essential component of ecological studies of flower-visiting animals (e.g. Waddington, 1983) or functional studies of floral biology (e.g. Zimmerman, 1988). Such measurements are therefore often required by biologists whose primary interests and expertise lie elsewhere. This paper is designed to facilitate their

task, complementing the major reviews of relevant techniques (Dafni, 1992; Kearns and Inouye, 1993) by resolving some discrepancies about units of measurement and explicitly addressing some uncertainties about equipment that have sometimes caused problems for workers using these methods for the first time.

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Résumé – La teneur en sucre du nectar : estimation de la quantité de nectar disponible dans les fleurs et du taux de sécrétion au champ. Cet article décrit les méthodes pour échantillonner et mesurer les taux de sécrétion et les quantités de nectar disponibles dans les fleurs au champ. Il vise à résoudre certaines omissions et certains désaccords présents dans d'autres articles de synthèse sur les techniques de mesure du nectar. Parce que la valeur énergétique du nectar est importante pour les animaux qui visitent les fleurs, la quantité de nectar est souvent exprimée par la teneur en sucre (mg sucre par fleur). Elle peut être calculée par les mesures au champ du volume du soluté et de sa concentration dans des fleurs prises individuellement. Pour l'échantillonnage, je recommande les pipettes microcapillaires en verre, suffisamment fines pour échantillonner quantitativement les fleurs pollinisées par les insectes sans les déchirer et je discute de méthodes alternatives d'échantillonnage pour les très petites quantités ou pour le nectar très visqueux. J'indique un type de réfractomètre à main qui peut mesurer la concentration du soluté (en g de saccharose pour 100 g de solution) dans de très petits volumes de nectar et je considère dans quelle mesure les calculs de la valeur énergétique du nectar basée sur les lectures du réfractomètre sont affectés par les facteurs suivants : présence de sucres autres que le saccharose ou de composés autres que les sucres, température, regroupement des échantillons de nectar provenant de plusieurs fleurs ou essai de dilution d'un échantillon de nectar dans la micropipette. La quantité de nectar est souvent distribuée irrégulièrement parmi les fleurs d'une parcelle et la quantité moyenne de sucre par fleur rencontrée par un insecte qui butine systématiquement peut dépasser celle échantillonnée par un écologiste non sélectif.

Le taux de sécrétion, communément exprimé en mg de sucre par fleur et par heure, est mesuré par le taux d'accumulation de nectar dans des fleurs vidées et dont on a exclu les visiteurs en ensachant les fleurs. Les sachets en voile de mariée ou en moustiquaire agissent moins sur le microclimat, et donc sur la concentration en nectar et le taux de sécrétion, que les sachets en papier ou en polyéthylène. Certaines espèces réabsorbent le nectar et cette réabsorption par les fleurs peut réduire le taux apparent de sécrétion. Pour minimiser cet effet, la durée pendant laquelle la sécrétion de nectar est mesurée doit être aussi brève qu'il est possible pour une mesure précise. Un protocole pour suivre la quantité de nectar disponible et le taux de sécrétion sur une journée de l'aube au crépuscule est indiqué.

nectar / quantité disponible / taux de sécrétion / concentration / réfractomètre / microcapillaire / nectarivore

Zusammenfassung – Der Zuckergehalt im Nektar: Schätzung der Nektarmenge und der Sekretionsrate im Freiland. Diese Arbeit beschreibt Methoden zur Sammlung von Proben und zur Messung von Sekretionsraten von Nektar in Blüten im Freiland. Das Ziel ist die Aufklärung von einigen Auslassungen und Diskrepanzen in anderen Darstellungen der Techniken zur Messung von Nektar. Da der Energiegehalt des Nektars für die Blüten besuchenden Tiere wichtig ist, wurde die Nektarmenge (anstehende Ernte) häufig als Zuckergehalt (mg Zucker pro Blüte) dargestellt. Dieser kann aus den Messungen des Volumens und der Konzentration der Lösung der einzelnen Blüten geschlossen werden. Zur Probensammlung empfehle ich mikrokapillare Glaspipetten, die dünn genug sind, um durch Insekten bestäubte Blüten quantitativ ohne Verletzung zu beproben. Außerdem diskutiere ich Sammlungsmethoden für sehr kleine Mengen oder sehr zähflüssigen Nektar. Ich setze mich für einen Typ eines handlichen Refraktometers ein, der in sehr kleinen Nektarvolumen Konzentration der Lösung messen kann (in g Sucrose per 100 g Lösung) und ich berücksichtige das Ausmaß des Vorkommens von zusätzlich zu Sucrose gelösten Stoffen wie nicht-Zucker Komponenten auf die auf den Ablesungen des Refraktometers basierenden Berechnungen des Energiegehalts. Auch der Einfluss von Temperatur und von Sammelproben des Nektars von mehr als einer Blüte oder der Versuch einer Verdünnung der Nektarprobe in der Mikropipette wurden einbezogen. Die Nektarmenge ist häufig ungleich in den Blüten in einer Stelle verteilt und die durchschnittliche Zuckermenge pro Blüte, die von einem systematischen Sammler angetroffen wird könnte über der Menge liegen, die von einem unselektive Ökologen gesammelt wird.

Die Sekretionsrate, allgemein als Zucker pro Blüte pro Stunde ausgedrückt, wird als die Rate der Akkumulierung von Nektar nach einer Leerung der durch Umhüllung vor Blütenbesuchern geschützten Blüte gemessen. Die Hüllen aus Brautschleiern oder Moskitonetzen haben einen geringeren Einfluss auf das Mikroklima und damit auf die Stoffkonzentration im Nektar und die Sekretionsrate als Hüllen aus Papier oder Polythen. Einige Arten resorbieren Nektar und diese Resorption durch die Blüten kann die scheinbare Sekretionsrate vermindern. Um diesen Effekt zu verringern, sollte das Intervall, in dem die Nektarsekretion gemessen wird, so kurz sein wie es für eine genaue Messung möglich ist. Ein Protokoll für ein Monitoring der Nektarmenge und der Sekretionsrate über einen Tag vom Morgengrauen bis in die Abenddämmerung wäre ausgezeichnet.

Sekretionsraten / Nektarmenge / Konzentration / Mikrokapillare / Refraktometer / Zucker / Aminosäuren

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