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Do flowers reabsorb nectar?

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Abstract. The rate of change in the standing crop of nectar allowed to accumulate in flowers, described here as the apparent secretion rate, can be resolved into two components: gross secretion rate and apparent reabsorption rate. A simple model shows how changes in these component rates may affect the apparent secretion rate. The ecological and physiological correlates of various temporal patterns of secretion are discussed in relation to whether the nectar carbohydrates originate from storage tissues or from immediate photosynthate.

Experiments with *Impatiens glandulifera* Royle, *Borago officinalis* L. and *Fritillaria imperialis* L. gave no evidence for reabsorption, but in *Brassica napus* L. apparent reabsorption was revealed by a difference between the apparent secretion rate and the cumulative rate of secretion derived by repeated sampling of individual flowers at short intervals, and true absorption was revealed by net solute loss from flowers protected from insect visits. Gross secretion rate and apparent reabsorption rate both peaked at midday on day 1. Thereafter secretion almost stopped, but reabsorption continued, peaking at night and at midday on day 2, until no more nectar remained in the flowers.

Reabsorption occurs in some species but not in others. We suggest that it does not occur in flowers in which nectar accumulates at a site remote from the nectary (e.g. Asclepiadaceae), or in those in which the nectary is lost when the corolla falls (e.g. *Impatiens*). The ecological implications of reabsorption are considered briefly.

Key-words: Brassica, nectar, pollinator reward, reabsorption, resorption, sugars

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Introduction

In nature, inputs to nectar comprise solutes (largely sugars) and water gained by secretion, and water gained by condensation from humid air. Outputs comprise solutes and water lost by reabsorption or removal by nectarivores, and water lost by evaporation in dry air. To isolate the component processes of secretion and reabsorption we have eliminated nectarivore visits by protecting the flowers, and eliminated the need to consider condensation and evaporation by expressing gains and losses in terms of solutes alone, disregarding water. An alternative way to control water exchange might be to conduct the experiments in a chamber in which the relative humidity was in equilibrium with nectar at the concentration at which it is secreted.

Reabsorption is here taken to mean net movement of solutes from the nectar into the plant (Table 1). Such reabsorption can be inferred if the solute content of nectar decreases when solute transfer to other destinations is prevented. In our experiments removal of nectar solutes by insect visitors was prevented by protecting flowers in a glasshouse or bag. We therefore infer reabsorption if the nectar solute content of protected flowers decreases over time.

Several authors have shown movement of labelled sugars from nectar into the nectaries (e.g. Bieleski & Redgwell, 1980) or to more remote parts of a plant (e.g. Zimmerman, 1988). Such transfer is a necessary, but not sufficient, condition for reabsorption. Labelled solutes can move in both directions between the nectar and the floral tissues (Bieleski & Redgwell, 1980). When influx (solute transfer from nectar into the plant) and efflux occur concurrently, the balance between the two rates determines whether the solute content of the nectar in an unvisited flower increases or decreases. If influx rate exceeds efflux rate, an increase in influx rate would reduce the solute content of the nectar (reabsorption). If efflux rate exceeds influx rate, in an unvisited, undisturbed flower, an increase in influx rate would lower the net rate of solute accumulation in the nectar (here called the apparent secretion rate). Increased influx rate is not the only possible cause for such lowering of the apparent secretion rate; it might

Table 1. Operational definitions of terms used here (in terms of solutes).

Apparent secretion rate: rate of change of solute content of nectar in undisturbed, unvisited flowers
Gross secretion rate: rate of change of solute content in nectar of repeatedly sampled flowers
Apparent reabsorption rate: difference between apparent secretion rate in undisturbed flowers and gross secretion rate
Reabsorption: rate of net solute loss from unvisited flowers; negative apparent secretion rate
Efflux rate: rate of movement of solutes from plant into nectar
Influx rate: rate of movement of solutes from nectar into plant
If repeated sampling prevents influx, without affecting efflux rate, gross secretion rate should approach efflux rate, and apparent reabsorption rate should approach influx rate

also be due to decreased efflux rate. Some distinction might be made between these two alternatives if influx could be slowed by removing the secreted nectar from the site of inward transfer (which may or may not be identical with the site of outward transfer). This might be done by repeatedly emptying the flower. If influx rate in full flowers exceeds that in recently emptied flowers, then the cumulative apparent rate of nectar secretion found when sampling individual flowers repeatedly at short intervals over a period will exceed that found when taking a single sample at the end of the same period. A similar result would be obtained if repeated emptying somehow slowed efflux rate, a possibility not eliminated in our experiments. Recognizing that without a study of the kinetics of solute flux we cannot distinguish these alternatives, we refer here to the apparent secretion rate in repeatedly sampled flowers as the 'gross secretion rate', and the difference between that and the apparent secretion rate in undisturbed, unvisited flowers as the 'apparent reabsorption rate'. If frequent sampling prevents influx, without affecting efflux rate, gross secretion rate should approach efflux rate and apparent reabsorption rate should approach influx rate.

Different diel patterns in the apparent secretion rate have been reported for different plant species. Peaks in the apparent secretion rate have been found in the morning (e.g. Pleasants & Chaplin, 1983), or at midday (e.g. Nuñez, 1977; Frankie & Haber, 1983; Corbet & Delfosse, 1984), or in the morning and again in the afternoon or evening (e.g. Nuñez, 1977; Corbet & Delfosse, 1984), or at dusk and at night (e.g. Martinez del Rio & Búrquez, 1986; Eguiarte & Búrquez, 1987). How can this diversity of nectar secretion patterns be described? Here, we present a simple model, aiming to describe the nectar secretion process with a minimum set of parameters. Although the model does not given an explanation of the actual process, some clues based on general physiological considerations are advanced. A general methodology is proposed, and is applied to four plant species with different pollination syndromes and physiology. The distribution of reabsorption among plant groups is also considered.

The model

We consider the apparent rate of secretion of nectar solutes as the resultant of two processes acting in opposite directions: solute efflux (from nectary to nectar) and solute influx (from nectar to nectary). The actual influx rate is sometimes less than the potential maximum rate because of the limits set by the amount of nectar in contact with the sites of influx in the nectary. In terms of solutes, the apparent nectar secretion rate will be the difference between efflux rate and influx rate.

The simplest assumption is that both efflux rate and influx rate of solutes change linearly with time. Depending on the slopes and relative positions of the curves, the apparent secretion rate will either increase or decrease linearly. Between these extreme cases lies a continuous family of curves, ranging from decreasing to increasing rates of apparent secretion.

In nature, however, the apparent nectar secretion rate does not change linearly with time. It generally shows at least one maximum each day. A further refinement of the model is therefore to make one of the curves curvilinear with at least one peak, while maintaining the other linear. This approach gives four possible general outcomes: two in which the apparent rate of secretion has one maximum (Fig. 1a and d), and two in which it has more than one maximum (Fig. 1b and c). A unimodal apparent secretion curve can be produced in two ways: by an efflux rate curve with one maximum or an influx rate curve with one minimum (Fig. 1a and d). Similarly, high rates of apparent secretion in the morning and evening can be produced either by an efflux rate curve with one minimum or by an influx rate curve with one maximum (Fig. 1b and c). This symmetry makes inference from the model difficult because two very different causal situations can produce the same result. Hypothetical examples illustrating particular cases of the model are provided in Fig. 2.

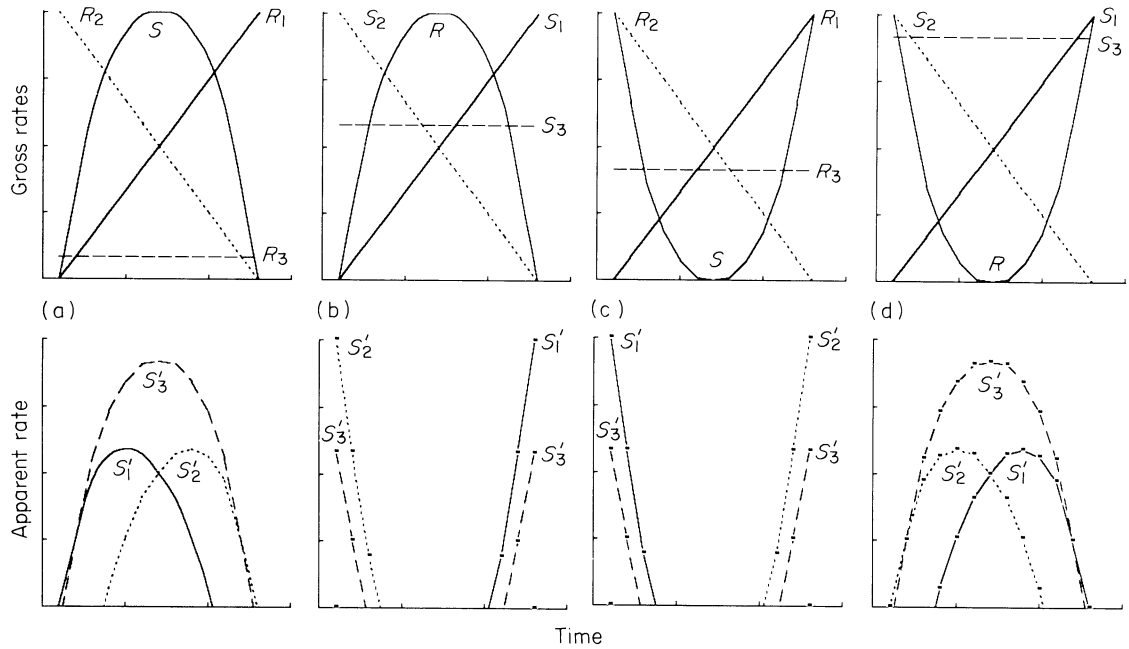

Fig. 1. Model showing the apparent secretion rate (lower graph of each pair) when the rate of one process (solute efflux or influx) varies linearly and that of the other varies non-linearly (upper graph of each pair). I = influx rate; E = efflux rate; S' = apparent secretion rate. The apparent secretion rate has one maximum per day if the efflux rate has a maximum (a) or if the influx rate has a minimum (d); the apparent secretion rate has two maxima per day if the influx rate has one maximum (b) or if the efflux rate has one minimum (c).

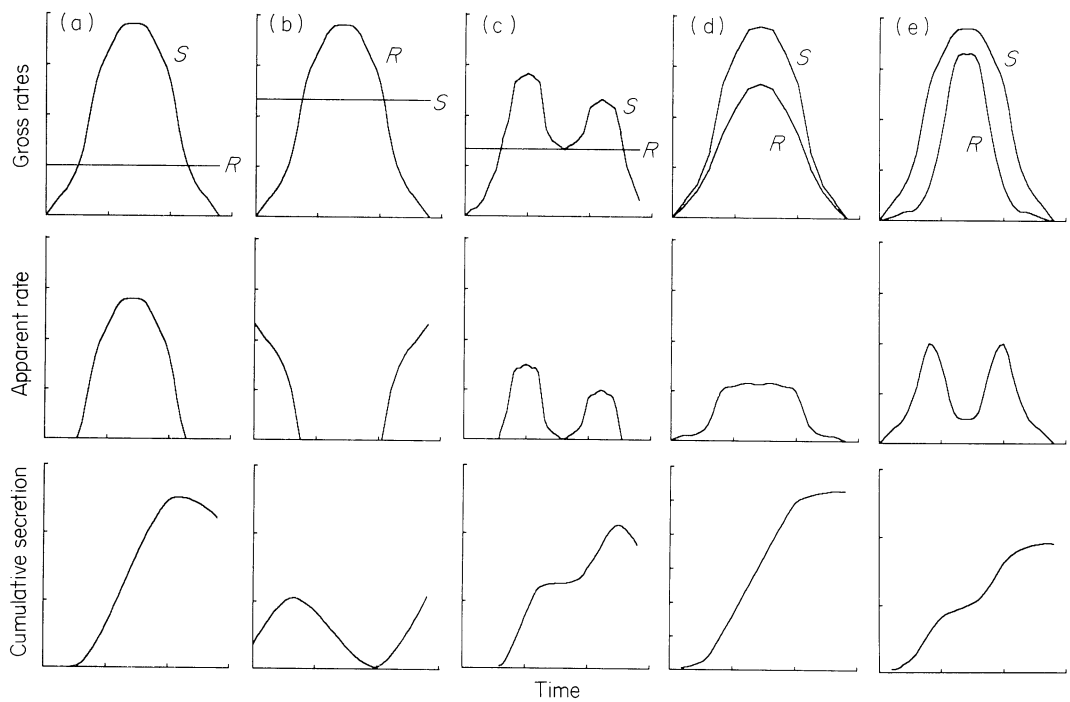

Fig. 2. Model illustrating the relationship between diel changes in rates of solute efflux (E) and influx (I) (upper row), apparent secretion rate (S') (middle row) and cumulative secretion curve (C) (=rate of accumulation of nectar) (bottom row). (a) Influx changes linearly, efflux shows one maximum; (b) efflux changes linearly, influx shows one maximum; (c) as (a) but efflux is reduced at midday; (d, e) two cases in which both efflux and influx show one maximum.

So far, we have assumed that the rate of one process changes linearly; but the rates of influx and efflux might both change non-linearly, perhaps in response to the same physiological or environmental factors. For simplicity, Fig. 2 does not include cases in which both efflux rate and influx rate are non-linear.

A model involving an efflux rate curve with one maximum, or an influx rate curve with one minimum, is biologically reasonable. Solute transfer rates are likely to be modified in a predictable way by changes in external factors such as air temperature. The apparent secretion rate seems to be influenced by factors such as irradiance, temperature and water balance (Huber, 1956; Nuñez, 1977; Búrquez, 1988). Because of this, a noon peak of secretion is likely to be common among diurnal flowers, but not universal.

In plants that do not mobilize carbohydrate reserves for nectar secretion, it is reasonable to suppose that the diel change in irradiance will affect the nectar secretion rate, if only because the supply of sugar depends on immediate photosynthesis (as shown by light deprivation or defoliation experiments, e.g. von Czarnowsky, 1952; Nuñez, 1977; Pleasants, 1983; Búrquez, 1988; but see Zimmerman & Pyke, 1988). At times of high irradiance, water deficit, leading to midday closing of stomata, could reduce the rate of photosynthesis. In plants that depend on the immediate supply of sugar, nectar secretion might decrease or even stop at such times, to begin again when photosynthesis resumes (Fig. 2c). Such plants are not expected to secrete nectar at night.

In plants in which the supply of nectar sugar depends on carbohydrate reserves rather than immediate photosynthesis, water balance could play a major role in secretion. In many plants water deficit might be severe enough to suppress translocation of photosynthates at midday, again limiting secretion to the morning and afternoon (Fig. 2c).

If plants are classified according to the source of photosynthates on which their nectar secretion depends, a remarkable corollary emerges for those plants that produce nectar during the night. In nocturnal or crepuscular nectar-producing plants, nectar sugar must come from storage tissues. Most plants producing nectar at night have storage tissues in the stem, leaves, and/or enlarged rhizomes (e.g. Bombacaceae, Nyctaginaceae). Many of them are CAM plants (e.g. Cactaceae, Agavaceae, Crassulaceae), in which the timing of nectar secretion may be linked with stomatal opening and translocation (see Ting, 1985).

Materials and methods

Nectar was sampled with 1 and 5 mm^3 disposable microcapillaries (Camlab, Cambridge) or, for larger volumes, autoclavable nylon tubing of 0·5 mm internal diameter (Portex, Hythe, Kent). The length of the column of nectar in the microcapillary was then measured to 0·1 mm with callipers. Nectar solute concentration was measured at once using pocket refractometers modified for small samples (Bellingham and Stanley, Tunbridge Wells), and expressed as percentage sucrose equivalent (g sucrose per 100 g solution). The sugar content of nectar was calculated after converting this to concentration by volume (Bolten *et al.*, 1979), using the quadratic equation resulting from the regression of percentage nectar solute concentration by weight (as g sucrose per 100 g solution, NCW), against nectar solute concentration by volume (as g sucrose per ml solution, NCV):

$$NCV = NCW^2 (59{\cdot}6 \times 10^{-6}) + NCW (9{\cdot}224 \times 10^{-3}) + 7{\cdot}08 \times 10^{-3}$$

This equation gives an error of less than 1% for values of nectar solute concentration between 10 and 80%.

The flowers

Flowers of oilseed rape, *Brassica napus* L. cv. Maris Haplona (Brassicaceae), typically last 30–50 h. Nectar secretion begins when the flowers open, ceases at night, and resumes the next day, usually at a much reduced rate. At the end of the flower's life, the petals shrivel and fall, but the nectaries remain attached. The pollination of *Brassica napus* has been described by Eisikowitch (1981), Williams (1985) and Búrquez (1988).

The nectaries are innervated by phloem alone. Two pairs are present, a medial cylindrical pair with a sparse phloem supply, and a lateral, flat, densely innervated pair. Most of the nectar is secreted by the lateral nectaries (Arber, 1931; Norris, 1941; Frei, 1955; Davis, Peterson & Shuel, 1986). In this study, 90–95% of the nectar sampled from *Brassica napus* flowers came from the lateral nectaries (Búrquez, 1988).

The flowers of *Impatiens glandulifera* Royle (= *I. roylei* Walpers) (Balsaminaceae) are zygomorphic with a saccate sepal into which bees crawl for nectar. This sepal ends in a spur lined with nectariferous tissue. The nectary is well innervated by phloem and xylem by a dorsal vein running the length of the sepal. Nectar secretion

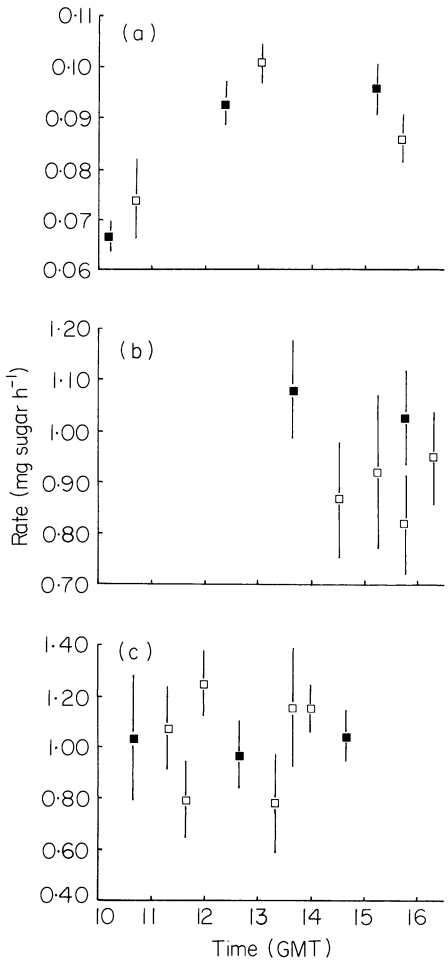

Fig. 3. Apparent nectar secretion rates over very short intervals (15–25 min; open squares) and over intervals of 2–3 h (filled squares) in flowers of (a) *Brassica napus*, (b) *Impatiens glandulifera* and (c) *Fritillaria imperialis*.

begins soon after the flower opens. As with *B. napus*, it ceases at night, and resumes next day. At the end of the flower's life the whole corolla falls, including the nectary. The pollination ecology of *Impatiens glandulifera* has been described by Daumann (1967), Valentine (1971, 1978) and Búrquez (1988).

The crown imperial, *Fritillaria imperialis* L. (= *Imperialis coronata* Dum-Cours) (Liliaceae) has large flowers with a nectary at the base of each of the six perianth segments. Flowers last 5–8 days, and are strongly protogynous. Nectar secretion begins as the flowers open, and lasts for the whole life of the flower. It peaks during the day and almost ceases at night. The rate of secretion decreases steadily as flowers age. If nectar is allowed to accumulate in the flowers, it forms a large droplet that easily falls if disturbed. After the active life of the flower, the perianth segments shrivel and dry up. *F. imperialis* pollination ecology has been described by Búrquez (1989).

Borage, *Borago officinalis* L. (Boraginaceae), has pendulous flowers arranged in cymose inflorescences. Nectar secretion begins shortly after flower opening, and lasts for most of the life of the flower. The flowers remains active for 24–35 h. Nectar is secreted by day; at night it ceases completely, to resume the next day. The nectaries of *Borago officinalis* are at the base of the ovary (Corbet, Chapman & Saville, 1988). As the flowers are pendulous, the nectar is likely to flow to a position on the five saccate lobes of the corolla, from which it is sucked by the visitors (Búrquez, 1988). By the end of the flower's life, a ring of abcission forms at the base of the corolla, which falls as a unit, carrying with it any accumulated nectar.

Results

Apparent secretion and the sampling interval

When the accumulation of nectar is monitored by sampling at intervals using a fresh sample of undisturbed flowers from the same cohort at each sampling time, the rate of change of accumulated nectar solutes represents an apparent secretion rate that may be considered as the resultant of the two opposing processes of solute influx and efflux. One way to explore these two processes separately would be to examine the effect of suppressing influx by removing all nectar from contact with the nectary as soon as it is secreted. In practice, this can be approched by repeatedly emptying a flower, and measuring the rate of increase in solute content over successive very short periods.

To accumulate a measurable quantity of nectar takes about 15 min in *Impatiens*, 20 min in *Fritillaria* and 25 min in *Brassica*. To see whether the period of accumulation could be increased from this minimum to 3 h without increasing apparent reabsorption, the apparent secretion rate in flowers sampled repeatedly at 2–3 h intervals was compared with that in flowers re-sampled the minimum period after emptying (Fig. 3).

No significant differences in nectar secretion rate were found between flowers sampled at very short intervals and flowers sampled every 2–3 h in *Brassica* or when comparing individual nectaries of *Fritillaria* (Table 2). In *Impatiens*, significant differences were found at midday between nectar secretion rates in flowers sampled every 3 h and in those sampled every 15 min. These observations

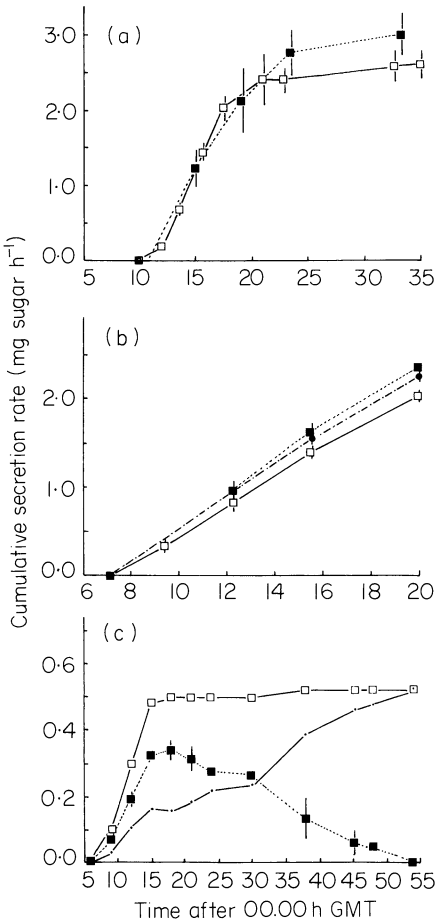

Fig. 4. Mean (±SE) rates of secretion in repeatedly sampled flowers and in flowers in which nectar is allowed to accumulate, in *Borago officinalis, Impatiens glandulifera* and *Brassica napus*. (a) *Borago officinalis* nectar sampled repeatedly every 3 h (open squares) or sampled from undisturbed flowers after being allowed to accumulate for intervals up to 24 h; (b) *Fritillaria imperialis* nectar sampled from individual nectaries repeatedly every 3 h starting 3 (open squares), 6 (black squares) or 9 (closed circles) h after isolation; (c) *Brassica napus*, cumulative secretion of nectar sampled repeatedly every 3 h (open squares), accumulated nectar in undisturbed flowers (black squares) and calculated (apparent) reabsorption rate (dots), 31 May 1985. Note that the *Brassica* graph spans 2 days.

were repeated on a different date, and the comparison resulted in differences that were significant only at the 10% level (Table 2). In both cases, the differences were in the opposite direction to those expected if nectar accumulation enhances solute influx; the shorter sampling interval yielded less nectar, suggesting a decline in nectar secretion rate, perhaps resulting from tissue damage or from experimental errors as the sampling interval, and therefore the volume sampled, diminished.

The rate of accumulation of nectar over very short intervals (15–30 min) was not higher than the rate for a longer sampling interval (2–3 h) (Fig. 3) in the species studied. This comparison suggests that a sampling interval of up to 3 h does not allow enough nectar to accumulate to produce a detectable increase in apparent reabsorption. These longer intervals were therefore used in subsequent studies.

Secretion and reabsorption

In *Fritillaria*, nectar was sampled in seven flowers on different plants. Each flower bears six independent nectaries. Two nectaries in each were randomly assigned to each of three experimental treatments. Some nectaries were emptied at dawn and sampled every 3 h until dark (repeatedly sampled, treatment 1). Some were sampled initially either 6 or 9 h after emptying, and then every 3 h (accumulated nectar, treatments 2 and 3, respectively). Thus each of the three treatments was applied to two nectaries on each of seven plants (Fig. 4). An analysis of variance on the cumulative nectar at the last sampling time shows no effects of treatment on nectar secretion. Most of the variance can be assigned to the effects of individual plants (Table 3). There is no evidence for apparent reabsorption (or a decline in nectar secretion rate resuling from repeated sampling), on the time scale studied. Observations on old bagged flowers support this inference. In these, nectar forms a large hanging droplet that eventually drips out of the nectary.

In *Borago*, a large sample of opening flowers was marked and bagged at 10.00 h GMT. A randomly selected sample of five flowers was sampled repeatedly every 3 h for about 24 h to give the gross secretion rate. At each sampling time, a destructive sample of five flowers was randomly drawn from the marked population. The rate of change of the standing crop in these flowers gave the apparent secretion rate in undisturbed flowers.

A significant effect of treatment on nectar secretion is evident in *Borago* (Table 3). The amount of nectar accumulated 24 h after flower opening was higher than the cumulative nectar in flowers sampled repeatedly every 3 h ($\bar{x}$ = 3·00 ± 0·30 (SEM) mg sugar, and $\bar{x}$ = 2·58 ± 0·22 mg sugar, respectively). The two curves separate after 20.00 h GMT (Fig. 4). The nectar secretion rates in both treatments were similar (about 0·3 mg h^{-1}), but secretion continued for a longer period in flowers sampled only once. This suggests that repeated sampling interfered with secretion, per-

Table 2. Mean nectar secretion rate (as mg sugar h^{-1}) at the peak of secretion, standard error and *F*-values and their probabilities for flowers sampled at either very short intervals or long time intervals (treatment 1 = 0·25–0·40 h and treatment 2 = 2–3 h, respectively).

Species	Treatment	Mean	SEM	*n*	*F*	*P*
Fritillaria[a]	1	0·1720	0·0117	30	0·0181	0·8935
	2	0·1693	0·0152	15		NS
Brassica[b]	1	0·0852	0·0028	72	0·1500	0·6990
	2	0·0868	0·0036	72		NS
Impatiens[c]	1	0·5557	0·0453	41	6·4158	0·0132
	2	0·7085	0·0401	43		*
Impatiens[d]	1	0·8889	0·0572	40	3·6090	0·0612
	2	1·0543	0·0648	39		NS

NS = not significant; * = significant differences between groups; *F* = *F*-values from ANOVA; *P* = exact probability; SEM = standard error of the mean (see Fig. 3). [a]*Fritillaria* values refer to only one nectary; to obtain the mean value per flower multiply by 6. [b]The factorial ANOVA showed significant effects of time of sampling but interaction time × treatment was not significant in all experiments. [cd]2 different days for *Impatiens*.

haps by damaging the nectaries. This experiment gave no evidence for apparent reabsorption.

In *I. glandulifera* no significant differences were found in the cumulative amounts of nectar sugar yielded between bagged flowers sampled every 3 h and those sampled only once at the time of abscission ($\bar{x}$ = 27·7 ± 2·0 (SEM) mg sugar, n = 22, and $\bar{x}$ = 25·1 ± 2·5 mg sugar, n = 17 respectively; ($F_{1,37}$ = 0·456, P = 0·5)). Again, as in *Borago*, nectar secretion did not increase and may even have diminished as sampling frequency increased.

Brassica gave more interesting results. As with *Borago*, a large sample of flowers at the opening stage was marked and bagged. At each sampling time, four to seven of these were picked and their nectar was sampled. This was repeated every 3 h from 05.00 h (GMT) until 24.00 h, and thereafter at longer intervals until 06.00 h, 49 h later. This period comprised the whole life of the flower. At the same time, a sample of seven flowers was repeatedly sampled. These observations were conducted in a large high-humidity polythene enclosure in a glasshouse with even-aged plants grown under uniform conditions. We kept the plants at high humidity because large volumes of dilute nectar facilitate sampling of small nectar quantities. This technique is useful as a way to explore secretory processes, but the volumes and concentrations measured in these conditions

Table 3. ANOVA for the cumulative and accumulated values of sugar secreted by plants of *Fritillaria imperialis* and *Borago officinalis*. (a) *F. imperialis* after 13 h sampling. Treatments: 1 = sampled repeatedly every 3 h; 2 = sampled 6 h after isolation; 3 = sampled 9 h after isolation. (b) *Borago officinalis* after 22 h of sampling. 1, repeated sampling every 2–3 h; 2, sampling only once at 4, 8, 12·5 and 22·5 h. See text for explanation of methods. The differences between treatments in *Brassica napus* were so great that the analysis was not needed.

Source of VAR	SS	d.f.	Mean square	*F*	*P*
(a) *Fritillaria imperialis*					
Main effects	20·855	8	2·607	13·118	<0·0001
Treatment	0·795	2	0·795	2·001	0·1600
Plant	20·060	6	3·343	16·823	<0·0001
Interaction					
Plant × treatment	3·146	12	0·262	1·319	0·2790
Explained	24·002	20	1·200	6·039	<0·0001
Residual	4·173	21	0·199		
Total	28·175	41	0·687		
(b) *Borago officinalis*					
Main effects	63·999	5	12·800	64·510	<0·0001
Treatment	0·972	1	0·972	4·898	0·0320
Plant	61.376	4	15·344	77·331	<0·0001
Interaction					
Plant × treatment	0·617	4	0·154	0·778	0·5460
Explained	64·617	9	7·180	36·184	<0·0001
Residual	8·334	42	0·198		
Total	72·950	51	1·430		

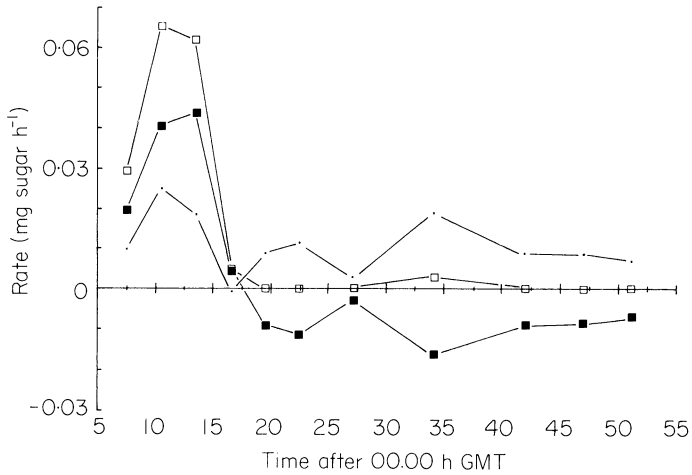

Fig. 5. Rates of secretion and reabsorption in *Brassica napus*, 31 May 1985 (see text). Filled squares: gross secretion rate; open squares: apparent secretion rate; dots: reabsorption rate.

differ from those found in the field on the sunny days when most pollinators probably visit *Brassica napus*.

In undisturbed *Brassica* flowers, the sugar content reached a peak and decreased slowly until none was left in the flower. When the apparent secretion rate in undisturbed flowers (rate of change in the standing crop of accumulated nectar) is subtracted from the gross secretion rate (measured in repeatedly sampled flowers), a curve of apparent reabsorption is revealed (Fig. 5).

Secretion was largely confined to the first day. Apparent reabsorption peaked and diminished in parallel with secretion on day 1. True reabsorption (net solute loss from the nectar) occurred from 15.00 h on day 1 onwards with two peaks, one on the first night and the second at midday on day 2, coinciding with a small second peak of secretion. The corresponding cumulative curves show that reabsorption continued until no nectar remained (Fig. 4).

Discussion

Reabsorption, in the sense of net solute transfer from nectar to nectary, is inferred when nectar solutes disappear from an unvisited flower. We have shown that this can occur in *Brassica napus*.

Our experiments also show that the apparent secretion rate in undisturbed flowers of *Brassica napus* is sometimes less than the cumulative gross secretion rate in repeatedly sampled flowers. They imply that the component rates of solute influx and/or efflux show regular changes through the day.

In the absence of net solute transfer, if solute influx rate from nectar to plant exceeds solute efflux rate, repeated sampling of a flower may yield cumulative nectar secretion greater than the apparent secretion rate measured by the rate of change of the standing crop in undisturbed flowers. This has often been demonstrated (e.g. Boëtius, 1948; Raw, 1953; Corbet & Delfosse, 1984; Gill, 1988). One explanation might be that repeatedly sampled flowers never have time to accumulate much nectar, and this reduced volume may reduce or abolish solute influx, which perhaps in undisturbed flowers might proceed concurrently with solute efflux.

If temporal changes in the balance between influx and efflux depend on the amount of nectar present in a flower, efflux rate might be limited by the availability of sugar within the plant and influx rate by the availability of nectar in the flower. In particular, if influx were limited to specific sites within a flower, it might be expected to occur only when the flower contained a minimum threshold volume of nectar, enough to bring nectar into contact with those reabsorptive sites. The resulting dependence of apparent secretion rate on the volume of the standing crop of nectar might contribute to the regulation of the volume of nectar in flowers. Our failure to find a difference in the rate of nectar accumulation between flowers sampled at 15-min intervals and flowers sampled at 3-h intervals (Figs. 3 and 4) may indicate that it takes more than 3 h to secrete enough nectar to

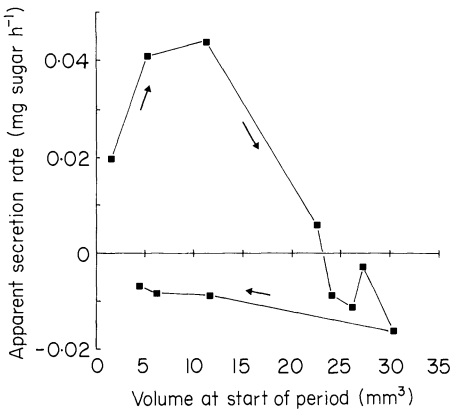

Fig. 6. *Brassica napus*, 31 May 1985 (see Figs. 4 and 5). Apparent secretion rate plotted against volume of accumulated nectar at the beginning of each sampling period. Successive samples are joined in sequence (arrows); the first six samples were taken at 3-h intervals on day 1.

reach the minimum threshold volume permitting influx to become detectable.

Alternatively, influx and/or efflux rate might depend on nectar volume in some other way, or on solute concentration (which would deviate further from the secretion concentration when nectar volumes are low, because of rapid equilibration with ambient humidity). In our experiments, correlations between apparent reabsorption rates and the volume or concentration of nectar do not allow inferences about causality, because successive samples are not independent. However, the absence of any correlation between apparent secretion rate on day 1 and the concentration of solutes in accumulated nectar at the beginning of each sampling period ($r = 0{\cdot}25$, $P > 0{\cdot}2$, $n = 6$) implies that any effect of concentration on secretion rate, if present, is unimportant. The correlation between apparent secretion rate on day 1 and the volume of accumulated nectar at the beginning of the sampling period (Fig. 6) was stronger but still not significant at the 5% level ($r = -0{\cdot}80$, $0{\cdot}05 < P < 0{\cdot}1$). It may be a corollary of the progression of secretion rate through time (Fig. 5), and does not necessarily give evidence for the expected negative relationship between secretion rate and the volume of nectar. Temperature has been shown to be a major determinant of apparent secretion rate in *Brassica napus*, in that at constant temperature the secretion rate is higher at 25 °C than at 18·5 °C, but temperature does not dictate the diel pattern, because the midday peak persists when the temperature is held constant (Búrquez, 1988). Perhaps nectar concentration or volume, like temperature, affects the peak level of secretion without dictating the diel pattern. Such effects would not be revealed by this experiment. An alternative way to explore the effects of volume and concentration on rates of secretion and reabsorption would be to put standard simulated nectars into flowers.

Surprisingly, the nectar yield of flowers in which nectar is allowed to accumulate has sometimes been found to be greater than that of the accumulated nectar in repeatedly sampled flowers (McDade & Kinsman, 1980; Corbet & Willmer, 1981). Perhaps sampling had damaged the nectary.

In some species (*Borago, Fritillaria, Impatiens*) we did not find apparent reabsorption. This conforms with the model shown in Fig. 1a, for the case with zero influx rate. *Brassica napus*, in which all nectar was eventually reabsorbed, conforms with the model shown in Fig. 2d.

Many workers, from Bonnier (1879) onwards, have shown that reabsorption does occur in some plants (Lüttge & Schnepf, 1976; Fahn, 1988). It has been demonstrated as net movement of nectar constituents into the plant (Wilson, 1881; Boëtius, 1948; Corbet & Delfosse, 1984), or inferred from the movement of radioactive tracers (e.g. Pederson, LeFevre & Wiebe, 1958; Ziegler & Lüttge, 1960; Shuel, 1961; Lüttge, 1962; Bieleski & Redgwell, 1980). On the other hand, true or apparent reabsorption has been sought but not found in other species, including *Asclepias syriaca* (Southwick, 1983), *Clintonia borealis* (Plowright, 1981) and *Ipomopsis aggregata* (Pleasants, 1983). Why should reabsorption occur in some species but not in others?

In some species, nectar accumulates after secretion at a site remote from the nectary. This is seen particularly in families with highly modified flowers, such as Asclepiadaceae and some Orchidaceae. In *Asclepias* species, for instance, nectar accumulates in the cucullus, where physical barriers separating it from the nectary would impede reabsorption (Galil & Zeroni, 1965; Southwick, 1983). Of the species studied here, *Borago* may represent another example of the same phenomenon.

In other species, nectar retains contact with the nectaries. Reabsorption might be expected in these, but it does not occur in all of them. It seems from the scant literature that reabsorption occurs mainly in those flowers in which the nectaries (with the nectar) remain attached to the plant after the corolla has fallen. This seems to be so for *Rubus, Trifolium, Vicia, Sinapis, Medicago, Abutilon, Streptosolen, Echium, Eucalyptus* and (as shown here) *Brassica* (Boëtius, 1948; Raw,

1953; Pedersen *et al.*, 1958; Shuel, 1961; Nuñez, 1977; Corbet & Delfosse, 1984). Species reported as lacking reabsorption, despite sustained contact of the nectar with the nectary, are those in which the nectaries are on the corolla or another floral structure which is shed soon after fertilization, as in *Impatiens glandulifera* (this paper). Reabsorption is therefore most unlikely in *Delphinium, Aquilegia, Symphoricarpos* and *Lonicera* (and probably other members of the Ranunculaceae, Caprifoliaceae, Fumariaceae and Lentibulariaceae, among others).

The ecological consequences of nectar reabsorption have rarely been considered. In many plants nectar accounts for a sizable proportion of the carbon budget during reproduction (Southwick, 1984). A flower that reabsorbs nectar not removed by visiting nectarivores can reclaim at least a part of the energy allocated to nectar production. If photosynthate is a limiting resource, and if the energetic cost of reabsorption (probably concentration dependent) is less than the energy content of the nectar, reabsorption can increase the resources available to developing seeds in this and other flowers on the same plant. If the nectar is not all removed by a nectarivore at the time when the flower is available for pollination, then the capacity for reabsorption permits the plant itself to compete with any thieves and gleaners for the remaining dregs of nectar.

Removal of nectar from flowers no longer available for pollination may have evident advantages. In some cases it has been shown that although seed set increases with the number of pollinator visits up to a point, further visits beyond that point may decrease seed set, perhaps because of damage to the flowers (Búrquez, Sarukhán & Pedroza, 1987; Young, 1988). The probability of potentially destructive post-pollination visits might be reduced by dilution or removal of the nectar from post-pollination flowers. One way in which the reward might be removed is by reabsorption. Another way is by allowing the corolla to fall, taking with it the residual nectar.

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