



## Flowers, Nectar and Insect Visits: Evaluating British Plant Species for Pollinator-friendly Gardens

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Twenty-four plant species native or naturalized in Britain were grown in the Cambridge University Botanic Garden, UK and evaluated as potential resources for nectar-foraging bees, butterflies and hoverflies. In ten plant species a series of measurements were made, at regular intervals from dawn to dusk, of nectar secretion rate and standing crop, and in all species insect visits were monitored throughout daylight hours. The study revealed differences between plant species in the composition of the assemblage of insect visitors, and in the magnitude and temporal distribution of the nectar reward. In some cases we found interesting correlations between temperature and secretion rates or patterns of insect visits. Species that received numerous insect visits in our study are potentially valuable forage plants that might be planted by gardeners to support local pollinator populations. Deep flowers whose nectar is accessible to long-tongued bumblebees (*Bombus hortorum*, *B. pascuorum*) but not to honeybees may provide long-tongued pollinators with a resource refuge relatively free from honeybee competition. Features that make some of those plant species particularly interesting to observe in the garden include robbing by short-tongued bumblebees in *Saponaria*, baseworking by honeybees on closed flowers in *Malva sylvestris*, and apparent displacement of bumblebees by territorial behaviour of the solitary bee *Anthidium manicatum* on species of *Stachys*.

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**Key words:** Wild flowers, gardens, nectar, *Silene*, *Lychnis*, *Saponaria*, *Stachys*, *Malva*, *Dipsacus fullonum*, *Lythrum salicaria*, pollinators, bumblebees, *Bombus*, honeybees, *Apis*, butterflies, Lepidoptera, hoverflies, Syrphidae, *Anthidium manicatum*, weeds.

### INTRODUCTION

The decline of bees and other flower-visiting insects in some areas of Britain and elsewhere (Peters, 1972; Williams, 1982, 1986; Rasmont, 1988; Thomas and Lewington, 1991; Berezin, 1995; Westrich, 1996) has been attributed, in part, to changes in land use resulting in losses of nectar-rich perennial herbaceous vegetation (Williams, 1982; Osborne, Williams and Corbet, 1991). By growing plants that attract and reward flower-visiting insects, gardeners can help to sustain local pollinator populations and enhance the natural history interest of the garden (Owen, 1991).

Under the auspices of Flora For Fauna, an organization established to encourage gardeners to grow plants valuable to wildlife, we have investigated the value of a number of plant species as nectar sources for bees and other flower-visiting insects. In an earlier paper (Comba *et al.*, 1999) we compared cultivated flowers with horticulturally-modified variants of the same species, and showed that less modified flowers were generally of greater value to foraging insects. Native plant species are expected to be attractive to local flower-visiting insects in the presence of which they have evolved. The reward offered by exotic or highly modified garden flowers that have coevolved with a different pollinator assemblage may be greater or less but is likely to be less accessible to native insect species. Native plant

species grown in gardens may help to support threatened local pollinator assemblages if they offer a rich reward to flower-visiting insects known to be declining. These include butterflies (Thomas and Lewington, 1991) and bumblebees, especially the long-tongued species (Rasmont, 1988), for which deep flowers with nectar inaccessible to the shorter-tongued bees are expected to provide a refuge free from competition by honeybees (Corbet *et al.*, 1995; Sugden, Thorp and Buchmann, 1995). We have focused on nectar, rather than pollen, because nectar is more easily quantified. This paper describes nectar production, insect visits and other relevant features of some native British species selected for their potential as pollinator-friendly wild flower species to be grown in gardens. Additional interest attaches to the pollinator relationships of some of these plant species which are crops (e.g. clovers, *Lotus*) or introduced weeds in North America (e.g. *Lythrum salicaria*, *Linaria vulgaris*) or Australia (e.g. *Dipsacus fullonum*; Parsons and Cuthbertson, 1992).

### MATERIALS AND METHODS

Twenty-four species that are native or well naturalized in Britain were grown (mostly in 5 × 1 m plots) in the research area of the Cambridge University Botanic Garden, UK and studied in July and August 1996 and 1997. Dawn-to-dusk studies of nectar and insect visits were conducted on species that were flowering well during the study period: white

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campion (*Silene latifolia* Poir.) red campion (*S. dioica* (L.) Clairv.), ragged robin (*Lychnis flos-cuculi* L.) and soapwort (*Saponaria officinalis* L.) (Caryophyllaceae, Caryophyllaceae); marsh woundwort (*S. palustris* L.) and hedge woundwort (*Stachys sylvatica* L.) (Lamiaceae); common mallow (*Malva sylvestris* L.) and musk mallow (*M. moschata* L.) (Malvaceae); and wild teasel (*Dipsacus fullonum* L.) (Dipsacaceae) and purple loosestrife (*Lythrum salicaria* L.) (Lythraceae). Observations on insect visitors were made on cornflower (*Centaurea cyanus* L.), greater knapweed (*C. scabiosa* L.), hemp agrimony (*Eupatorium cannabinum* L.), common toadflax (*Linaria vulgaris* Mill.), marjoram (*Origanum vulgare* L.), common vetch (*Vicia sativa* L.), common bird's foot trefoil (*Lotus corniculatus* L.), field scabious (*Knautia arvensis* (L.) Coult.), small scabious (*Scabiosa columbaria* L.), meadow clary (*Salvia pratensis* L.), wild clary (*S. verbenaca* L.), foxglove (*Digitalis purpurea* L.), white deadnettle (*Lamium album* L.), red clover (*Trifolium pratense* L.) and white clover (*T. repens* L.). Plant species names follow Stace (1997). Digital calipers (Mitutoyo (UK) Ltd, Andover, UK) were used for measuring floral parts.

Rates of nectar secretion and removal by insects vary with weather and time of day. Therefore, where possible we monitored nectar secretion rate, nectar standing crop and insect visit frequency, in conjunction with microclimate, at regular intervals throughout a day from dawn until dusk. Nectar was withdrawn from flowers into glass microcapillaries (Microcaps; Drummond Scientific Co., Broomall, Pa, USA) of standard volume (0.5 to 5  $\mu$ l), and nectar volume was calculated from the length of the fluid column in the Microcap. Solute concentration (as g sucrose per 100 g solution) was measured at once with a pocket refractometer modified for small volumes (down to about 0.1  $\mu$ l) by the makers (Bellingham & Stanley Ltd, Tunbridge Wells, UK). Nectar sugar content per flower (*s*, mg) was calculated from the equation

$$s = dvC/100$$

where *v* is the volume calculated as above ( $\mu$ l), and *d* is the density of a sucrose solution at a concentration *C*% (g sucrose per 100 g solution) as read on the refractometer (Bolten *et al.*, 1979; Prys-Jones and Corbet, 1991). The density was obtained as

$$d = 0.0037921C + 0.0000178C^2 + 0.9988603$$

(Prys-Jones and Corbet, 1991). When there was too little nectar for refractometer readings, nectar volumes were recorded as zero if the extracted volume was less than 0.1  $\mu$ l, or a missing value if it was more than 0.1  $\mu$ l. Samples contaminated by dew (giving concentration readings below 5%) were treated as missing values and were not included in the calculation of means.

The nectar content of unprotected flowers at a given time (standing crop) is expressed in terms of sugar content (mg sugar per flower). Nectar standing crop was monitored through the day by sampling nectar from about ten previously undisturbed flowers at intervals of approx. 120 min, except where reported otherwise. To estimate nectar secretion rate (mg nectar sugar per flower h<sup>-1</sup>) at each

sampling time, the ten flowers that had been drained for standing crop measurement were bagged in bridal veiling (1 mm mesh, secured with a numbered tag) to prevent nectar removal by insects, and resampled after a known interval of about 120 min. The flowers were marked so that they would not be sampled again. Teasel flowers were difficult to drain without causing damage that might affect secretion rate. Preliminary studies showed that the standing crop of nectar was almost zero, presumably because of removal by insects. After sampling for standing crop, we bagged the inflorescence and later sampled previously unsampled flowers on the same inflorescence to estimate secretion rate, assuming that the flowers had been empty when bagged. In a dawn-to-dusk study on white campion, red campion and ragged robin on 10 Jul. 1997, secretion rate was measured in a different way. Tagged flowers were emptied in the morning, bagged as described above, and sampled repeatedly through the day. If a flower fell off or suffered obvious damage from repeated probing, another flower on the same plant was substituted for it.

Flower-visiting insects could usually be identified without capture. Bumblebees were named to the following colour groups, each now represented by only one or a few species in the impoverished Cambridge area (Williams, 1982): browns (represented in the Cambridge area only by *Bombus pascuorum* Scopoli); black-bodied red tails [represented by the common *B. lapidarius* (L.) and possibly occasional specimens of the much rarer *B. ruderarius* (Müller)]; and banded white-tails [including two-banded white tails, *Bombus terrestris* (L.) and/or *B. lucorum* (L.), and three-banded white tails, *B. hortorum* (L.) with possibly occasional specimens of the rare *B. ruderatus* (Fabr.)] (Prys-Jones and Corbet, 1991). Bumble bee names follow Prys-Jones and Corbet (1991), hoverfly names follow Stubbs and Falk (1993) and butterflies follow Thomas (1986). When possible, we recorded species, sex and caste and foraging behaviour (whether collecting nectar, pollen or both) for each visitor. Voucher specimens were taken for identification where necessary.

Visitor counts were made at regular intervals of about 120 min except where reported otherwise, just before each nectar-sampling session. Insects seen visiting the flowers were counted during a standard slow walk along the relevant plot, usually repeated three times in quick succession to give a mean insect count in each plot at each sampling time.

Microclimate measurements were made 100 cm above the ground throughout the day, usually at hourly intervals. Ambient temperature (*T<sub>a</sub>*) was measured in the shade using a fine K-type thermocouple. Black globe temperatures, *T<sub>g</sub>*, were measured in full sunlight as the temperature of a K-type thermocouple inserted in the centre of a 8-mm-diameter sphere of Blu-tack (Bostik Ltd, Leicester, UK) (a sticky, elastic deformable dough-like material) painted matt black (Joy Blackboard Black, Matt Finish, Turnbridges Ltd, London SW17) (Corbet *et al.*, 1993). Temperatures are expressed as the mean of five readings taken in quick succession. Relative humidity (RH) was measured with a miniature wet-and-dry thermocouple psychrometer (Unwin, 1980; Unwin and Corbet, 1991). Cloud cover was estimated

TABLE 1. Whole-plot counts of flowers or flower heads, corolla depths (mean  $\pm$  s.e.m.) and numbers of visits made by the four most numerous species of bee on 29 Jul. 1997 (see text)

| Common name                        | Scientific name              | Annual/biennial/<br>perennial | Flowers<br>(or heads*) | Corolla depth<br>(mm)                                | Massed? | No. visits from      |             |                     |                  |
|------------------------------------|------------------------------|-------------------------------|------------------------|--|---------|----------------------|-------------|---------------------|------------------|
|                                    |                              |                               |                        |  |         | <i>B. lapidarius</i> | <i>Apis</i> | <i>B. pascuorum</i> | <i>Anthidium</i> |
| White clover                       | <i>Trifolium repens</i>      | p                             | 40*                    | 2.65 $\pm$ 0.01 (a)                                  | yes     | 0                    | 1           | 1                   | 0                |
| Hemp agrimony                      | <i>Eupatorium cannabinum</i> | p                             | 10192*                 | 2.71 $\pm$ 0.08 (b)                                  | yes     | 1                    | 15          | 0                   | 0                |
| Small scabious                     | <i>Scabiosa columbaria</i>   | p                             | 222*                   |  | yes     | 13                   | 15          | 2                   | 0                |
| Marjoram                           | <i>Origanum vulgare</i>      | p                             | 8440                   | 4.25 $\pm$ 0.17 (b)                                  | yes     | 11                   | 49          | 0                   | 0                |
| Field scabious                     | <i>Knautia arvensis</i>      | p                             | 35*                    | 6.37 $\pm$ 0.25 (c)                                  | yes     | 8                    | 1           | 0                   | 0                |
| Red clover                         | <i>Trifolium pratense</i>    | p                             | 417*                   | 8.65 $\pm$ 0.07 (a)                                  | yes     | 0                    | 1           | 23                  | 0                |
| Cornflower                         | <i>Centaurea cyanus</i>      | a                             | 1080*                  |  | yes     | 0                    | 62          | 0                   | 0                |
| Wild teasel                        | <i>Dipsacus fullonum</i>     | b                             | 44*                    | 12.1 $\pm$ 0.14                                      | yes     | 8                    | 0           | 0                   | 0                |
| Common mallow                      | <i>Malva sylvestris</i>      | p                             | 296                    | open   |         | 18                   | 22          | 0                   | 0                |
| Musk mallow                        | <i>Malva moschata</i>        | p                             | 122                    | open   |         | 1                    | 16          | 0                   | 0                |
| Common vetch                       | <i>Vicia sativa</i>          | a                             | 7164                   | 4.8 $\pm$ 0.18 (d)                                   |         | 2                    | 10          | 63                  | 0                |
| Purple loosestrife<br>(trimorphic) | <i>Lythrum salicaria</i>     | p                             | 410                    | 5.6 $\pm$ 0.18;<br>5.9 $\pm$ 0.23;<br>6.4 $\pm$ 0.20 |         | 4                    | 6           | 0                   | 0                |
| Wild clary                         | <i>Salvia verbenaca</i>      | p                             | 652                    |  |         | 0                    | 12          | 0                   | 0                |
| Common bird's foot trefoil         | <i>Lotus corniculatus</i>    | p                             | 3324                   | 6.7 $\pm$ 0.12 (c)                                   |         | 3                    | 13          | 2                   | 0                |
| Foxglove                           | <i>Digitalis purpurea</i>    | b/p                           | 17                     | 7.6 $\pm$ 0.15 (e)                                   |         | 0                    | 0           | 0                   | 0                |
| Hedge woundwort                    | <i>Stachys sylvatica</i>     | p                             | 1050                   | 8.5 $\pm$ 0.10                                       |         | 0                    | 0           | 14                  | 4                |
| Meadow clary                       | <i>Salvia pratensis</i>      | p                             | 56                     | 8.8 $\pm$ 0.88                                       |         | 1                    | 5           | 2                   | 0                |
| Ragged robin                       | <i>Lychnis flos-cuculi</i>   | p                             | 368                    | 9.4 $\pm$ 0.37                                       |         | 6                    | 0           | 2                   | 0                |
| Marsh woundwort                    | <i>Stachys palustris</i>     | p                             | 6492                   | 9.8 $\pm$ 0.08                                       |         | 0                    | 1           | 18                  | 14               |
| White deadnettle                   | <i>Lamium album</i>          | p                             | 248                    | 11.37 $\pm$ 0.12 (g)                                 |         | 0                    | 0           | 5                   | 0                |
| Red campion<br>(dioecious)         | <i>Silene dioica</i>         | p                             | 692                    | 13.3 $\pm$ 0.42 (f);<br>15.5 $\pm$ 0.43 (m)          |         | 0                    | 0           | 0                   | 0                |
| Toadflax                           | <i>Linaria vulgaris</i>      | p                             | 744                    | 16.5 $\pm$ 0.28 (c)                                  |         | 0                    | 1           | 2                   | 0                |
| White campion<br>(dioecious)       | <i>Silene latifolia</i>      | (a)/p                         | 208                    | 20.2 $\pm$ 0.51 (m);<br>21.5 $\pm$ 0.62 (f)          |         | 0                    | 0           | 0                   | 0                |
| Soapwort                           | <i>Saponaria officinalis</i> | p                             | 6480                   | 24.8 $\pm$ 0.23                                      |         | 0                    | 87(robb)    | 0                   | 0                |
| Total visits                       |                              |                               |                        |  |         | 75                   | 214         | 133                 | 18               |

f, Female; m, male. Corolla lengths were measured in this study or taken from Williams (1997) (a), SAC's observations in Cornwall in 1998 (b), Williams (1985) (c), Barrow and Pickard (1985) (d) or Prys-Jones (1982) (e).

in tenths of the sky covered, and relative wind strength was measured with an integrating cup anemometer.

Times were reported as British Summer Time (BST). Intervals are rounded to the nearest 0.5 h to the end of the session.

## RESULTS

### Comparative survey

On 29 Jul. 1997 we made bee counts at regular intervals from 0730 to 2130 h on the 24 plant species flowering in our plots at that time. The profitability of a given flower type is expected to depend on patch size as well as on attributes of the individual flowers, and the unequal flower counts for the different species (Table 1) limit the resolution of this study; however, some overall conclusions can be drawn.

Of a total of 625 bee visits recorded, most were made by honeybees (317), *Bombus pascuorum* (134) and *B. lapidarius* (76). The other species making more than two visits were *Anthidium manicatum* (18) and species groups of banded white tail bumblebees (*B. terrestris/lucorum/hortorum*) (37) and cuckoo bumblebees (*Psithyrus* spp.) (27).

Visit counts for the four major visitors identified to species are listed in Table 1, in which plant species are arranged with those having massed inflorescences first, followed by species with individual flowers in approximate increasing order of corolla length. Ranked in terms of visits per flower (or per head, in those asterisked in Table 1), the ten plant species most used by honeybees were *Malva moschata*, *Salvia pratensis*, *Malva sylvestris*, *Scabiosa columbaria*, *Centaurea cyanus*, *Knautia arvensis*, *Trifolium repens*, *Salvia verbenaca*, *Lythrum salicaria* and *Saponaria officinalis*. Honeybees have tongues only about 6–6.5 mm long (Corbet *et al.*, 1995) and they acted as secondary robbers on the deep-flowered *Saponaria*. A comparable ranked list for

*Bombus pascuorum* is *Trifolium pratense*, *Salvia pratensis*, *Trifolium repens*, *Lamium album*, *Stachys sylvatica*, *Scabiosa columbaria*, *Vicia sativa*, *Stachys palustris* and *Linaria vulgaris*. For *B. lapidarius* the ranked list is *Knautia arvensis*, *Dipsacus fullonum*, *Malva sylvestris*, *Scabiosa columbaria*, *Salvia pratensis*, *Lychnis flos-cuculi*, *Lythrum salicaria*, *Malva moschata* and *Origanum vulgare*. *Anthidium* was recorded on *Stachys palustris* and *S. sylvatica*.

### Campions, Caryophylloideae (family Caryophyllaceae)

We made dawn-to-dusk studies on four members of the subfamily Caryophylloideae (Silenoideae) in the family Caryophyllaceae: *Silene latifolia*, *Silene dioica*, *Lychnis flos-cuculi* and *Saponaria officinalis*.

*White campion* *Silene latifolia* Poiret. White campion is native and widespread in Britain. It is native in Europe, W Asia and N Africa, and introduced in N America (Baker, 1947). The large white flowers are dioecious. They sometimes wilt on dry days, but regain turgor in the evening. Nectar of these and other *Silene* species is secreted at the base of the corolla and conducted via cryptic channels down the base of the carpophore to accumulate in the base of the calyx tube (Vogel, 1998). The corolla depth was  $20.2 \pm 0.51$  mm ( $n = 10$ ) in male flowers and  $21.5 \pm 0.62$  mm ( $n = 10$ ) in female flowers (Table 1).

On 10 Jul. 1997 we undertook a dawn-to-dusk study. There were 543 flowers in the plot (about 109 flowers  $m^{-2}$ ). The nectar secretion rate of male flowers peaked early in the morning, decreased around midday and rose again in the evening (Fig. 1). There was some indication of a similar temporal pattern in female flowers. There was no significant correlation between secretion rate and black globe temperature for flowers of either sex (females: Spearman correlation coefficient  $-0.195$ , 2-tailed  $P = 0.29$ ,  $n = 31$ ;

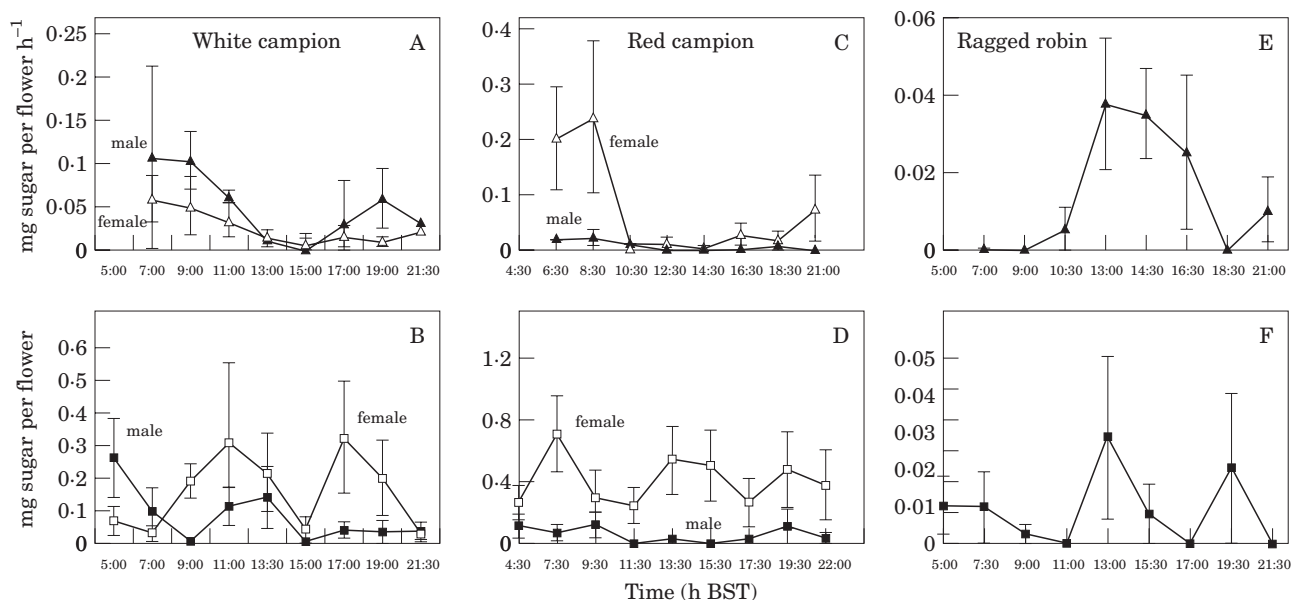


FIG. 1. Campions: nectar secretion rate (A, C, E) and standing crop (B, D, F) of white campion *Silene latifolia* (A, B), red campion *Silene dioica* (C, D) and ragged robin *Lychnis flos-cuculi* (E, F) (mean  $\pm$  s.e.m.) on 10 Jul. 1997. Note different vertical scales. Male ( $n = 5-7$ ) (solid symbols) and female ( $n = 4-6$ ) (open symbols) flowers of red and white campion are treated separately.

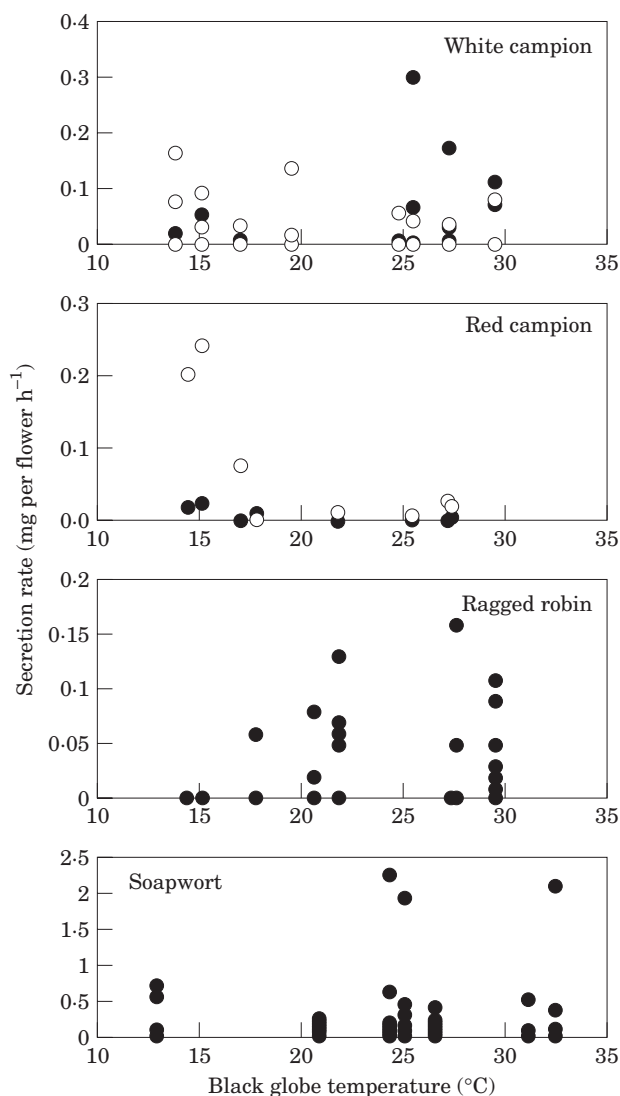


FIG. 2. Caryophyllaceae: nectar secretion rate (mean  $\pm$  s.e.m.) in relation to the most recent black globe temperature measurement before the sampling run began (about 30–60 min beforehand) for male flowers (●) and female flowers (○) of white campion (*Silene latifolia*) and red campion (*Silene dioica*) and for ragged robin (*Lychnis flos-cuculi*) all on 10 Jul. 1997, and soapwort (*Saponaria officinalis*) on 29 Jul. 1997. There was a significant correlation between globe temperature and secretion rate in female flowers of red campion (Spearman correlation negative;  $P = 0.043$ ) and in ragged robin (positive;  $P < 0.005$ ), but not in white campion or soapwort.

males: correlation coefficient  $-0.238$ ,  $P = 0.13$ ,  $n = 41$ ) (Fig. 2). The standing crop was variable, reaching about 0.3 mg per flower (Fig. 1).

During the day's observations we recorded only seven insects visiting the 543 flowers: four hoverflies, one solitary bee and two banded white-tail bumblebees (*Bombus hortorum* or *terrestris/lucorum*). We made no observations at night. Nocturnal moths have been recorded visiting the flowers by Baker (1947), Brantjes (1976), and Goulson and Jerrim (1997).

**Red campion** *Silene dioica* (L.) *Clairv.* Red campion is native and widespread in Britain, but rare around Cam-

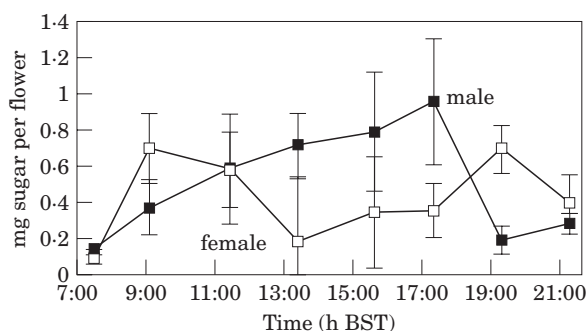


FIG. 3. Red campion *Silene dioica*: nectar standing crop (mg sugar per flower, mean  $\pm$  s.e.m.) in male (■) and female (□) flowers, West Cornwall, 27 May 1996.

bridge (Baker, 1947). It is common in much of Europe (Baker, 1947; Huxley, 1992). It is dioecious, and the mean corolla depth (from the insertion of the pedicel to the mouth of the flower) was  $15.5 \pm 0.43$  mm in male flowers and  $13.3 \pm 0.42$  mm in females ( $n = 10$  for each gender;  $t = 3.66$ ,  $P = 0.002$ , d.f. = 18) (Table 1).

In a dawn-to-dusk study on 10 Jul. 1997, the mean nectar secretion rate was higher in females than in males at seven of the eight sampling times (Sign test;  $P = 0.035$ ; Siegel and Castellan, 1988); males secreted no measurable nectar between 1230 and 1630 h (Fig. 1). The mean standing crop of nectar was higher in female flowers than in males at all of the nine sampling times (Sign test;  $P = 0.002$ ; Siegel and Castellan, 1988), varying between about 0.24 and 0.71 mg sugar per flower (Fig. 1). Secretion rate in flowers of both sexes showed a negative correlation with black globe temperature, which was significant in the case of female flowers (Spearman correlation coefficient  $-0.307$ ,  $P = 0.043$ ,  $n = 44$ ) but not males (Spearman correlation coefficient  $-0.185$ ,  $P = 0.204$ ,  $n = 49$ ) (Fig. 2). In a dawn-to-dusk study on 27 May 1996 in West Cornwall insect visits were few, and nectar removal by insects was probably negligible. This study again showed remarkably high standing crops with marked differences in temporal pattern between male and female flowers (Fig. 3). In contrast to the findings of 10 Jul. 1997 in Cambridge, the standing crop was not always higher in female flowers than in males.

Although temperatures were permissive for social bee activity all day on 10 Jul. 1997 (Corbet *et al.*, 1993; Table 2), few insect visits were recorded to the 422 open flowers in the plot (about 84 flowers m<sup>-2</sup>): four hoverflies, one honeybee (*Apis mellifera* L.), and one banded white tail bumblebee. In West Cornwall (50° N, 5.5° W), where red campion is abundant, insect visitors recorded during a survey between 27 Mar. and 28 Aug. 1996 included long-tongued bees [*Bombus hortorum*, *B. pascuorum*, *Eucera longicornis* (L.)] and lepidopterans (large white butterfly *Pieris brassicae* (L.), silver Y moth *Autographa gamma* (L.) and the hummingbird hawkmoth *Macroglossum stellatarum* L.) taking nectar legitimately via the mouth of the flower; and insects seen taking pollen on male flowers included the hoverflies *Rhingia campestris* Meigen, *Platycheirus al-bimanus* (Fabr.) and *Episyrphus balteatus* (Degeer), the beetles *Oedemera nobilis* (Scopoli) and *Haltica* sp. and

TABLE 2. Summary of microclimate measurements for days on which dawn-to-dusk studies were performed in Cambridge University Botanic Garden in 1997

| Date      | Sun (h BST)            | Rain (h BST) | Ta (°C)   | Tg (°C)   | RH (%) | Wind | Cloud (tenths) |
|-----------|------------------------|--------------|-----------|-----------|--------|------|----------------|
| 10 July   | 1130–1930              | —            | 13.9–23.2 | 13.8–29.5 | 68–95  | 4–36 | 0–10           |
| 15 July   | 0730–1600              | 0530–0630    | 14–24.3   | 15.7–29.4 | 58–95  | 0–42 | 5–10           |
| 22 July   | 0830–1900              | —            | 11.8–24.6 | 11.6–29.1 | 62–95  | 0–64 | 0–10           |
| 29 July   | 0630–1930              | —            | 10.5–28.0 | 10.1–32.5 | 39–96  | 0–53 | 0–5            |
| 5 August  | 0530–2000              | —            | 13.7–24.2 | 13.3–25.5 | 32–90  | 9–68 | 0–8            |
| 12 August | 0700–1000<br>1300–1800 | 1000         | 18.1–30.1 | 17.6–32.9 | 75–92  | 0–19 | 3–10           |
| 19 August | 0730–1830              | —            | 15.9–30.1 | 16.5–35.4 | 44–95  | 0–60 | 0–4            |

Relative windspeed is given as numbers of revolutions of a cup anemometer per minute. Ta, Ambient temperature; Tg, black globe temperature (see text); RH, relative humidity.

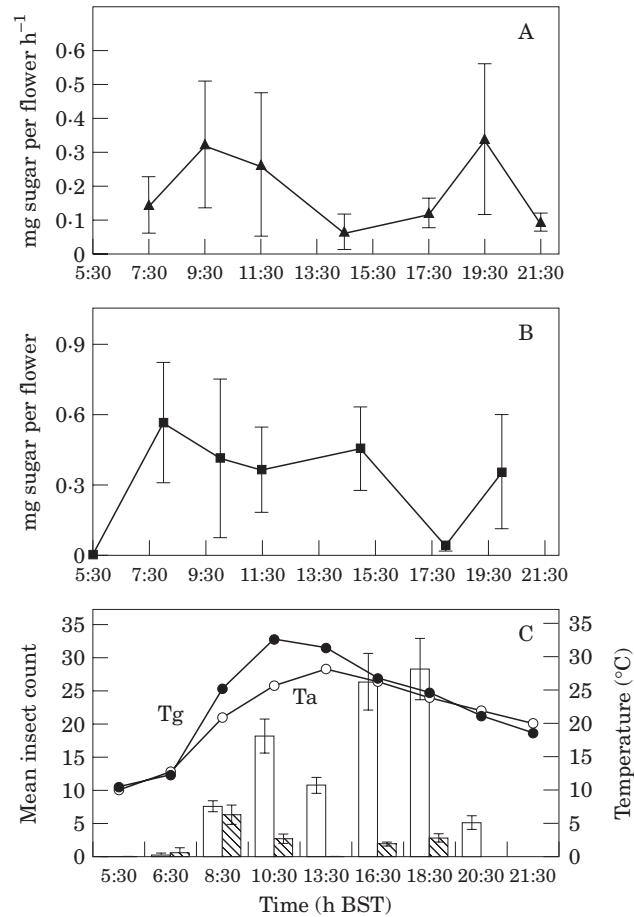


FIG. 4. Soapwort (*Saponaria officinalis*): nectar secretion rate (A), standing crop (B) and insect visits (C) (mean  $\pm$  s.e.m.), 29 Jul. 1997; with air temperature and black globe temperature.  $\square$ , *Apis mellifera*;  $\square$ , small hoverflies.

a halictine bee. The relatively short-tongued bumble-bee *Bombus terrestris* robbed the flowers and probed through a hole bitten at the base of the calyx. Kay *et al.* (1984) recorded legitimate visits by *Bombus hortorum*, *B. pascuorum* and the white butterflies *Pieris brassicae* and *P. napi*, with *B. terrestris* acting as a primary robber and *Apis mellifera* as a secondary robber, re-using its holes, and collecting pollen

TABLE 3. Butterfly species recorded making at least one visit to plant species in the Cambridge Botanic Garden between 29 July and 19 August 1997

|                              | No. spp. butterfly |                         |                        |             |                       |                   |                         |                         |                     |                            |                       |                           |                          |   |
|------------------------------|--------------------|-------------------------|------------------------|-------------|-----------------------|-------------------|-------------------------|-------------------------|---------------------|----------------------------|-----------------------|---------------------------|--------------------------|---|
|                              | <i>Pieris napi</i> | <i>Vanessa atalanta</i> | <i>Maniola jurtina</i> | Hesperiidae | <i>Lycæna phlaeas</i> | <i>Inachis io</i> | <i>Pieris brassicae</i> | <i>Pyronia tithonus</i> | <i>Pieris rapae</i> | <i>Celastrina argiolus</i> | <i>Aglais urticae</i> | <i>Polyommatus icarus</i> | <i>Gonepteryx rhamni</i> |   |
| <i>Lythrum salicaria</i>     | 9                  | +                       | +                      |             | +                     | +                 | +                       | +                       | +                   | +                          | +                     | +                         | +                        |   |
| <i>Saponaria officinalis</i> | 6                  |                         | +                      | +           |                       | +                 | +                       | +                       | +                   |                            | +                     |                           |                          |   |
| <i>Scabiosa columbaria</i>   | 4                  |                         |                        | +           | +                     |                   | +                       | +                       | +                   |                            | +                     |                           |                          |   |
| <i>Knautia arvensis</i>      | 4                  |                         |                        | +           | +                     |                   | +                       | +                       | +                   |                            | +                     |                           |                          |   |
| <i>Origanum vulgare</i>      | 4                  |                         |                        |             | +                     | +                 |                         | +                       |                     |                            |                       | +                         |                          |   |
| <i>Malva sylvestris</i>      | 2                  |                         |                        |             |                       |                   | +                       |                         | +                   |                            |                       |                           |                          |   |
| <i>Lychnis flos-cuculi</i>   | 2                  |                         |                        |             |                       |                   |                         | +                       |                     |                            |                       | +                         |                          |   |
| <i>Eupatorium cannabinum</i> | 2                  |                         |                        |             |                       |                   |                         | +                       |                     |                            |                       | +                         |                          |   |
| <i>Vicia sativa</i>          | 2                  |                         |                        |             |                       |                   |                         |                         | +                   |                            |                       | +                         |                          |   |
| <i>Centaurea scabiosa</i>    | 2                  |                         |                        |             |                       |                   |                         |                         |                     |                            | +                     |                           | +                        |   |
| <i>Stachys sylvatica</i>     | 1                  |                         |                        |             |                       |                   | +                       |                         |                     |                            |                       |                           |                          |   |
| <i>Malva moschata</i>        | 1                  |                         |                        |             |                       |                   |                         |                         |                     |                            | +                     |                           |                          |   |
| <i>Dipsacus fullonum</i>     | 1                  |                         |                        |             |                       |                   |                         |                         |                     |                            |                       | +                         |                          |   |
| <i>Trifolium pratense</i>    | 1                  |                         |                        |             |                       |                   |                         |                         |                     |                            |                       | +                         |                          |   |
| <i>Linaria vulgaris</i>      | 1                  |                         |                        |             |                       |                   |                         |                         |                     |                            |                       |                           | +                        |   |
| <i>Silene dioica</i>         | 1                  |                         |                        |             |                       |                   |                         |                         |                     |                            |                       |                           |                          | + |
| No. plant spp. visited       | 1                  | 1                       | 1                      | 1           | 4                     | 2                 | 4                       | 5                       | 7                   | 2                          | 9                     | 4                         | 2                        |   |

Small tortoiseshells became frequent from 16 August, predominantly on *Scabiosa columbaria*, *Knautia arvensis* and *Lythrum salicaria*.

on male flowers. Additional visitor records include small tortoiseshell butterflies, *Aglais urticae*, the small elephant hawkmoth *Deilephila porcellus* (L.) (Baker, 1947) and muscid flies in the genus *Thricops* (Westerbergh and Saura, 1994).

**Ragged robin** *Lychnis flos-cuculi* L. Ragged robin is native in Britain and common in much of Europe, Caucasus and Siberia. White and pink, single and double variants are

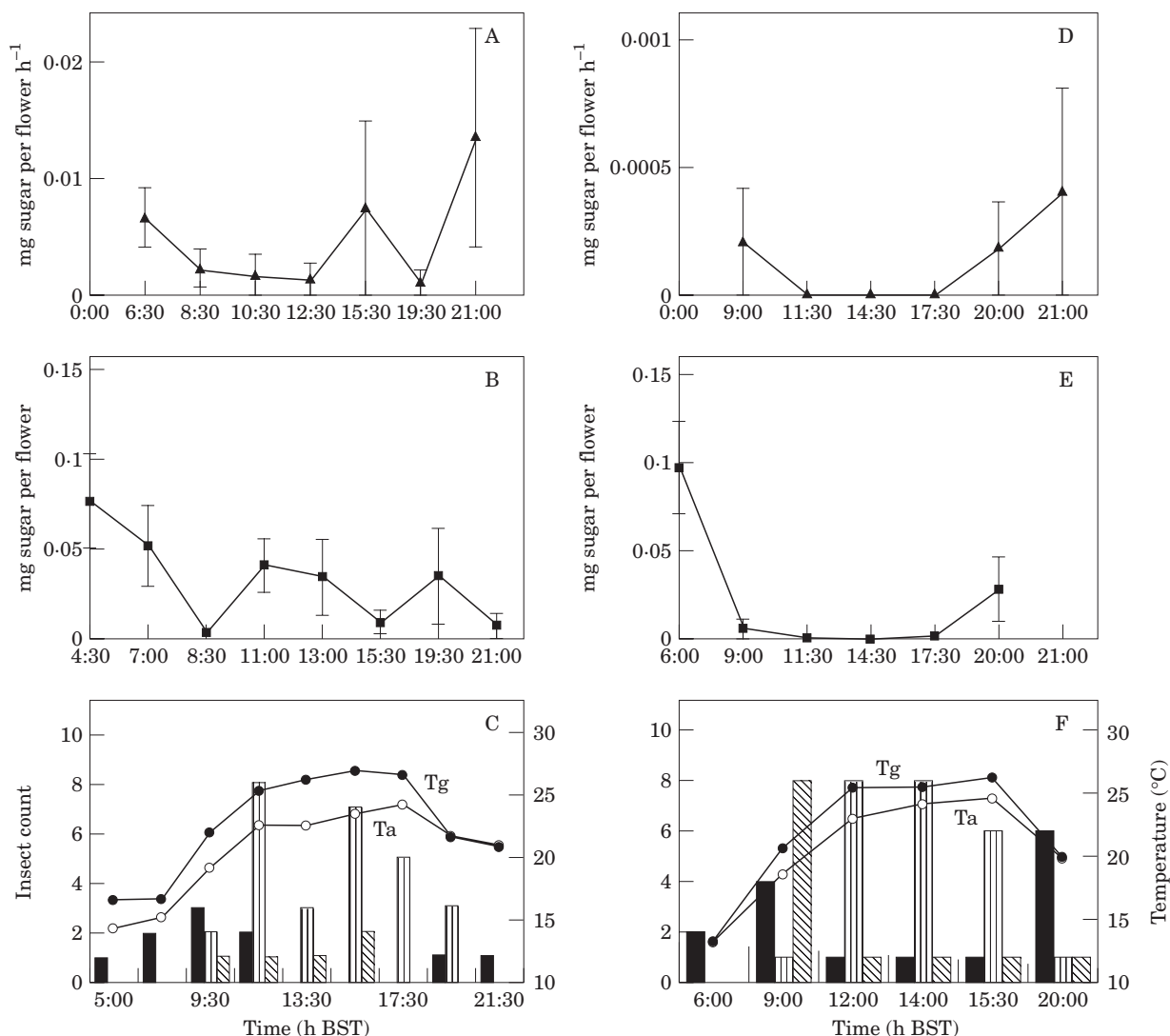


FIG. 5. Marsh woundwort (*Stachys palustris*): nectar secretion rate (A, D, note different scales), nectar standing crop (B, E) (mean  $\pm$  s.e.m.) and 1-min insect counts (C, F) on 15 July (A, B, C) and 22 July (D, E, F) 1997, with air temperature and black globe temperature. ■, *Bombus pascuorum*; ▨, *Anthidium manicatum*; □, hoverflies.

known in cultivation (Huxley, 1992). The flowers are bisexual and the corolla length, measured from the insertion of the pedicel to the mouth of the corolla, was  $9.4 \pm 0.37$  mm ( $n = 10$ ) (Table 1).

When a dawn-to-dusk study was performed on 10 Jul. 1997 there were 396 open flowers on the plot (equivalent to about 79 flowers m<sup>-2</sup>). The secretion rate was low morning and evening, and peaked at about 0.04 mg per flower h<sup>-1</sup> around midday (Fig. 1). The standing crop was lower than that of the other members of the subfamily studied (Fig. 1). The secretion rate was positively correlated with black globe temperature (Spearman correlation coefficient 0.409,  $P < 0.005$ ,  $n = 74$ ) (Fig. 2).

Despite temperatures permissive for activity of *Bombus* and *Apis* (Table 2), the only insects recorded visiting the flowers during the day were five *B. lapidarius* workers, one *B. pascuorum* and a hoverfly.

*Soapwort* *Saponaria officinalis* L. Soapwort is native in Europe, but its status in Britain is uncertain. Perhaps native

in SW England, it is well naturalized throughout Britain and behaves as an escape from cultivation (Huxley, 1992; Walters, 1993; Stace, 1997). The single form was naturalized in Britain by the early seventeenth century; the double variant, 'Flore Pleno', came later (Coats, 1956). The corolla tube of the single pink-flowered form was  $24.8 \pm 0.23$  mm long ( $n = 30$ ) (Table 1).

On 29 Jul. 1997, when we undertook a dawn-to-dusk study, there were 6480 flowers in the 5 m<sup>2</sup> plot (1296 flowers m<sup>-2</sup>). Nectar was sampled from unwilted flowers at the stage when the stigma was fully developed and the anthers had dehiscence. The secretion rate was high, reaching about 0.3 mg per flower h<sup>-1</sup>, and so was the standing crop, with up to about 0.5 mg sugar per flower (Fig. 4). There was no significant correlation between secretion rate and black globe temperature (Spearman correlation coefficient  $-0.187$ ,  $P = 0.121$ ,  $n = 70$ ) (Fig. 2).

On 29 July temperatures were permissive for social bee activity (Corbet *et al.*, 1993, 1995) all day except early in the



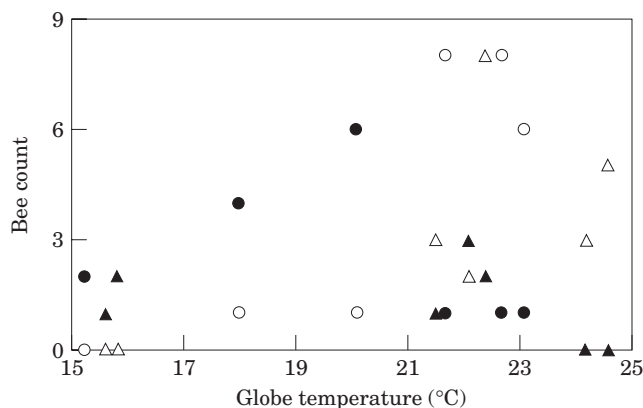


FIG. 6. Marsh woundwort (*Stachys palustris*): numbers of *Bombus pascuorum* (solid symbols) and *Anthidium manicatum* (open symbols) in 1-min counts on 15 ( $\Delta$ ,  $\blacktriangle$ ) and 22 Jul. ( $\circ$ ,  $\bullet$ ) 1997, in relation to black globe temperature at the time of the count. Below  $T_g = 21^\circ\text{C}$ , bumblebee numbers increased with temperature and there was never more than one *Anthidium* present. Above that temperature, *Anthidium* numbers were high and few bumblebees were present.

morning, when air temperature was below  $11^\circ\text{C}$  (Table 2). Honeybees (*Apis mellifera*) were frequent visitors to the flowers (Fig. 4). They acted as secondary robbers, taking nectar via holes bitten through the calyx by a few individuals of the short-tongued bumblebees *Bombus terrestris/lucorum*, which acted as primary robbers (*sensu* Inouye, 1983). In 1997 we recorded visits from single queens of *B. lapidarius* and *B. hortorum/ruderatus* (the only insect seen to take nectar legitimately, via the mouth of the flower), and in 1996 we saw *Bombus pascuorum* and *B. pratorum* (L.) acting as secondary robbers on both single and double variants of soapwort. Other visitors in 1997 included pollen-collecting hoverflies [small ones including *Episyrphus balteatus* (Degeer) and species of *Platycheirus* Lepeletier & Serville and *Melanostoma* Schiner, and large ones including *Eristalis tenax* (L.) and *E. intricarius* (L.)], a solitary bee, a solitary wasp, moths and six species of butterflies (Table 3). Ants were frequently seen crawling in through the holes bitten by primary robbers, presumably collecting nectar.

#### Woundworts, *Stachys* spp. (Lamiaceae)

**Marsh woundwort** (*Stachys palustris* L. *S. palustris* is native and common in damp places throughout most of Britain (Stace, 1997). It is widespread in Europe (Blamey and Grey-Wilson, 1989). The mean corolla depth was  $9.8 \pm 0.08$  mm ( $n = 30$ ) (measured in 1998).

Dawn-to-dusk studies were performed on 15 and 22 Jul. 1997, when there were about 2080 open flowers  $\text{m}^{-2}$  (10404 open flowers in a  $5\text{ m}^2$  plot) and  $1580\text{ m}^{-2}$  (7899 in  $5\text{ m}^2$ ), respectively. Open, unwilted flowers were sampled for nectar. Nectar secretion rate was below  $0.02\text{ mg per flower h}^{-1}$  on 15 July and did not exceed  $0.001\text{ mg per flower h}^{-1}$  on 22 July (Fig. 5). The standing crop was below  $0.1\text{ mg sugar per flower}$  on 15 July and undetectable for most of the day on 22 July (Fig. 5).

The main visitors to the flowers were *Bombus pascuorum* and *Anthidium manicatum*, both taking nectar (Fig. 5).

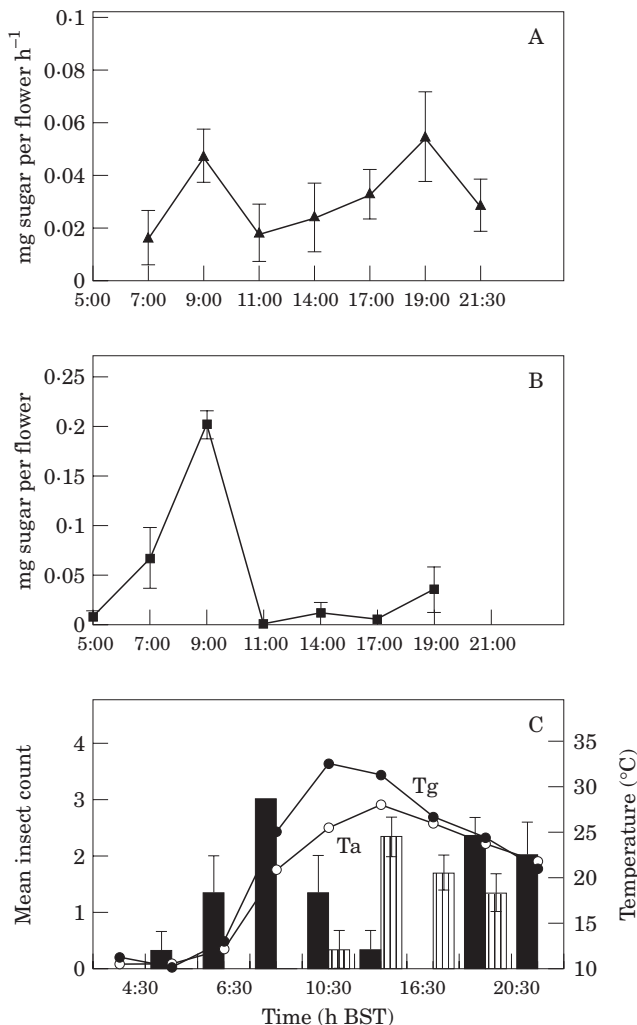


FIG. 7. Hedge woundwort (*Stachys sylvatica*): nectar secretion rate (A), standing crop (B) (mean  $\pm$  s.e.m.) and insect visits (C) (mean  $\pm$  s.e.m. of three 1-min counts), with air temperature and black globe temperature, on 29 Jul. 1997.  $\blacksquare$ , *Bombus pascuorum*;  $\square$ , *Anthidium manicatum*.

Other visitors were hoverflies taking pollen (four on 15 July and 12 on 22 July), honeybees (two on 15 July and none on 22 July), solitary bees (two on 15 July and 13 on 22 July) and single individuals of *Bombus terrestris/lucorum* and *B. lapidarius* (on 22 July). No butterflies were recorded during either dawn-to-dusk study.

On both dates, bumblebees were more numerous on marsh woundwort early and late in the day than they were around midday, and *Anthidium* showed the converse pattern. A plot of counts of these species against globe temperature for the two dates (Fig. 6) is consistent with the hypothesis that *Anthidium* was numerous only at globe temperatures above  $21^\circ\text{C}$ , and that *B. pascuorum* could forage at lower temperatures than that, but was discouraged from visiting at times when *Anthidium* was present. An *Anthidium* male would patrol a group of inflorescences and dart towards any bee that visited *Stachys* within the patrolled area (as described by Westrich, 1989). When approached in this way bumblebees usually departed. Their absence during the



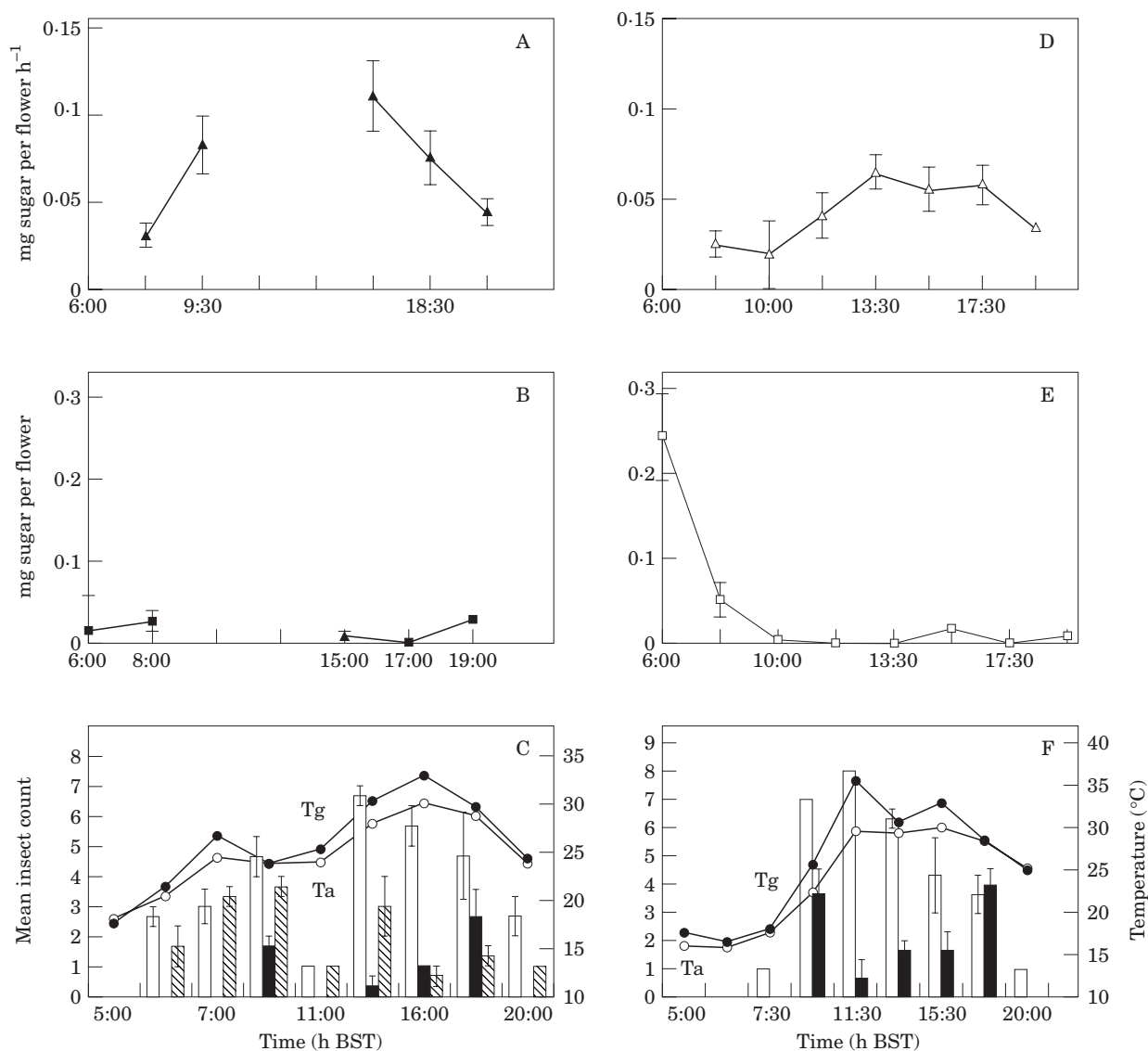


FIG. 8. Musk mallow (*Malva moschata*): nectar secretion rate (A, D), standing crop (B, E) and insect visits (C, F) (mean  $\pm$  s.e.m.), with air temperature and black globe temperature, on 12 (A, B, C) and 19 Aug. (D, E, F) 1997. ■, *Bombus pascuorum*; □, *Apis mellifera*; ▨, hoverflies.

warmer parts of the day may have been due to this interference competition.

**Hedge woundwort** *Stachys sylvatica* L. Native and common over most of Britain (Stace, 1997), this perennial is widely distributed in Europe (Blamey and Grey-Wilson, 1989). The dark purple flowers last for 1 or 2 d. Flowers were marked as buds and monitored at regular intervals. Of nine that opened on 5 August, none were open at 0540 h, six were fully open by 0847 h with dehiscent anthers but the stigma not exposed, all had reached that stage by 1457 h and one had its stigma exposed, and by 2105 h five had the stigma exposed and some stamens withered. Nectar accumulates in a trichome-rimmed chamber at the base of the corolla. Measured from the base to the point of maximum flexure in the centre of the lower lip, the corolla tube was  $8.5 \pm 0.10$  mm long ( $n = 30$ ) (Table 1).

On 29 Jul. 1997, when there were 1050 open flowers in the

plot ( $210 \text{ m}^{-2}$ ), we performed a dawn-to-dusk study sampling nectar from flowers that were fully open and unwilted, with anthers dehiscent and the stigma exposed. The secretion rate appeared bimodal, with morning and evening peaks of about  $0.05 \text{ mg per flower h}^{-1}$  and lower values at midday (Fig. 7). The standing crop peaked around 0900 h with about  $0.2 \text{ mg sugar per flower}$ , and then fell sharply to remain low for the rest of the day (Fig. 7).

*Bombus pascuorum* and the solitary bee *Anthidium manicatum* (L.) dominated the flowers (Fig. 7); less frequent flower visitors included the small hoverflies *Episyrphus balteatus* and species of *Platycheirus* and *Melanostoma* taking pollen, two other species of solitary bee and the gatekeeper butterfly *Pyrionia tithonus* (L.) (Table 3). *B. pascuorum* was probably largely responsible for depleting the high early-morning standing crop. The pattern of visits by *Anthidium* and *B. pascuorum* was similar to that on

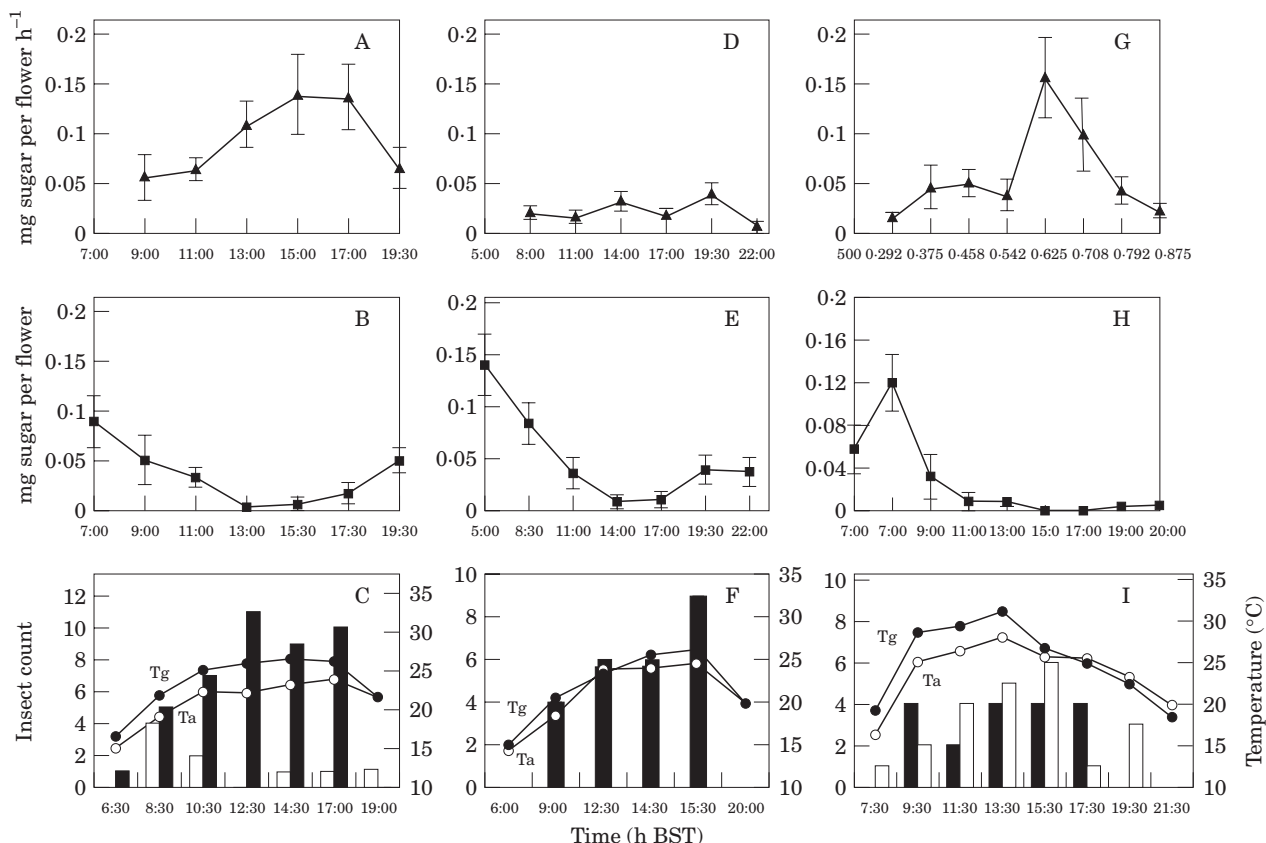


FIG. 9. Common mallow (*Malva sylvestris*): nectar secretion rate (A, D, G), standing crop (B, E, H) (mean  $\pm$  s.e.m.) and insect visits (C, F, I), with air temperature and black globe temperature, on 15 (A, B, C), 22 (D, E, F) and 29 Aug. 1997 (G, H, I). ■, *Bombus* spp. (mainly *B. lapidarius* in C and F; all *B. lapidarius* in I); □, *Apis mellifera*.

marsh woundwort (Fig. 6). In the afternoon *Anthidium* visited the flowers and bumblebee numbers fell, to rise again as *Anthidium* numbers fell towards evening (Fig. 7).

#### Mallows, *Malva* spp. (family Malvaceae)

**Musk mallow** *Malva moschata* L. Musk mallow is native and common over most of the British Isles except in parts of Ireland and North Britain where it is less common and probably not native (Stace, 1997). It is native in much of Europe and in NW Africa, and naturalized in North America (Huxley, 1992).

The flowers are large, with petals more than 16 mm long (Stace, 1997). The nectaries of *Malva* species are on the upper surface of the sepals (Holm, 1979; Weberling, 1989), and bees probe down between the bases of adjacent petals to reach the nectar.

Two dawn-to-dusk studies were undertaken on 12 and 19 August 1997, when the flower density was about 61 flowers  $m^{-2}$  (307 flowers in a 5  $m^2$  plot) and 44 flowers  $m^{-2}$  (220 flowers in the plot), respectively. Nectar was sampled from flowers with dehiscent anthers. On 12 August rain at 0945 h wetted the flowers and prevented nectar sampling until 1500 h (Table 2). On both dates the secretion rate was lower in the morning and evening than it was around the middle of

the day (Fig. 8). The standing crop was low throughout the day on 12 August and for most of the day on 19 August, but on that date it was high early in the morning reaching about 0.25 mg per flower.

On both dates the most frequent visitors were *Apis mellifera* and *Bombus lapidarius* (Fig. 8). Honeybees were often covered in pollen, presumably reflecting failure to groom; pollen of Malvaceae has been found to be unacceptable to honeybees (Vaissiere and Vinson, 1994). Other visitors were one *B. pascuorum*, one solitary bee and a common blue butterfly (Table 3). Taking pollen were the large hoverfly *Eristalis tenax*, the small hoverflies *Episyrphus balteatus* and species of *Syrphus* and *Platycheirus*. Air temperature did not fall below 15.9 °C on either date (Table 2). Despite these permissive temperatures, honeybees were not numerous before 0900 h on 19 August, perhaps because the nectar solute concentrations were low, with means of  $20.0 \pm 0.88$  ( $n = 10$ ) and  $19.4 \pm 2.43$  ( $n = 9$ )% sucrose at 0547 h and 0744 h, respectively. Through much of the day standing crops were too low to permit concentration measurement, but by 1542 h the mean had risen to  $57.3 \pm 1.70$ % sucrose ( $n = 4$ ).

**Common mallow** *Malva sylvestris* L. Common mallow is native and common throughout lowland England, Wales and the Channel Islands (Stace, 1997). It is native

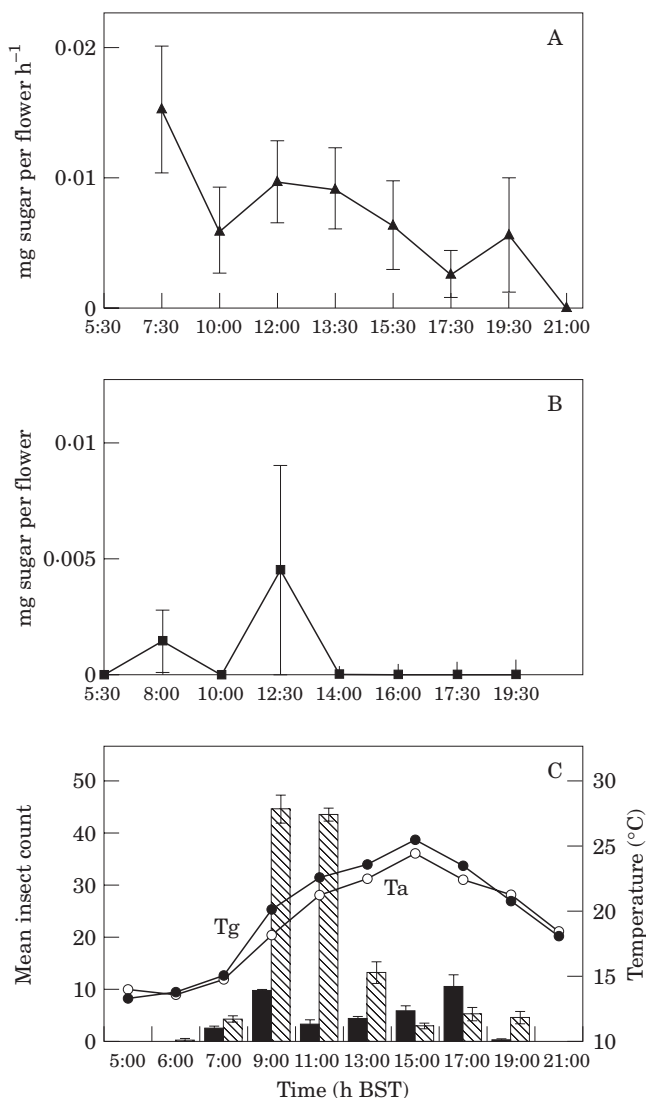


FIG. 10. Teasel (*Dipsacus fullonum*): nectar secretion rate (A), standing crop (B) and insect visits (C), 5 Aug. 1997 (mean  $\pm$  s.e.m.), with air temperature and black globe temperature. ■, *Bombus* spp.; ▨, small hoverflies.

throughout Europe, N Africa and SW Asia, and naturalized in N America (Huxley, 1992). Fifteen flowers that were monitored through a day were all buds at 0430 h and had all passed through the open stage and closed by 1900 h.

We undertook three dawn-to-dusk studies, on 15, 22 and 29 Jul. 1997. Nectar was sampled from open, unwilted flowers. Secretion rates were high on 15 and 29 Jul. 1997, peaking at about 0.15 mg per flower h<sup>-1</sup> in early afternoon, but on 22 July the rate did not exceed about 0.04 mg per flower h<sup>-1</sup> (Fig. 9). The standing crop was high in the morning, with about 0.1 mg per flower or more, and fell to a minimum below 0.01 mg sugar per flower in early afternoon (Fig. 9).

On all dates *B. lapidarius* was a frequent visitor, taking nectar legitimately from open flowers, working systematically around a flower probing each gap between adjacent petals. Honeybee numbers were variable; *Apis* was absent

on 22 July, present in small numbers on 15 July and numerous on 29 July (Fig. 9). Honeybees often acted as base workers (*sensu* Inouye, 1983), visiting flowers that had closed and probing into the calyx from outside the flower without touching the sexual parts of the flower.

A few legitimate visits to open flowers were also made by *B. terrestris/lucorum* and *B. pascuorum*, and by hoverflies, a solitary bee and small white and large white butterflies (Table 3). The microclimate is summarized in Table 2.

#### Other species

*Wild teasel* *Dipsacus fullonum* L. This biennial species is native in Britain and elsewhere in Europe and Asia, and naturalized in North America (Huxley, 1992; Stace, 1997). The pale violet flowers are massed in a capitulum, on which the flowers at the equator open first; a wave of flowering progresses both upward and downward over a period of about 10 d. The mean corolla length was  $12.1 \pm 0.14$  mm ( $n = 30$ ) (Table 1), and the corolla tube was less than 1 mm diameter at the base. The dehiscent anthers protrude about 5 mm from the mouth of the corolla. An individual flower's life is completed, from bud-opening to abscission, in a single day. The flowers usually fall off at nightfall.

At the time of our dawn-to-dusk study on 5 Aug. 1997, there were 93 capitula in the plot, each with an average of 73.7 flowers, giving approx. 6850 flowers in all. The secretion rate was low, hardly exceeding 0.01 mg per flower h<sup>-1</sup> (equivalent to 0.74 mg per capitulum h<sup>-1</sup>), and declined from early morning onwards (Fig. 10). The standing crop was always low (Fig. 10).

Despite the small quantities of nectar per flower, the massed flowers on a capitulum evidently provided profitable foraging for insects. The most frequent visitors were the small hoverflies *Episyrphus balteatus*, and species of *Meta-syrphus*, *Platycheirus* and *Melanostoma*. Hoverflies generally took pollen, and were very numerous between 0900 and 1100 h (Fig. 10), following a pattern similar to that seen on purple loosestrife (Fig. 11). Less numerous were bumblebees (*B. lapidarius*, *B. pascuorum* and *B. terrestris/lucorum* taking nectar and pollen) and cuckoo bumblebees *Psithyrus* species, of which an average of two–four were collecting nectar between 0900 h and 1700 h. Occasional visitors were honeybees taking nectar and the large hoverfly *Eristalis tenax* taking pollen. No butterflies visited teasel during the study day, but small tortoiseshells visited it at other times in the season (Table 3).

*Purple loosestrife* *Lythrum salicaria* L. Purple loosestrife is native in Europe, and naturalized as a weed in North America (Huxley, 1992). It is common in wet places throughout most of the British Isles except N Scotland (Stace, 1997). The flowers are trimorphic. Our plants had about 30 open flowers per spike. The mean length of the effective corolla tube (that is, the region enclosed within the fused region of the calyx) differed according to morph ( $F_{2,33} = 3.92$ ,  $P = 0.03$ , one-way Anova). It was longer in long-styled flowers ( $6.4 \pm 0.20$  mm) than in flowers with styles of medium length ( $5.9 \pm 0.23$  mm) or flowers with short styles ( $5.6 \pm 0.18$  mm;  $n = 12$  for each morph) (Table 1).

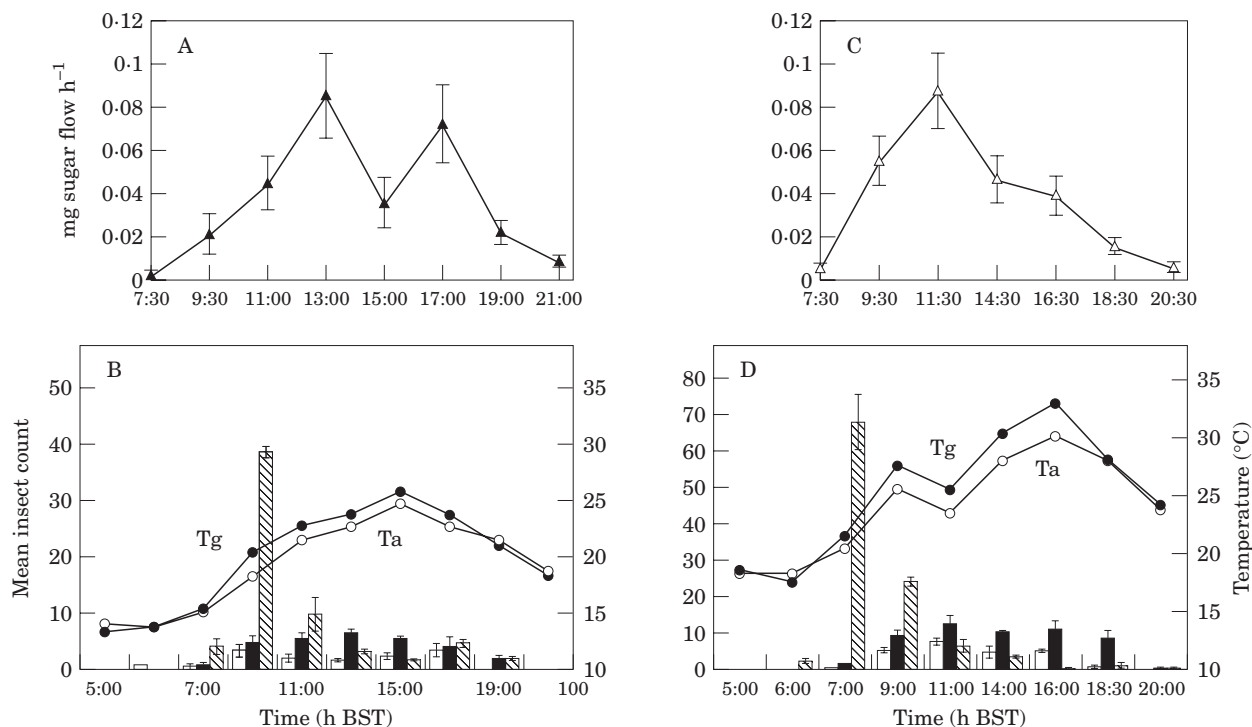


FIG. 11. Purple loosestrife (*Lythrum salicaria*): nectar secretion rate (A, C) and insect counts (mean  $\pm$  s.e.m.) with air temperature and black globe temperature (B, D) on 5 (A, B) and 12 Aug. (C, D) 1997. The standing crop of nectar was undetectable on both dates. ■, *Bombus* spp. □, *Apis mellifera*; ▨, small hoverflies.

We sampled nectar from open flowers with dehiscid anthers. In a preliminary investigation (1000–1600 h on 1 Aug. 1997) we did not find any difference in nectar secretion rate between the three morphs ( $H = 1.70$ , d.f. = 2,  $P = 0.43$ , Kruskal-Wallis test), so we sampled nectar from all three morphs during dawn-to-dusk studies on 5 and 12 Aug. 1997. On these dates the numbers of open flowers in the plot were about 2575 and 4920, respectively, with 32.6 flowers per spike and 79 spikes, equivalent to a density of 515 flowers m<sup>-2</sup>, and 29.7 flowers per spike and 168 spikes, equivalent to 996 flowers m<sup>-2</sup>.

On both dates the rate of nectar secretion was low in the morning and evening, peaking around the middle of the day at about 0.09 mg sugar per flower h<sup>-1</sup> (Fig. 11). The standing crop was very low indeed. We could not detect any nectar in unprotected flowers.

Temperatures were high enough for social bee activity throughout both days (Table 2). The flowers were visited by small hoverflies foraging for pollen [*Episyrphus balteatus*, *Sphaerophoria scripta* (L.) and species of *Syrphus* and *Metasyrphus*, and occasionally *Helophilus pendulus* (L.)]. These were very numerous early in the morning on 5 August (with an average of 38 at 0900 h) and 12 August (68 at 0700 h, of which 25 were *Syrphus* sp.). On both dates hoverfly numbers fell after the early peak, and few individuals were recorded for the rest of the day (Fig. 11). The large hoverflies *Eristalis tenax* and *E. intricarius* (L.) were present in smaller numbers and probed for nectar as well as pollen. Honeybees and the bumblebees *Bombus terrestris/lucorum*, *B. lapidarius* and *B. pascuorum* took

nectar. Butterflies were numerous; seven species took nectar (Table 3).

## DISCUSSION

The nectar production of a plant species cannot be evaluated on the basis of a single sample because the standing crop of nectar sugar in a flower changes with time. The standing crop at a given time depends on the rate of depletion by insects, as well as the rate of supply by secretion, and both of these depend on weather and other variables (Burquez, 1988; Corbet, 1990). A dawn-to-dusk study involving measurements of both standing crop and secretion rate gives information on rates of supply as well as depletion, and if insect visits and microclimate are monitored at the same time it is possible to gain a clearer understanding of the causes of observed fluctuations in standing crop. For example, steep declines in standing crop in *Stachys palustris* on 15 and 22 Jul. 1997 (Fig. 5) coincided with (and may have been caused by) peak periods of foraging by *Bombus pascuorum*; the appearance of *Anthidium* at the flowers followed (and may have depended on) elevation of the black globe temperature above 21 °C (Fig. 6); and the disappearance of *B. pascuorum* followed (and may have depended on) the arrival of territorial males of *Anthidium* (Fig. 6).

Even when dawn-to-dusk studies are performed, the potential nectar production of a plant species cannot be reliably established on the basis of a single day's sampling. There are sometimes marked day-to-day differences in rates of nectar secretion and depletion (e.g. compare Fig. 5A, and

D), presumably related to such factors as plant status as well as immediate weather conditions. For that reason we conducted more than one dawn-to-dusk study on the same plant species where possible. When comparing two related plant species, we performed dawn-to-dusk studies of both on the same day (e.g. Fig. 1) unless differences in flowering period made that impossible.

Limited studies on insect visits can also be misleading. Insect visits to a given plant species varied from day to day (e.g. Fig. 9C and F). Use of flowers by an insect species must depend not only on the accessible reward in individual flowers and patches, but also on seasonal and hourly patterns of availability of alternative forage flowers and competing insects. Thus *Digitalis*, normally much visited by the long-tongued bumblebees *B. hortorum* and *B. pascuorum* (SAC, pers. obs.), was past its flowering peak when our study began, and *Saponaria* and *Eupatorium* flowered towards the end of the period. The insect fauna changed with time. In 1997 small hoverflies were numerous between 28 July and 18 August, and butterflies, especially small whites, small tortoiseshells and common blues, from 16 August onwards.

Insect visit frequencies also vary from place to place, depending on the pool of insects available in each location and the availability of alternative forage. Our study site was in a town, where the pool of potential visitors may be smaller than that in the countryside, and in a botanic garden, where alternative forage may have been particularly abundant. For these reasons we cannot conclude that a plant species rarely visited in our study is unattractive to insects, but we can conclude that nectar-rich species that received many visits here can (at least sometimes) provide valuable forage for flower-visiting insects.

Species of bumblebee differ in the attributes of the flowers they select as nectar sources (Fussell and Corbet, 1992). *B. lapidarius* commonly visits massed flowers, yellow Fabaceae and mallows. The longest-tongued species, *B. hortorum*, visits deep flowers such as *Silene dioica* and *Digitalis purpurea*, but was not distinguished from the short-tongued *B. terrestris/lucorum* in this study. *B. pascuorum*, the only other species present with a moderately long tongue, visits moderately long flowers, especially in the families Lamiaceae and Fabaceae. Honeybees, *Apis mellifera*, forage for nectar on shallower flowers than most bumblebees. *Dipsacus* is of interest as an overnight resting place for male bumblebees and *Psithyrus* species.

Lepidoptera take nectar. In this study butterflies were particularly frequent on *Lythrum salicaria*, *Scabiosa columbaria*, *Knautia arvensis* and *Origanum vulgare* (Table 3). Other good butterfly flowers, in terms of numbers of individuals if not species diversity, were *Eupatorium cannabinum* and *Dipsacus fullonum*. In a survey of butterfly nectar flowers, Porter, Steel and Thomas (1992) list all these as commonly used, except *Lythrum*, which is listed as a butterfly nectar flower by Vickery (1991), and *Scabiosa*.

Hoverflies often take pollen on flowers too deep to supply them with nectar. Hoverflies were particularly numerous on *Dipsacus*, *Lythrum*, *Saponaria*, *Stachys palustris* and *Malva moschata*.

All the plant species described here offer abundant nectar.

The four species of Caryophylloideae, *Silene dioica*, *S. latifolia*, *Lychnis flos-cuculi* and *Saponaria officinalis*, are all strong candidates for pollinator-friendly gardens because of their deep, nectar-rich flowers. They received relatively few daytime visits in this study, but in other circumstances they may be well visited. *S. dioica* showed a significant negative correlation between globe temperature and secretion rate (Fig. 2), perhaps implying that nocturnal pollinators are important, or have been so during its recent evolutionary history. This species is visited elsewhere by long-tongued bees, butterflies, day-flying moths and pollen-collecting hoverflies (SAC, pers. obs.); we did not observe it at night. For white campion, *S. latifolia*, the correlation between temperature and secretion rate (Fig. 2) was not significant, but the hypothesis of adaptation to nocturnal visitors is supported by the tendency of the corolla to wilt by day and become turgid at night, and by observations elsewhere of visits by moths including pine hawkmoths, *Hyloicus pinastri* (L.) (SAC, pers. obs.) and others (Proctor, Yeo and Lack, 1996). *L. flos-cuculi* showed a positive correlation between temperature and secretion rate (equivalent to a daytime secretion peak) and is known as a butterfly flower (Proctor *et al.*, 1996). *Saponaria* secretion rate may peak at an intermediate temperature (Fig. 2). This species is visited by moths (Proctor *et al.*, 1996) in addition to the bees, hoverflies and butterflies recorded here (Table 3). *Saponaria* and *Silene dioica* offer added interest to gardeners by providing the opportunity to observe primary and secondary robbing by insects with tongues too short to reach the nectar directly.

Where *Silene dioica* and *S. latifolia* occur together hybrids form between them (Baker, 1947; Goulson and Jerrim, 1997; Stace, 1997), implicating a shared pollinator such as a moth or *Bombus hortorum*.

The species of *Stachys* secrete less nectar per flower than some campions, but profitability is increased because the flowers are grouped in an inflorescence, reducing interflower travelling costs for foraging insects. Both *S. palustris* and *S. sylvatica* are well used by *Bombus pascuorum*, with very little competition from honeybees (Table 1). Both woundworts are important components of long-tongued bumblebee forage in hedgerows and waste ground. *Stachys* species have added interest for gardeners because they frequently host the solitary bee *Anthidium manicatum* (tongue length about 7.5–8.5 mm; SAC, pers. obs.), which provides fascinating entertainment due to the male territorial behaviour and the female's habit of collecting downy hairs from plants of *Stachys byzantina* K. Koch and other woolly species and carrying them to the nest to line the cells (Westrich, 1989). Further, the interaction between territorial male *Anthidium* and foraging bumblebees (and even, in Umbria, Italy, the very large carpenter bee *Xylocopa* spp.; LC, pers. obs.) provides a rare opportunity to observe interference competition in action. The high temperature threshold for *Anthidium* activity leaves the nectar resource of *S. palustris*, *S. sylvatica* and *S. byzantina* (SAC, pers. obs.) available in the morning and evening for long-tongued bumblebees such as *B. pascuorum* and *B. hortorum*.

Hybrids between *Stachys sylvatica* and *S. palustris* (Stace, 1997) presumably result from cross pollination by an insect

species that visits both, such as *Anthidium manicatum*, *Bombus pascuorum* or *B. hortorum*. In West Cornwall such hybrids were visited by both these species and by the hummingbird hawkmoth, *Macroglossum stellatarum* in July 1998 (SAC, pers. obs).

The mallows, *Malva sylvestris* and *M. moschata*, attracted a different assemblage of visiting insects including *Bombus lapidarius*, a bumblebee with a relatively short tongue and a relatively high temperature threshold for flight activity (Corbet *et al.*, 1993, 1995), as well as honeybees. Musk mallow is perhaps more delicate and attractive as a garden flower, but on common mallow extra interest is provided by the honeybees' habit of probing into the calyx of closed flowers from outside (baseworking), especially towards the late afternoon and evening. Other attractive native mallows include the magnificent 3-m-high *Lavatera arborea* L., in which the nectaries are enclosed within the basally-fused epicalyx making the nectar less accessible to short-tongued bees. That species is much visited by *B. pascuorum* in Cornwall (SAC, pers. obs.).

Our comparative studies revealed differences between plant species in reward and visitor spectrum, and differences between insect species in the plants they select. A knowledge of these differences may help gardeners to choose plant species for insect-friendly gardens. By providing forage for selected groups of insects, they may help to sustain populations of pollinators on which crops and wild plants depend for pollination; and they may also add greatly to the biological interest of the garden.

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## LITERATURE CITED

- Baker HG.** 1947. Biological flora of the British Isles. *Melandrium* (Roehling em.) Fries. *Journal of Ecology* **35**: 271–292.
- Barrow DA, Pickard RS.** 1985. Estimating corolla length in the study of bumble bees and their food plants. *Journal of Apicultural Research* **24**: 1–8.
- Berezin M.** 1995. Bumble bees of the Moscow region. *Entomologist's Monthly Magazine* **131**: 259–268.
- Blamey M, Grey-Wilson C.** 1989. *The illustrated flora of Britain and Northern Europe*. London: Hodder & Stoughton.
- Bolten AB, Feinsinger P, Baker HG, Baker I.** 1979. On the calculation of sugar concentration in flower nectar. *Oecologia* **41**: 301–304.
- Brantjes NBN.** 1976. Riddles around the pollination of *Melandrium album* (Mill.) Garcke (Caryophyllaceae) during the oviposition by *Hadena bicurvis* Hufn. (Noctuidae, Lepidoptera). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C* **79**: 1–12.
- Burquez A.** 1988. *Studies on nectar secretion*. PhD Thesis. University of Cambridge, UK.
- Coats AM.** 1956. *Flowers and their histories*. London: Hulton Press.
- Comba L, Corbet SA, Barron A, Bird A, Collinge S, Miyazaki N, Powell M.** 1999. Garden flowers: insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany* **83**: 73–86.
- Corbet SA.** 1990. Pollination and the weather. *Israel Journal of Botany* **39**: 13–30.
- Corbet SA, Saville NM, Prys-Jones OE, Unwin DM.** 1995. The competition box: a graphical aid to forecasting pollinator performance. *Journal of Applied Ecology* **32**: 707–719.
- Corbet SA, Fussell M, Ake R, Fraser A, Gunson C, Savage A, Smith K.** 1993. Temperature and the pollinating activity of social bees. *Ecological Entomology* **18**: 17–30.
- Fussell M, Corbet SA.** 1992. Flower usage by bumble-bees: a basis for forage plant management. *Journal of Applied Ecology* **29**: 451–465.
- Goulson D, Jerrim K.** 1997. Maintenance of the species boundary between *Silene dioica* and *S. latifolia* (red and white campion). *Oikos* **79**: 115–126.
- Holm E.** 1979. *The biology of flowers*. Harmondsworth, Middx: Penguin Books Ltd.
- Huxley A.** 1992. *The new Royal Horticultural Society dictionary of gardening*. London: MacMillan.
- Inouye DW.** 1983. The ecology of nectar robbing. In: Bentley B, Elias T, eds. *The biology of nectaries*. New York: Columbia University Press, 153–173.
- Kay QON, Lack AJ, Bamber FC, Davies CR.** 1984. Differences between sexes in floral morphology, nectar production and insect visits in a dioecious species, *Silene dioica*. *New Phytologist* **98**: 515–529.
- Osborne JL, Williams IH, Corbet SA.** 1991. Bees, pollination and habitat change in the European Community. *Bee World* **72**: 99–116.
- Owen J.** 1991. *The ecology of a garden: the first fifteen years*. Cambridge: Cambridge University Press.
- Parsons WT, Cuthbertson EG.** 1992. *Noxious weeds of Australia*. Melbourne: Inkata Press.
- Peters G.** 1972. Ursachen für den Rückgang der seltenen heimischen Hummelarten (Hym., *Bombus* et *Psithyrus*). *Entomologische Berichte* **9**: 85–90.
- Porter K, Steel CA, Thomas JA.** 1992. Butterflies and communities. In: Dennis RHL, ed. *The ecology of butterflies in Britain*. Oxford: Oxford University Press, 139–177.
- Proctor M, Yeo P, Lack D.** 1996. *The natural history of pollination*. London: HarperCollins.
- Prys-Jones OE.** 1982. *Ecological studies of foraging and life history in bumblebees*. PhD Thesis, University of Cambridge, UK.
- Prys-Jones OE, Corbet SA.** 1991. *Bumblebees*. 2nd edn. Slough: The Richmond Publishing Co. Ltd.
- Rasmont P.** 1988. *Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae)*. PhD Thesis. Faculté des Sciences Agronomiques de l'Etat, Gembloux, Belgium.
- Siegel S, Castellan NJ.** 1988. *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill International.
- Stace C.** 1997. *New flora of British Isles*. 2nd edn. Cambridge: Cambridge University Press.
- Stubbs AN, Falk SJ.** 1993. *British hoverflies*. London: British Entomological and Natural History Society.
- Sugden EA, Thorp RW, Buchmann SL.** 1996. Honey bee–native bee competition: focal point for environmental change and apicultural response in Australia. *Bee World* **77**: 26–44.
- Thomas JA.** 1986. *The RSNC guide to butterflies of the British Isles*. London: Guild Publishing.
- Thomas J, Lewington R.** 1991. *The butterflies of Britain and Ireland*. London: Dorling Kindersley.
- Unwin DM.** 1980. *Microclimate measurement for ecologists*. London: Academic Press.

- Unwin DM, Corbet SA. 1991. *Insects, plants and microclimate*. Slough: The Richmond Publishing Co. Ltd.
- Vaissiere BE, Vinson SB. 1994. Pollen morphology and its effect on pollen collection by honey bees, *Apis mellifera* L. (Hymenoptera, Apidae), with special reference to upland cotton, *Gossypium hirsutum* (Malvaceae). *Grana* 33: 128–138.
- Vickery M. 1991. National garden butterfly survey. 1990 report—part 2. *Butterfly Conservation News* 48: 26–30.
- Vogel S. 1998. Remarkable nectaries: structure, ecology, organo-phyletic perspectives. III. Nectar ducts. *Flora* 193: 113–131.
- Walters M. 1993. *Wild and garden plants*. London: HarperCollins.
- Weberling F. 1989. *Morphology of flowers and inflorescences*. Cambridge: Cambridge University Press.
- Westerbergh A, Saura A. 1994. Gene flow and pollinator behaviour in *Silene dioica* populations. *Oikos* 71: 215–224.
- Westrich P. 1989. *Die Wildbienen Baden-Württembergs*. Stuttgart: Ulmer.
- Westrich P. 1996. Habitat requirements of central European bees and the problem of partial habitats. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH, eds. *The conservation of bees*. London: Academic Press, 2–16.
- Williams CS. 1997. *Foraging ecology of nectar-collecting bumblebees and honeybees*. PhD Thesis, University of Cambridge, UK.
- Williams PH. 1982. The distribution and decline of British bumblebees. *Journal of Apicultural Research* 21: 236–245.
- Williams PH. 1985. *On the distribution of bumble bees (Hymenoptera, Apidae) with particular regard to patterns within the British Isles*. PhD Thesis, University of Cambridge, UK.
- Williams PH. 1986. Environmental change and the distribution of British bumble-bees (*Bombus* Latr.). *Bee World* 67: 50–61.