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Nectary biology of *Cucurbita pepo*: ecophysiological aspects

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SUMMARY

Nectary structure, nectar secretion and composition and insect visits were studied in male and female flowers of *Cucurbita pepo* in which anthesis lasts only 6 hours. The nectaries of male and female flowers develop in the same way, with presecretory, secretory and postsecretory phases; the flowers are dimorphic with regard to the position, quantity and composition of their nectar. The nectary is formed by an epidermis with stomata and a nectariferous parenchyma with phloem vessels. The epidermis is devoid of cuticle. Starch is stored in the presecretory phase in the amyloplasts of parenchyma and epidermis; it disappears a few hours before anthesis and nectar flows through stomata. The nectar of the female flower is higher in quantity, sugars and proteins and therefore more attractive than that of the male flower. Flowers whose nectar is collected by bees fall the day after anthesis; unvisited flowers fall after 3 days. Nectar not collected by bees is reabsorbed and sugars temporarily stored inside amyloplasts.

Key-words: Cucurbita pepo, nectaries, nectar composition and secretion.

INTRODUCTION

The dispersal of moss and fern spores and most gymnosperm pollen is always passive. In angiosperms, however, nectaries producing rewards for pollinators are common (Fahn 1979). The quantity and composition of nectar vary widely from species to species (Fahn 1979; Baker & Baker 1983). There is also wide intraspecific variability due to environmental (temperature, soil moisture, humidity) (Fahn 1979; Cruden *et al.* 1983; Marden 1984; Freeman & Head 1990; Wyatt *et al.* 1992) and physiological factors (health of the plant, damage to floral parts) (Gottsberger *et al.* 1990). In monoecious zoophilous plants, nectaries may be present in the male or female flower or in both (Dafni 1984). In the former case, nectary position and nectar quantity and composition differ in flowers of the two sexes (Devlin & Stephenson 1985; Klinkhamer & De Jong 1990; Delph & Curtis Lively 1992; Wunnachit *et al.* 1992). All these differences affect pollinator behaviour.

The position of the nectaries in the flowers determines the path of the pollinator and the mode in which pollen is loaded and unloaded (Nepi & Pacini 1993). Depending on

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its composition and accessibility, nectar may be collected by insects, birds, small mammals and marsupials (Baker & Baker 1983). Some nectaries are accessible to many and others to few pollinators, such as those situated deep inside long spurs or that of *Antirrhinum*, in which the closed corolla prevents access to all but very large insects. Certain insects perforate spurs containing nectaries and steal the nectar without effecting pollination (Inouye 1983; Pacini 1992).

Nectar may be consumed directly by the animal that collects it (Lepidoptera, Diptera, birds and bats) or taken to the nest to feed larvae (social Hymenoptera) (Baker & Baker 1983). Nectar differs from other secretions as it consists mainly of substances derived from photosynthesis; this is why nectaries cost the plant a significant proportion of its products of photosynthesis (Southwick 1984).

The present study was performed in the framework of a research programme on the reproductive biology of the Cucurbitaceae. One of its main aims was to investigate the cytology, chemistry and ecology of the floral nectaries of *Cucurbita pepo*. The species in question is monoecious. Both sexes of flower have a brief anthesis, opening between 05.00 h and 06.00 h (local time) and closing around noon of the same day (Nepi & Pacini 1993). Both have nectaries but their position and accessibility are different (Nepi & Pacini 1993). Pollination is mostly performed by *Apis mellifera*; bumble bees (*Bombus* sp.) are common visitors and other insects (Diptera, Coleoptera and Lepidoptera) are occasionally observed (Philippe 1991). Nectary development was only studied in male flowers because preliminary work indicated that it is the same in both sexes. All the other observations were made on flowers of both sexes.

MATERIALS AND METHODS

Morphology, cytology and ecology of the nectaries of *Cucurbita pepo* cv. Greyzini, were studied in plants growing in the open air in the Botanical Gardens of Siena University in the summers of 1992 and 1993. The protein component of the nectar was studied in plants growing in a greenhouse at the Plant Cytology and Morphology Department of the Agricultural University of Wageningen in October and November 1992.

Light microscopy and histochemistry

Nectary specimens were obtained from male flowers in the time span beginning 5 days before anthesis and ending 2 days afterwards. At anthesis, some flowers were bagged to keep pollinators out. The specimens were fixed in 4% paraformaldehyde in phosphate buffer at pH 7·2, dehydrated in an ethanol series and embedded in LR white (London Resin Co. Ltd.). Semithin sections were stained as follows:

1. PAS for insoluble polysaccharides (O'Brien & McCully 1981);
2. Bromophenol blue for total proteins (Pearse 1968);
3. Auramine O for cuticle (Heslop-Harrison 1977);
4. Toluidine blue (O'Brien & McCully 1981) as general stain.

Hand sections of parenchyma and epidermis were tested for starch by staining with Lugol (Johansen 1940) and by observation with polarized light for starch birefringence.

The number of stomata per unit surface area of nectary was estimated by taking an impression of the surface of 10 male and 10 female nectaries with nail varnish (Hilu & Randall 1984). The varnish was allowed to dry and was removed with tweezers, placed between a microscope slide and cover slip and observed by optical microscope.

Scanning electron microscopy

Nectaries dissected immediately before and after anthesis were fixed on stubs and gold coated in an Edwards vaporizer. They were then observed with a Philips 501 scanning electron microscope at 7·2 Kv.

Nectar production

To determine how nectar secretion rate varied with time, five male and five female flowers from different plants were bagged to exclude bees. Nectar volume was measured in each flower with a micropipette at intervals of an hour from 05.00 h until the end of anthesis. The same measurements were repeated on fresh sets of flowers on three consecutive days.

Nectar composition

The sugar concentration of the nectar was measured with a portable refractometer and it was expressed as sucrose equivalents (g of sucrose per 100 g of solution). The percentage of sugars, measured in 20 flowers of both sexes, was determined 3, 6, 27 and 51 h after anthesis. Nectar sampled 3, 6 and 27 h after anthesis was used to determine protein concentration and pattern. Nectar sampled at the beginning of anthesis was placed in an open Eppendorf tube inside the flower to exclude the contact with the nectary.

The protein concentration determination was performed by spectrophotometry after treatment with the Micro BCA Protein Assay kit (Pierce). To concentrate the protein component, the same nectar samples were centrifuged in a cold room in a Millipore ultra-free-MC, 10 000 NMwL filter that only allowed the passage of molecules with a molecular weight less than 10 000 D. They then underwent isoelectric focusing (IEF) and two-dimensional electrophoresis on polyacrylamide gel (native-Page) in Phast System equipment, using PhastGel IEF 3-9 and PhastGel Gradient 8-25, respectively. The gels were stained with silver nitrate, dried and photographed.

Nectar reabsorption

In order to determine whether nectar is reabsorbed, five flowers were bagged to exclude bees the day before anthesis. At 11.00 h on the day of anthesis, the nectar was removed with a micropipette and replaced with three aqueous sucrose solutions at different concentrations (30%, 40% and 50%), coloured with the vital stain neutral red (0·05%) (O'Brien & McCully 1981). The quantity of artificial nectar was the same as the average amount taken from the flowers (Table 1). Three days after anthesis, we checked to see whether the artificial nectar had been absorbed.

Bee activity

Bee visits were observed directly and by videocamera. The mean visit duration was calculated from video images. The number of visits per flower was calculated by observing bees collecting nectar from 20 male and 10 female flowers on a sunny day (26 June 1992). The bees came from hives about 300 m from the plants.

Table 1. Anatomical features of the nectary of *Cucurbita pepo*, and chemical properties of the nectar. Mean ± SE is shown

	Male flower	Female flower
Nectary surface area (mm^2) (mean ± SE)	97 ± 28 $n=10$	169 ± 37 $n=10$
Stomata number (mm^{-2}) (mean ± SE)	93·9 ± 13·2 $n=10$	152·4 ± 14·5 $n=10$
Nectar volume (µl) (mean ± SE)	93 ± 26 $n=5$	118 ± 22 $n=5$
Sugar content (% by weight) (09.00 h) (mean ± SE)	36·3 ± 6·2 $n=20$	45·6 ± 4·7 $n=20$
Protein content (µg ml^{-1}) (09.00 h) (mean ± SE)	6·3 ± 0·8 $n=20$	5·4 ± 0·5 $n=20$

RESULTS

Flower and nectary morphology

Both male and female flowers have a pentameric perianth with radial symmetry. The female flower has an inferior ovary and three partially fused style columns, each of which supports a bipartite stigma lobe. The nectary is in the form of a circular channel surrounding the base of the triple column (Fig. 1). It is open above and easily accessible to pollinators. The male flower has three fused filaments and five anthers which are united and bent to form an anther-bearing column. The nectary is in a cavity inside the base of the filaments and is accessible through three nectary pores (Fig. 1).

Anthesis of both flowers lasts about 6 h; that of the female flower starts about half an hour before that of the male. Once the flowers have closed, they do not open again (Nepi & Pacini 1993). Male flowers that have been visited by bees drop 2 days later, whereas male and female flowers that have not been visited, that is, those the nectar of which has not been collected, drop after 3 days.

Structure and histochemistry

The male and female nectaries are structurally, cytologically and histochemically similar; they differ proportionally in surface area and stomata per unit surface area (Table 1). Nevertheless, we only studied male nectaries. The nectary surface has stomata for nectar secretion; they are open from the early stages of development (Figs 2a,b). Nectar flows from the stomata at anthesis (Fig. 2f). The number of stomata per mm^2 differs in the two sexes, with a higher number in the mature nectary of the female flower (Table 1). The stomata are always open. The external walls of the epidermal cells are thicker than the internal walls. From the early stages, no trace of cuticle could be detected with Auramine O. The nectar-producing parenchyma, consisting of large cells with small intercellular spaces, is situated under the epidermis (Fig. 2c). Xylem vessels end at the base of the nectar producing tissue and phloem vessels divide repeatedly near the stomata.

From 4 days before anthesis, the cells of the nectar-producing parenchyma were seen to contain starch grains (Fig. 2c) which stain black with Lugol and showed a double refraction with polarized light. From 2 days before anthesis, parenchyma and epidermal cells contain starch grains (Fig. 2d). Two hours before anthesis, the starch began to

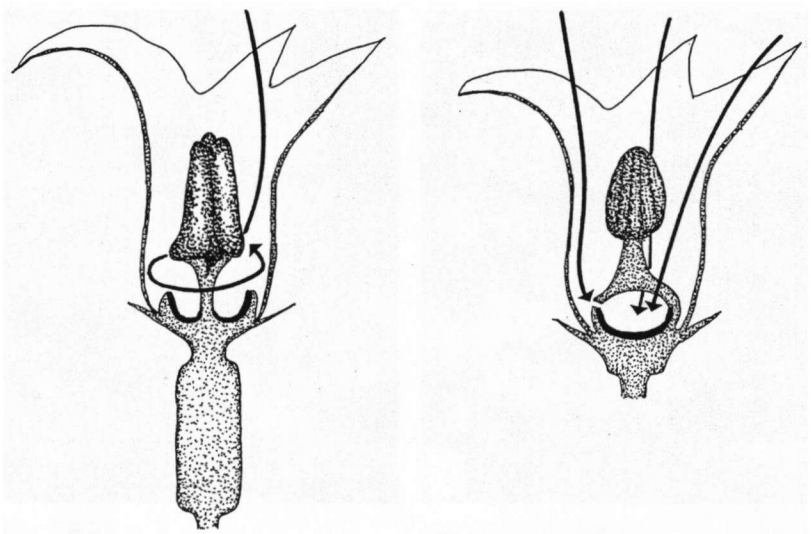
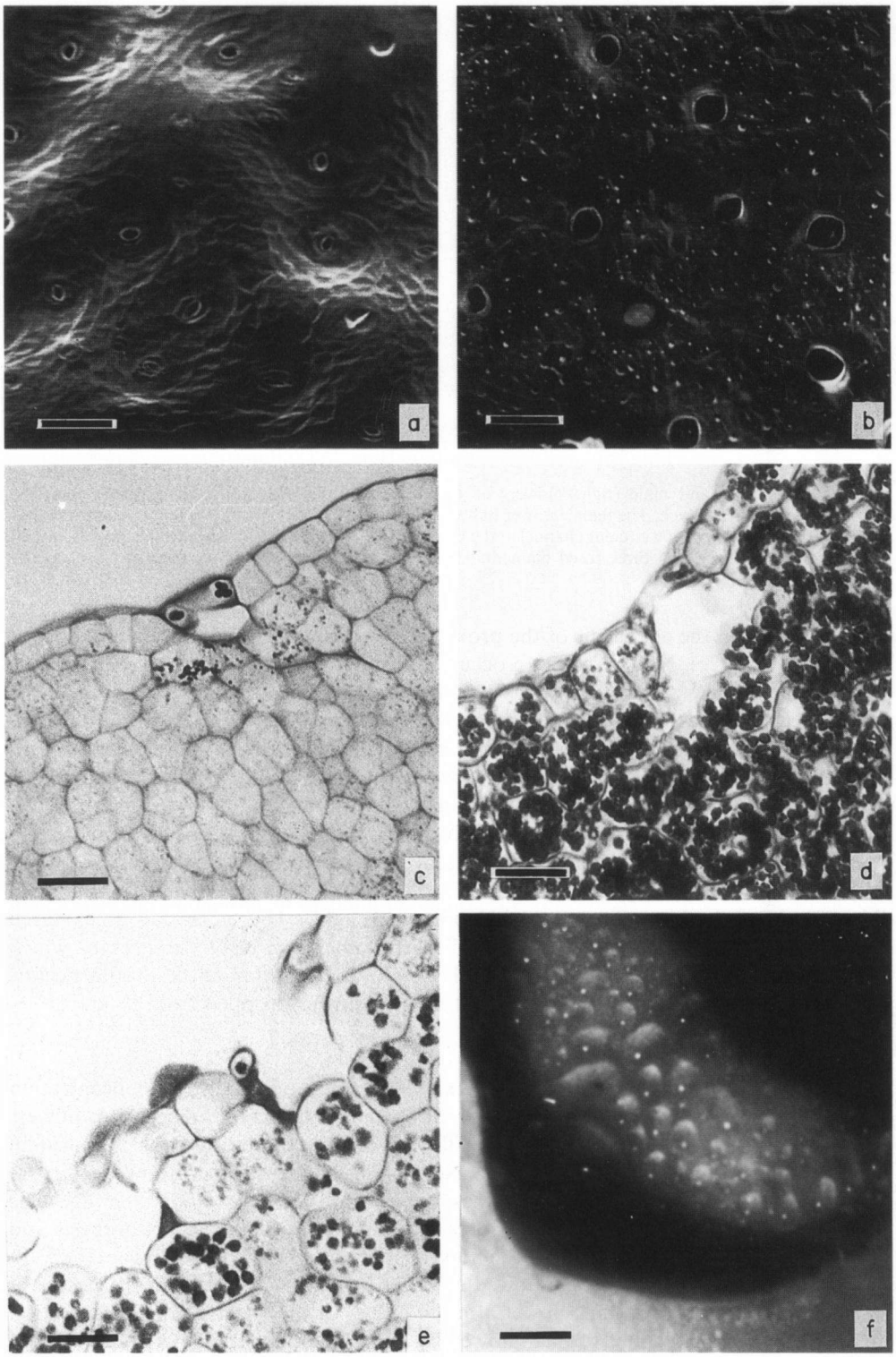


Fig. 1. Female (left) and male (right) flowers of *Cucurbita pepo* showing pollinator pathway (arrows). Nectaries are shown in black. The female flower has an inferior ovary and a stigma with three bipartite lobes. The nectary is in the form of a circular channel at the base of the style column. The male flower has five anthers bent to form a column, and three fused filaments. The nectary is in a cavity at the base of the filaments, accessible through three pores.

disappear, first in the epidermis of the proximal and then spreading to the distal part of the nectary (Fig. 2e). Nectar secretion occurred through the stomata which were greatly dilated (Fig. 2b). A drop of nectar exuded from each stomata and was visible on the surface (Fig. 2f); the drops joined to form a layer of nectar. At the end of anthesis, when the flowers of both sexes had closed, the starch of the parenchyma and epidermal cells was depleted (Fig. 3a). In non-bagged flowers deprived of their nectar by bees, the parenchyma cells developed vacuoles and shrivelled, and the flower dropped the day after anthesis. In bagged flowers, that obviously retained their nectar, amyloplasts containing small starch grains were present around the vascular bundles in the afternoon after closure of the flower (Fig. 3b). This starch stained brown with Lugol and did not show double refraction with polarized light. The next day this starch disappeared, but more starch was formed in the outer region of the nectary which disappeared in the afternoon (Fig. 3c). The second day after anthesis, the nectar-producing tissue degenerated, and the next day the flower dropped from its stalk.

Nectar composition

Nectar produced by male and female flowers differed in protein and sugar concentration content. Electrophoresis gels showed different protein patterns in the nectar of flowers of the two sexes (Fig. 3d–f). Nectar of male flowers had more or less comparable protein patterns during the different intervals. Nectar of female flowers showed a more incomplete pattern at the onset of anthesis compared with the other intervals. The number of bands detected on electrophoresis gels increased at the end of anthesis and increased again 24 h after closure of the flower especially in the female flower (Fig. 3d). Two-dimensional electrophoresis showed a higher number of proteins in the nectar of the female flower than the male flower after 24 h (Fig. 3e,f). The protein concentration curves were similar but that of male flowers at the start of anthesis was higher (Fig. 4



and Table 1). By 09.00 h the next day, protein concentration was drastically reduced (Fig. 4).

The sugar concentration as sucrose equivalents (g of sucrose per 100 g of solution) at the beginning of anthesis was higher in nectar of female flowers (45·6 ± 4·7% vs. 36·3 ± 6·2% of male flowers) (Fig. 5 and Table 1). This concentration did not vary substantially in the course of anthesis. By 09.00 h the next day, the sugar concentration of both nectars was much less and it continued to decrease during the following 24 h. By 09.00 h of the third day, the sugar concentration was the same in both nectars and had dropped to less than 10% of its original value (Fig. 3e,f).

Cucurbita pepo nectar is quite viscous so that a few drops remained on the nectary surface even in samples fixed for microscopic observations, and were visible in PAS-stained sections (Fig. 2e).

Nectar secretion as a function of time

Nectar secretion rate was different in flowers of the two sexes (Fig. 6). In the male flower secretion began at anthesis and reached a maximum about 2 h later; it subsequently decreased and was less than 8 $\mu l\ h^{-1}$ when the flower closed. In the female flower nectar secretion began after the start of anthesis, reaching a maximum between 07.30 and 08.30 h, about 1 h later than in the male flower (Fig. 6). The female flower secreted a higher total quantity of nectar (Table 1).

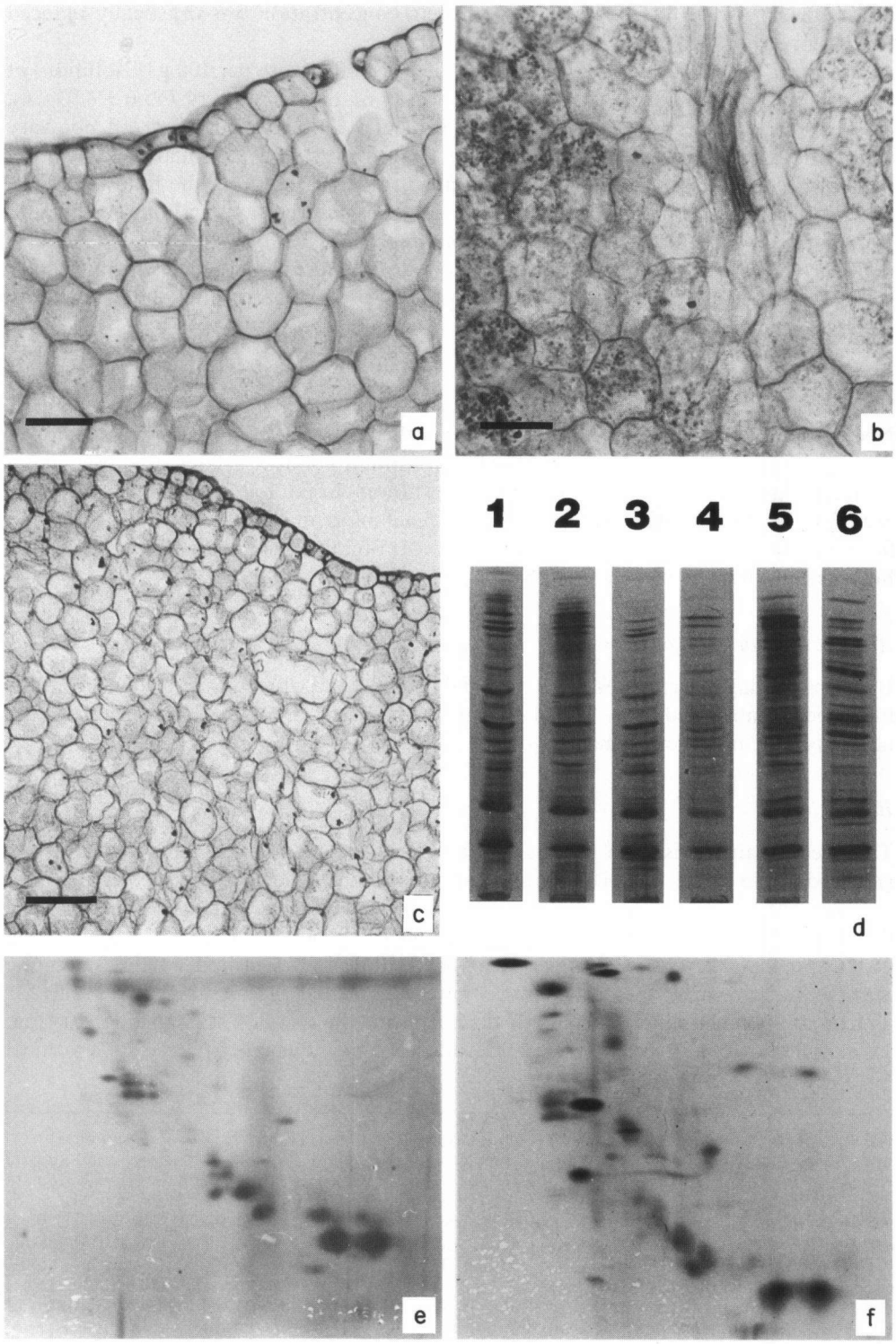
Artificial nectar reabsorption

By the third day after anthesis, the artificial nectars at all three sucrose concentrations had been reabsorbed and the dye was translocated into the cytoplasm of the nectar-producing parenchyma.

Bee activity

The bees began to visit the flowers of *Cucurbita pepo* as soon as they opened. They gathered nectar only; the pollen that sticks to their bodies seems to annoy them because they remove it with the first and second pair of legs (Nepi & Pacini 1993). The male flowers are visited first (Fig. 7). The maximum frequency of visits occurred between 07.00 and 09.00 h. During anthesis each male flower was visited 60 times, on the average, for a mean of 41 s. Each female flower was visited 78 times, on the average, for a mean of 90 s each time. The path of the bee inside the two flowers was different (Fig. 1): in male flowers the bee inserted the proboscis into the nectary pore from a vertical

Fig. 2. Nectary of male flower of *Cucurbita pepo* 2 days before anthesis (a) and at the end of anthesis (b): (a) open stomata are visible; (b) the stomata are completely dilated and are further apart as a result of growth. Scale bar=60 μm. (c) Nectary 4 days before anthesis. The nectary consists of epidermal cells with stomata overlying the largest parenchyma cells, in which starch storage is beginning (PAS). Scale bar=30 μm. (d) Nectary in the afternoon of the day before anthesis. Amyloplasts almost totally fill the space between cell walls and nucleus of nectar-producing parenchyma cells; some are also visible in epidermal cells (PAS). Scale bar=25 μm. (e) Nectary at 07.00 h of day of anthesis. The starch disappears first from the epidermis and the cells near the epidermis. Drops of nectar are visible on the surface of the nectary and in the chamber underlying the stomata (PAS). Scale bar=25 μm. (f) Nectary at 07.00 h on the day of anthesis. Droplets of nectar are visible on the surface. As secretion proceeds, the droplets join up and form a continuous layer of nectar. Scale bar=0·5 mm.


a
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position; in female flowers it circled the nectar vessel with its body more or less horizontal. Bee activity stopped at about 11.00 h (Fig. 7).

DISCUSSION

Nectary structure

The nectar-producing tissue of *Cucurbita pepo* has a general structure comparable with that of many other species of angiosperms. An epidermis with stomata is also observed on the nectary surface of species of Fabaceae (Davis & Gunning 1992), Labiatae (Zer & Fahn 1992), in *Vinca rosea*, *V. major* and *Citrus sinensis* (Rachmilevitz & Fahn 1973), *Passiflora* (Durkee *et al.* 1981), *Colchicum*, and *Tropaeolum* (Fahn 1979). The nectary stomata are modified having lost the capacity to close completely (Davis & Gunning 1992). When nectaries have stomata, the nectar exudes through them. In species without modified stomata, nectar flows from the cuticle which may be permeable, provided with pores, or may rupture (Fahn 1979). In *Cucurbita pepo*, there is no trace of cuticle and secretion only seemed to occur through the stomata; however, the possibility that nectar permeates the epidermis without a cuticle cannot be excluded. In Cucurbitaceae such as *Luffa aegyptiaca* and *Sechium edule*, we observed a cuticle which ruptures to release the nectar (unpublished data). Moreover, in the same family there are other types of nectary organization, for example *Sechium edule* and *Cyclanthera pedata* with multicellular glandular hairs and a cuticle.

Nectar sugar precursors

Sugars for nectar production may be derived from substances previously stored or from substances newly photosynthesized by floral or other parts of the plant (Fahn 1979). In *Cucurbita pepo*, the plastids of the nectar-producing parenchyma store a large quantity of starch before secretion starts. Unlike the situation in most other plants, a few amyloplasts also differentiate in the epidermis. A similar situation is found in the floral nectaries of *Passiflora biflora* (Durkee *et al.* 1981). In this species too, anthesis lasts only a few hours. In the floral nectaries of other species, starch accumulation is extremely modest (Rachmilevitz & Fahn 1973; Fahn & Benouaiche 1979; Davis *et al.* 1986; Figueiredo & Pais 1992) and no storage occurs in many extrafloral nectaries (Baker *et al.* 1978; Durkee 1982; Eleftheriou & Hall 1983; Fahn 1987; Grout & Williams 1980; Galetto & Bernardello 1992; Vinoth & Yash 1992). The quantity of starch stored is probably related to the quantity of nectar secreted and the duration of secretion. If much nectar is produced in a short time, starch must be stored in advance. This is true of *Cucurbita pepo* and *Passiflora*, in which much nectar is produced for a limited period, presumably about equal to the period of anthesis. When nectar production is prolonged, the substances necessary for the sugar component are formed by photosynthesis just before secretion.

Fig. 3. (a) Nectary at noon of the day of anthesis. The starch has all disappeared (PAS). Scale bar=30 μm. (b) Nectary of a bagged flower at 06.00 h on the day of anthesis. Starch grains appear in parenchyma cells near phloem vessels (PAS). Scale bar=25 μm. (c) Nectary of bagged flower at 06.00 h of the day after anthesis. All starch has disappeared. The parenchyma cells begin to shrink (PAS). Scale bar=100 μm. (d) Isoelectric focusing gel stained with silver nitrate. Protein bands of nectar from male (1–3) and female (4–6) flowers at the start of anthesis (09.00 h, 1 and 4), at the end (12.00 h, 2 and 5) and at 09.00 h the next day (3 and 6). (e)–(f) Two-dimensional electrophoresis on polyacrylamide gel of the protein component of nectar of the male (e) and female (f) flower 1 day after anthesis (09.00 h), see Fig. 5 (3 and 6). Silver nitrate staining.

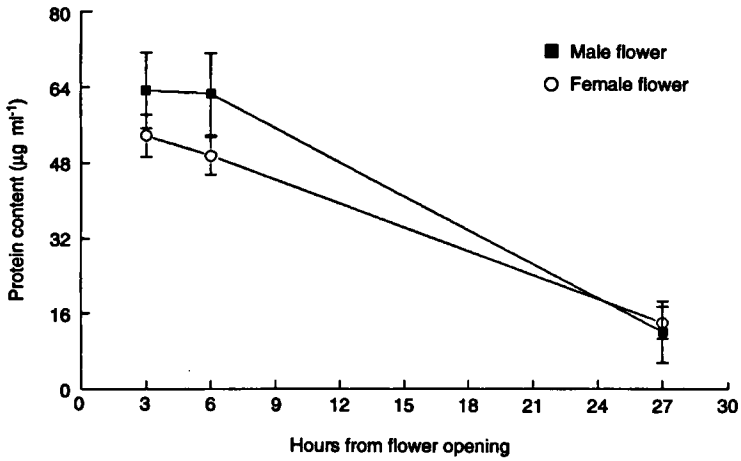

Fig. 4. Protein concentration of nectar of male (■) and female (○) flowers of *Cucurbita pepo* 3, 6 and 27 h after anthesis (mean ± SE). At the beginning of anthesis the nectar of the male flower has a slightly higher protein concentration. In both sexes protein content decreased the day after anthesis.

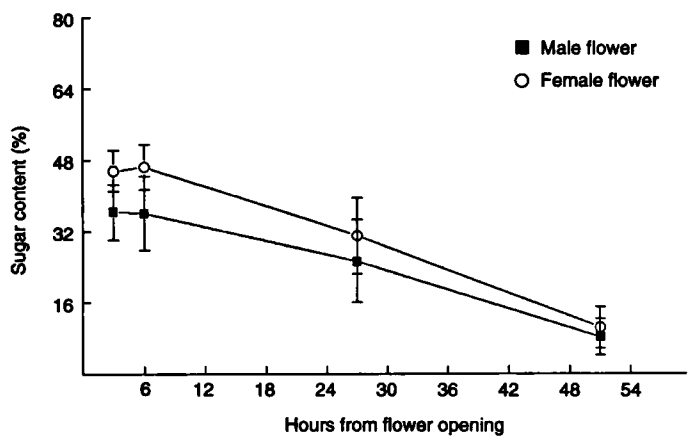

Fig. 5. Sugar concentration of nectar of male (■) and female (○) flowers of *Cucurbita pepo* 3, 6, 27 and 51 h after anthesis (mean ± SE). The nectar of the female flower had a higher sugar concentration. In both flowers, sugar concentration decreased drastically after anthesis.

Nectar composition and production in male and female flowers

Monoecious species pollinated by animals have morphologically similar flowers. Both sexes of flowers or only one may have nectaries. In the latter case, the pollinators are attracted to the nectarless flower by deception (Aronne *et al.* 1993). If flowers of both sexes have nectaries, the composition and quantity of nectar is generally different (Devlin & Stephenson 1985; Klinkhamer & De Jong 1990; Delph & Curtis Lively 1992; Wunnachit *et al.* 1992). In *Cucurbita pepo*, the female flower produces more and sweeter nectar with a lower protein content than the male flower (Table 1). Two-dimensional electrophoresis showed different protein patterns that varied with time. This means that the protein synthesis occurs and new proteins are added or proteins undergo structural changes by enzymatic breakdown during anthesis. The nature of nectar proteins is not

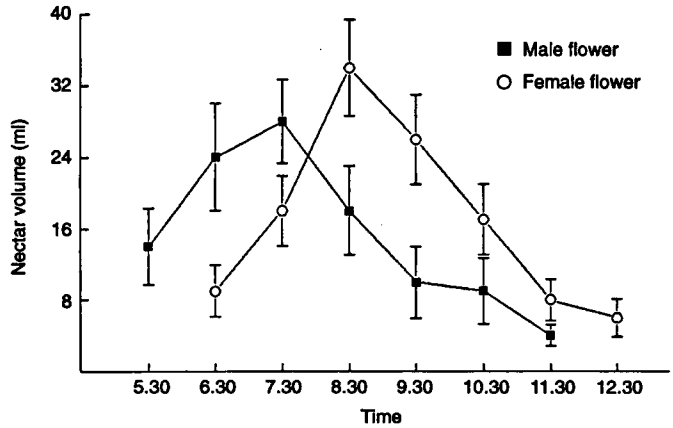

Fig. 6. Nectar secretion rate of male (■) and female (○) flowers of *Cucurbita pepo* during anthesis (mean ± SE). The nectaries of the two flowers are out of phase by about an hour. The female flower produces a greater quantity of nectar than the male flower.

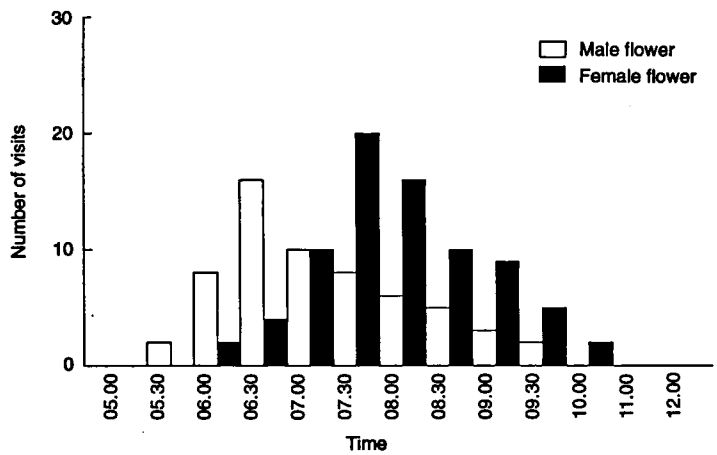

Fig. 7. Histogram of the mean number of bee visits to male (■) and female (□) flowers of *Cucurbita pepo*. Male flowers are visited first but female flowers receive a larger total number of visits. Bee activity was a maximum between 07.00 h and 09.00 h and ceased by about 11.00 h.

known, but according to Baker & Baker (1983) they are generally enzyme-related. The activity of nectaries of the two sexes was found to be out of phase and the secretion rates of the two differed during the hours of anthesis. Maximum nectar production was between 07.30 and 08.30 h for female and 06.30 and 07.30 h for male flowers. Male flowers were visited first because they contain nectar with a complete protein set as soon as they open, unlike female flowers. The nectar production curves correlate well with the frequency of pollinator visits. Until 07.30 h, the male flowers produced more nectar and received more visits; after 07.30 h it was the turn of the female flowers to produce a complete nectar and be visited. By the end of anthesis, although female flowers were fewer in number than male, they had received more bee visits. The fact that bees preferred female flowers is explained by the sweeter nectar, easier access and no pollen to annoy them (Nepi & Pacini 1993). This preference is important because it guarantees

that sufficient pollen reaches the stigma to fertilize the many ovules in the ovary of this species (Nepi & Pacini 1993).

Nectar reabsorption

The present observations provide fairly clear evidence that in *Cucurbita pepo*, the nectar not gathered by insects is reabsorbed by the nectary. The sugars are stored as starch in the parenchyma the day after anthesis. The amount of starch is decreased the following day and the sugars transferred presumably to the vegetative part of the plant. The starch stored in the nectar-producing parenchyma stains black with Lugol reagent and shows double refraction with polarized light, whereas that formed during reabsorption is brown and does not show double refraction. This signifies that the former contains a larger proportion of amylose, which has a linear molecule bent in a spiral, whereas the latter contains a larger proportion of amylopectin which has a branched molecule (Morrison 1992). The fact that amylopectin is branched accelerates hydrolysis. The fate of the nectar proteins is unknown although in the nectar the rate of breakdown of proteins must be low because of the persisting pattern during 24 h. Apart from the observation of increasing parenchymal starch reserves in the postsecretory stage, there is also the following evidence in favour of nectar resorption in this species.

1. The flower closes at the end of the secretory period, creating a high relative humidity microenvironment inside the corolla. This might facilitate reabsorption by preventing the increase in concentration of the nectar by evaporation.

2. The nectary epidermis has no cuticle.

3. Nectar kept in the vial inside the flower did not vary in protein content.

4. Three days after anthesis, no trace of solution remained in flowers in which the nectar had been replaced with sucrose solution.

A possible objection to the hypothesis of active reabsorption is that the protein and sugar contents may be modified by micro-organisms in the nectar. In extrafloral nectaries of *Ailanthus altissima*, a mould that destroys these components has been described (Clair-Maczulajtys & Bory 1982). In floral nectaries of *Asclepias syriaca*, a yeast that inhibits pollen germination is common (Eisikowitch *et al.* 1990). These micro-organisms may be carried from flower to flower by insects. In our study protein and sugar declined even in flowers that were bagged to prevent access by pollinators. Moreover, measurement of the protein concentration of control nectar showed that it did not decrease if the nectar was kept in a vial outside the nectary. It should also be considered that antibiotic substances have been found in certain nectaries (Baker & Baker 1983).

Other examples exist of reabsorption of substances produced for reproductive purposes: although its function is different, the micropylar drop of certain gymnosperms is periodically emitted and reabsorbed (Moussel 1980; Owens *et al.* 1981). Pollen grains are transferred into the micropylar chamber together with the droplet.

The reabsorption of nectar does not seem to be a common phenomenon, to judge from the small number of cases in which it has been documented. Bonnier (1878) was the first to demonstrate that nectar not collected from flowers of *Platanthera* was reabsorbed. Pedersen *et al.* (1958) showed nectar reabsorption in alfalfa by autoradiography of sucrose marked with C^{14}. Cruden *et al.* (1983) reported a decrease in sugar concentration of *Penstemon gentianoides* nectar. Burquez & Corbet (1991) revealed reabsorption in *Brassica napus* by net solute loss from flowers protected from insect

visits. Our observations suggest that in *Cucurbita pepo*, nectar is not merely a secretion provided for pollinators but a material that is secreted, but may subsequently be actively transformed, reabsorbed and metabolized by the plant. The fate of the substances reabsorbed is different in male and female flowers: in the former they are probably recycled to the vegetative part of the plant; in the latter any substances that are not gathered by insects may be used by the developing ovary.

Since up to 37% of the photosynthetic energy of a plant may be invested in nectar production (Southwick 1984), reabsorption represents an important energy saving. A similar saving occurs in plants that are about to lose their leaves (Fischer & Feller 1994).

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