Oecologia (1990) 83:191–196

*Oecologia*

# Pollen limitation and distance-dependent fecundity in females of the clonal gynodioecious herb *Glechoma hederacea* (Lamiaceae)

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Received November 8, 1989 / Accepted January 25, 1990

**Summary.** Pollen movement is often restricted in natural populations, and insufficient pollination is a potential constraint on sexual reproduction in outcrossing species. Seed-set should decrease with increased distance from the pollen source in outcrossing plants. This prediction was tested using females of the clonal, gynodioecious herb *Glechoma hederacea* in three natural populations. In controlled pollinations, both hermaphrodites and females had similar high percentages of fruit-set and seed-set. In a natural population where a female clone was isolated from the nearest hermaphroditic clone by c. 100 m, fruit-set was low (1%). In another population where hemaphroditic clones were rare and female clones had a patchy distribution, fruit- and seed-set in females were pollen-limited and decreased with increased distance from the nearest pollen source. The estimated mean pollen dispersal distance was 5.9 m when calculated on fruit-set and 5.3 m when calculated on seed-set. The most frequent pollinators were bumblebees. The mean and median distances moved by pollinators between ramets were 0.13 m and 0.05 m. In a third population where female clones were isolated from the nearest hermaphrodites by more than 200 m, fruit-set was 0%. After introduction of 16 hermaphroditic ramets in the center of the female clone, fruit-set varied between 0% and 100% in individual female ramets. Fruit-set decreased with increased distance from the pollen source. The mean and median pollen movement distances were 1.06 m and 0.54 m.

**Key words:** *Glechoma* – Clonal plant – Gynodioecy – Pollen flow

Clonal growth is widespread among plants, with some clones reaching enormous sizes (Harberd 1967). In clonal plants flowers become increasingly surrounded by flowers of the same individual as clone size increases (Handel 1985). Most movements by pollinators in natural populations are between very near neighbors (Levin and Kerster 1974). With increased flower density on an individual, geitonogamous pollination increases (Bateman 1956; Arroyo 1976; Handel 1985; Hessing 1988) and a negative correlation between fecundity per flower and plant size, attributed to insufficient out-pollination, has been reported for self-incompatible species (Carpenter 1976; Willson et al. 1979; Andersson 1988). Insufficient pollination could therefore be a special problem to the females of a gynodioecious species with extensive clonal growth. Gynodioecious species are often insect-pollinated, and restrictions in pollen production and dispersal could therefore play a part in determining the fecundity of the females, since they must outcross (Lewis 1941; Lloyd 1974). We test the prediction that the fecundity of the females is pollen limited in the gynodioecious herb *Glechoma hederacea,* a widespread perennial weed. Patches of unisexual ramets ranging from a few $dm^2$ to hundreds of $m^2$ in size, probably consisting of individual clones (M. Widén unpubl.), occur in southern Sweden. We examine fecundity in female clones of different distances from hermaphrodite clones.

In this paper we also introduce a novel method to measure movements of pollen grains in natural populations. We have used the experimental introduction of hermaphrodites into an isolated female clone to study the distance that pollen travels and actually achieves fertilization and produces mature seeds in a natural population. As far as we know this is the first study to use this approach to measure gene flow. This is a profitable method, easy to use in undistributed natural populations as well as in experimental populations of dioecious and gynodioecious species. Although the number of dioecious and gynodioecious species are small (cf. Godley 1979; Bawa 1980), our method has obvious advantages over other methods for species in which it can be used.

## Material and methods

### *The species and the study sites*

*Glechoma hederacea* (Lamiaceae) is a perennial herb bearing flowers on erect or ascending stems from May to early July in southern

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**Table 1.** Population characteristics of three natural populations of *Glechoma hederacea* in Skåne, Southern Sweden

| Site | Latitude (°N) | Longitude (°E) | Sex ratio | Area ($m^2$) | Minimum distance to adjacent hermaphroditic population (m) |
|---|---|---|---|---|---|
| Vrams-Gunnarstorp | 56°08′ | 12°58′ | >25 female clones 4 hermaphrodites | 3000 | 250 |
| Billebjär | 55°41′ | 13°19′ | Only female ramets | 50 | 200 |
| Fredriksdal | 56°04′ | 12°43′ | Only female ramets | 50 | 110 |

Sweden. The flowers are arranged in whorls with acropetal development but with much overlap between whorls. After flowering, the vegetative growth of the upright ramet continues, and eventually the whole branch bend down becoming horizontal (Slade and Hutchings 1987). Hermaphroditic flowers are protrandrous and self-compatible (M. Widén unpubl. and this paper, but see Gill 1979). Flowers of females usually lack any sign of stamens and are smaller than hermaphroditic flowers. The differences between female and hermaphroditic clones are usually distinct, but rarely the functional females possess shriveled anthers. Each flower produces up to four seeds (=nutlets). The calyx bends down at fruit maturation and the seeds are passively dropped. Ovaries that develop into nutlets leave distinct scars at the bottom of the calyx, making it easy to record fruit- and seed-set even after dispersal. Individuals spread vegetatively by horizontal stolons except after flowering when the tips of the vertical stems bend down and become vertical stolons (cf. Slade and Hutchings 1987). In cultivation without competition, stolons can spread several meters during one growing season (personal observation).

This study was based on the analysis of fecundity in three natural populations of *G. hederacea* in the region of western Skåne, in southern Sweden (Table 1). At Vrams-Gunnarstrop, a predominantly female population of *G. hederacea* has become established on a deposition of bark from a sawmill. Four hermaphroditic clones of *G. hederacea* cover only a fraction of the area of female clones. The populations at Billebjär (at the edge of an open forest) and Fredriksdal (a roadside at the botanical garden, Helsingborg) contain only female ramets (probably one clone at each site).

### *Fecundity in natural populations*

In order to establish the fecundity level in the study populations without experimental manipulations, natural seed-set was measured at Vrams-Gunnarstorp in 1986, at Billebjär in 1978 and at Fredriksdal in 1987 and 1988. At Vrams-Gunnarstorp all hermaphroditic and female clones were mapped, and at the peak of fruit-set in early July, ten random samples from each hermaphroditic clone and from 15 randomly sampled female clones were taken except from the small clones where all ramets were sampled. Each sample consisted of all ramets within a 1 $dm^2$ area. Stolon connections between ramets in a clone older than one year are difficult to trace. We therefore considered each group of ramets separated from the nearest group of ramet by >1 m to be a clone. This probably overestimated the number of female clones. At Billebjär all ramets were counted and examined in situ for fruit-set. Fredriksdal was examined in situ for fruit-set twice during the early part of the fruiting period in 1987, and 10 ramets were randomly sampled in 1988.

### *Pollination and fecundity*

To test for pollen limitation we hand-pollinated ramets of two female clones and of two hermaphroditic clones sampled at Vrams-Gunnarstorp in early May 1987. The ramets were cultivated outdoors in insect-free cages at Fredriksdal botanical garden in soil taken from the site; the soil was fertilized once just after transplantation. Flowers on the female ramets were hand-pollinated using a mixed pollen load from the two hermaphrodites, and the hermaphroditic flowers were artificially self-pollinated.

In treatment 1 we examined the fecundity level when all flowers are pollinated; here all flowers in a ramet were hand-pollinated as soon as the stigma became receptive. In treatment 2 we hand-pollinated half of the flowers in each ramet; all flowers in the axil of one of the opposite bracts at each inflorescence-whorl were hand-pollinated and the flowers at the other bract were used as controls of automatic self-pollination. We hypothesized that if there are any resource constraints on fecundity this would give rise to lower seed set per flower in treatment 1. Seed-set was recorded when no more flowers developed in a ramet and when the last hand-pollinated flower had started to develop seeds.

### *Pollen flow distances*

Billebjär was used for the experimental study of gene flow. Just before anthesis in early May 1979, 16 ramets of a hermaphroditic clone were transplanted from another population (at Lomma, situated 15 km west of Billebjär) to the centre of the female clone. The transplants covered an area of about 2 $dm^2$. In late June all hermaphroditic and female ramets were sampled, fruit-set per ramet was recorded, and that of female ramets was related to distance from the pollen source. In order to examine fruit-set under optimal conditions random samples of ramets were transplanted from Billebjär and from Lomma to the experimental garden at the University of Lund 1978. Individual ramets were grown in randomly located pots ($\approx 25$ pots per $m^2$) for one season and fruit-set was measured after open flowering in 1979.

To estimate the potential pollen flow distances we followed 20 flower visitors 21 May 1985 at Vrams-Gunnarstorp (just before peak flowering). The flight distances of the 20 pollinators between ramets were marked with numbered tags. In order not to disturb the behaviour of the pollinators, flight distances <10 cm were not marked, only estimated. We used the spatial distribution of hermaphrodic clones and seed-set in female clones at Vrams-Gunnarstorp to estimate realized gene flow distances by pollen.

## Results

### *Fecundity in natural populations*

Fruit-set in the natural population at Vrams-Gunnarstorp was lower in females than in hermaphrodites (Table 2). It varied from 52.2% to 69.2% (mean = 59.2%) in the four hermaphroditic clones and from 0% to 51.5% (mean = 10.5%) in the 15 female clones.

The isolated female ramets at Billebjär (N = 1122) produced no fruits in 1978. After transplantation of the hermaphrodites in 1979, fruit-set in female ramets was 5.5% (S.D. = ±13.65, $N = 1156$) and in hermaphroditic ramets 56.8 (S.D. = ±23.81, $N = 16$, $P < 0.001$, Mann-Whitney U test). Fruit-set after open flowering in culti-

**Table 2.** Reproductive characters of the females and hermaphrodites of *G. hederacea* at Vrams-Gunnarstorp in 1986. The differences in fruit set among clones were significant at $P<0.01$ and $P<0.001$ for hermaphrodites and females respectively (Kruskal-Wallis). $P$ referes to differences between hermaphrodites and females, ns = non-significant, ** $P<0.01$, *** $P<0.001$ (Mann-Whitney U test)

| Trait | Hermaphrodites | Females | $P$ |
|---|---|---|---|
| No. of clones | 4 | 15 | |
| No. of ramets | 127 | 560 | |
| No. of flowers per ramet (mean and S.D.) | 11.9 ± 6.76 | 12.0 ± 7.04 | ns |
| Fruit-set (%) (mean and S.D.) | 59.2 ± 21.59 | 10.5 ± 17.53 | *** |
| Range of fruit-set (%) among clones | 52.2–69.2 | 0–51.5 | |
| Seed-set % (mean and S.D.) | 43.6 ± 19.59 | 6.1 ± 11.95 | *** |
| No. of ramets per $dm^2$ (mean and S.D.) | 3.8 ± 1.82 | 5.4 ± 3.0 | ** |

vation at the University of Lund 1979 was higher among the hermaphroditic ramets (87.5% ± 19.43, $N=7$) derived from the Lomma site than the females (68.0% ± 16.10, $N=8$) derived from Billebjär ($P=0.015$, Mann-Whitney U test).

No fruit-set could be detected in the isolated female clone at Fredriksdal during the early part of the fruiting period 1987. Unfortunately no ramets were sampled because the road side was mowed off by accident just at the peak of fruiting. In 1988 two fruits were found on one of the ten ramets (fruit-set = 1.0%, seed-set per flower = 0.38%).

### *Pollination limitation*

Fruit-set and seed-set per fruit of hand-pollinated flowers in cultivation were high and approached 100% in both female and hermaphroditic clones. Flowers used as controls (not hand-pollinated flowers at each inflorescence-whorl in treatment 2) did not set fruit. Fruit-set did not differ between hermaphroditic and female clones but seed-set per fruit was significantly higher (Mann-Whitney U test, $P=0.013$) in female clones (Table 3). There is a non-significant trend that fecundity per flower is greatest in treatment 2, where half of the flowers at each inflorescence-whorl were pollinated (Mann-Whitney U test, $P=0.09$). Thus, there could be resource constraints on seed-set, resulting in some compensation growth of the inflorescence as suggested by the significant increase in number of flowers per ramet when only half of the flowers are pollinated ($P=0.004$).

### *Pollinator flight distances*

The main visitors were bumblebee queens (Table 4), but occasionally honeybees, syrphids, beetles, and ants were observed (personal observation). Visitors were frequent early in the flowering season but less so later in early to middle June. The reward offered by the plant is nectar, and in hermaphroditic flowers pollen as well (no pollen collecting visitors were, however, observed at Vrams-Gunnarstorp). The bumblebees usually visited all fresh flowers on a ramet before moving to the next. Because hermaphrodites were rare at Vrams-Gunnarstorp, only one of the 20 flower visitors was observed to move between the two clone types. There were few other herbs than *G. hederacea* flowering at the site, and only one bumblebee was observed to switch flower species (from *G. hederacea* to *Taraxacum vulgare*). The mean and median distances moved by pollinators between ramets were 0.13 m (SD = 0.467) and 0.05 m. The shape of the pollinator flight distribution (Fig. 1) is leptokurtic ($g_2=148.8$; $P<0.001$).

### *Distance dependent fecundity*

Fruit-set in female clones on unmanipulated plants depended on distance from nearest pollen source. Female

**Table 3.** Fruit-set and seed-set (mean and S.D.) after hand-pollination in cultivated female (F) and hermaphroditic (H) clones of *G. hederacea* derived from Vrams-Gunnarstorp in 1987. In treatment 1 (Treat.) all flowers per ramet were hand-pollinated, and in treatment 2 only half of the flowers at each inflorescence whorl were hand-pollinated; the un-hand-pollinated flowers were used as controls. Fruit-set refers to the percentage of hand-pollinated flowers that set fruit; no control flowers in treatment 2 set fruit. Seed-set was calculated assuming a maximum of four seeds per fruit. The differences in number of flowers and fruits per ramet, and in seed-set (treatment 1 + treatment 2) are significant among the four clones ($P<0.001$, Kruskal-Wallis), but not in fruit-set ($P=0.121$). The difference in seed-set between hermaphroditic and female clones is significant ($P=0.013$, Mann-Whitney U test), but not in the other characters ($P>0.09$)

| Clone | Type | Treat. | Flowers per ramet | Fruits per ramet | Fruit-set (%) | Seed-set per fruit (%) | Number of ramets |
|---|---|---|---|---|---|---|---|
| 1 | F | 1 | 10.2 ± 7.18 | 9.1 ± 6.47 | 89.0 | 90.9 | 22 |
| | | 2 | 20.4 ± 8.7 | 9.9 ± 4.35 | 94.8 | 94.7 | 15 |
| 9 | F | 1 | 11.4 ± 7.92 | 11.1 ± 8.11 | 96.1 | 88.5 | 14 |
| | | 2 | 12.2 ± 5.25 | 6.5 ± 3.36 | 96.1 | 90.4 | 17 |
| 10 | H | 1 | 15.7 ± 12.37 | 15.2 ± 12.01 | 97.1 | 82.7 | 16 |
| | | 2 | 19.7 ± 9.44 | 10.2 ± 5.18 | 99.5 | 86.2 | 14 |
| 19 | H | 1 | 7.1 ± 5.23 | 6.8 ± 5.33 | 94.9 | 84.9 | 20 |
| | | 2 | 5.4 ± 2.8 | 2.7 ± 1.27 | 100.0 | 83.2 | 11 |

**Table 4.** Pollinator flights for groups of visitors on *G. hederacea* at Vrams-Gunnarstorp on 21 May 1985, 9.00–12.00. The bumblebees (*Bombus*) were not captured, and some individuals could not be determined to species with certainty; therefor *B. hortorum* and *B. subterraneus* as well as *B. lucorum* and *B. terrestris* have not been separated in the table. Number of flights are movements between ramets

| Type of pollinator | No. of visitors | No. of flights | Mean (±S.D.) flight distance (cm) | Median flight distance (cm) | Maximum flight distance (cm) |
|---|---|---|---|---|---|
| *Apis mellifera* | 2 | 43 | 14.4±22.04 | 5.0 | 115.0 |
| *B. hortorum/subterraneus* | 1 | 10 | 28.7±26.56 | 22.5 | 90.0 |
| *B. lapidarius* | 2 | 155 | 8.2±10.82 | 5.0 | 95.0 |
| *B. lucorum/terrestris* | 3 | 272 | 11.2±55.57 | 3.0 | 805.0 |
| *B. pascuorum* | 10 | 319 | 17.1±52.7 | 5.0 | 603.0 |
| *B. pratorum* | 1 | 12 | 10.3±6.34 | 9.0 | 23.0 |
| *Syrphidae* | 1 | 7 | 21.4±12.70 | 26.0 | 35.0 |

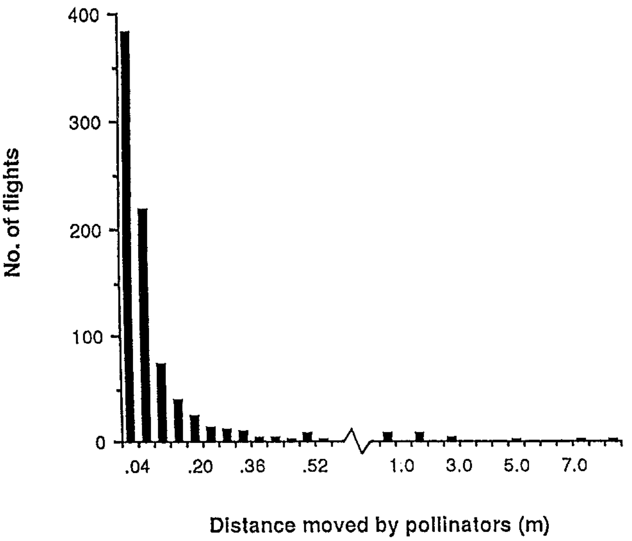

**Fig. 1.** Pollinator flight distances of 20 visitors on *G. hederacea* at Vrams-Gunnarstorp on 21 May 1985 (cf. Table 4). Note change of scale between 52 and 100 cm

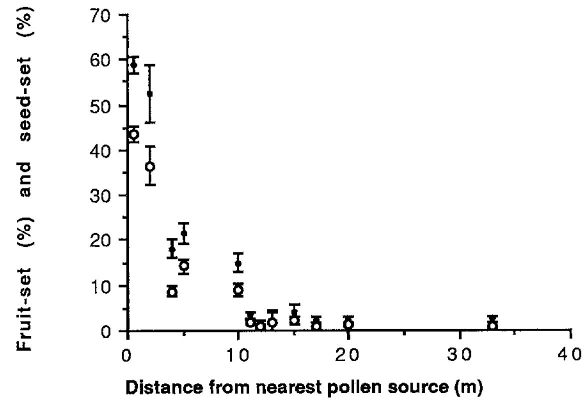

**Fig. 2.** Average percentage fruit- and seed-set (±SE) of ramets in *G. hederacea* at different distances from the nearest pollen source at Vrams-Gunnarstorp in 1986 (the distances were measured from the middle of clones). Fruit- and seed-set at a distance near to 0 m refer to hermaphrodites, the rest to females. ● fruit-set; ○ seed-set

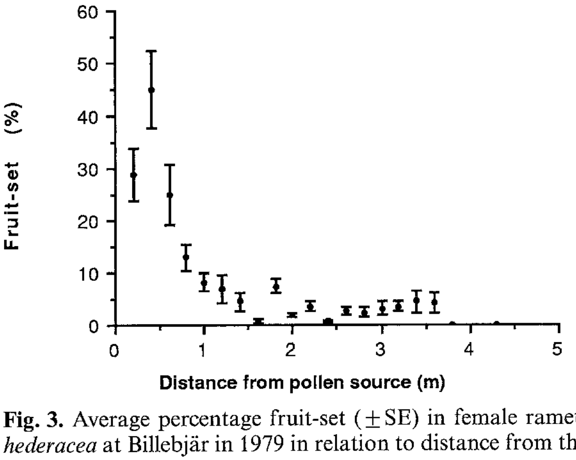

**Fig. 3.** Average percentage fruit-set (±SE) in female ramets of *G. hederacea* at Billebjär in 1979 in relation to distance from the introduced pollen source. $N=1154$

fruit-set and distance from the nearest hermaphroditic clone were negatively correlated (Spearman $r=-0.60$, $P<0.01$) at Vrams-Gunnarstorp (Fig. 2). Fruit-set (52%) in the most fecund female clone did not differ significantly from fruit-set (54%) in the nearest (2 m) hermaphroditic clone. Fruit-set decreased markedly at longer distances and was never more than 4% at a distance $\geq 11$ m from the nearest pollen source (Fig. 2). The mean pollen dispersal distance can be calculated if we assume that pollen travel from the nearest hermaphroditic clone, and that each pollen grain gives rise to fertilization; being 5.9 m when calculated on fruit-set and 5.3 m when calculated on seed-set.

Fruit-set (%) of female ramets at Billebjär showed a significant negative correlation (Fig. 3) with distance from the transplanted hermaphrodites (Spearman $r=-0.28$, $P>0.001$). Fruit-set for female ramets was never as high as for introduced hermaphrodites, and it was never more than 8% at 1.0 m and longer distances when averaged for each distance. The shape of the pollen flow distribution is leptokurtic ($g_2=0.97$; $P<0.02$) with mean and median distances of 1.06 m and 0.54 m, respectively.

The number of fruits (%) on female ramets show a tendency to have two maxima at Billebjär, one at a distance of 0.4 m from the pollen source and the other at a distance of 1.8 m (Fig. 3). The second distance corresponds to the most dense patches of female ramets, which could indicate density dependent fruit-set. However, no significant correlation between fruit set and flower density (per $dm^2$) was found at this sites (females; $r=0.06$, $P>0.05$), nor at Vrams-Gunnarstorp (females; $r=-0.14$, $P>0.05$, hermaphrodites; $r=0.11$, $P>0.05$).

## Discussion

Hermaphroditic flowers of *G. hederacea* are self-compatible; when artificially selfed they showed nearly full seed-set. However, they are not automatically selfed (cf. Gill 1979); an insect visit is needed for pollination. Fruit- and seed-set of females of *G. hederacea,* in the natural populations that we examined in Sweden, are pollen-limited. The isolated female clone at Billebjär did not set fruit in 1977–78, and fruit-set decreased with increased distance from pollen sources both in the transplant experiment at Billebjär and in the natural population at Vrams-Gunnarstorp. There were no indications of fruit-set in the female clone at Fredriksdal in 1987 and only 1% fruit-set in 1988. Low fruit- and seed-set of females in *G. hederacea* are rather common in natural populations in southern Sweden, and there are also indications of pollen-limited seed-set in hermaphrodites (M. Widén, unpublished work).

The only indication that fecundity in *G. hederacea* could depend on resource allocation come from the artificially hand-pollinated ramets. The ramets developed more flowers when only half of the flowers at each inflorescence-whorl were pollinated, and the fecundity per flower increased slightly compared to the results when all flowers were pollinated. However, the differences in fecundity between ramets where all flowers were pollinated and ramets where flowers only on one side of each whorl were pollinated are very small compared to the differences between female and hermaphrodites in the natural populations used in the present study, indicating that resource constraints are of minor importance for fecundity in natural populations of *G. hederacea.*

Pollen limitation of seed-set in natural populations has been documented in several studies (for a review see Rathcke 1983). We conclude that seed-set in females of *G. hederacea* is significantly reduced when distance from hermaphrodites increases. Effects of this type were found by Wyatt and Hellwig (1979) in a study of spatial pattern and fecundity in distylous populations of *Houstonia caerulea.* On the other hand, Barrett and Thomson (1982) found no distance-effect on fecundity in dioecious *Aralia nudicaulis,* probably due to a male-biased flower ratio, nor did Hicks et al. (1985) in the distylous *Mitchella repens.* A distance-dependent fecundity would have particularly severe effects on seed fitness in clonal species occurring in large unisexual patches, such as *G. hederacea.*

Our results support the view of restricted gene flow both within and between populations. The median pollen flow distance was only 0.5 m at Billebjär. Seed-set in female 9, situated about 35 m from the nearest pollen source at Vrams-Gunnarstorp, was only 0.64%, which should be compared with the average seed-set in hermaphrodites of 45%. No gene flow occurred at an interpopulation distance of about 200 m at Billebjär, and we had no indication of gene flow at an interpopulation distance of 100 m at Fredriksdal in 1987. In 1988, however, there was interpopulation gene flow at Fredriksdal, indicated by the 0.4% seed set. The contemporary view is that gene flow, measured by direct observations of potential or actual movements of genes, is highly restricted both within populations and between populations (Ehrlich and Raven 1969; Levin and Kerster 1974; Levin 1981, 1984; but for indirect methods to measure gene flow, see Slatkin 1985; Govindaraju 1988). Recent studies, however, have found unexpectedly high levels of gene flow. Meagher (1986) found that long-distance pollination within a population of the dioecious herb, *Chamaelirium luteum,* was much higher than expected on the basis of previous studies. Ellstrand and Marshall (1985) estimated the rate of interpopulation gene flow by pollen per generation in the annual, self-incompatible weed, *Raphanus sativus,* to be as high as 9%.

Much has been published in recent years about the evolutionary advantages of females in a population of hermaphrodites, and the conditions required for the maintenance of gynodioecy (Charlesworth and Charlesworth 1978). Hemaphroditic plants transmit genes through gametes of both sexes, while females contribute only through seeds. Models for maintenance of females in gynodioecious populations make several predictions involving increased fecundity of females (Lewis 1941), superiority of outcrossed progeny (Valdeyron et al. 1973), and differential adult survival (Van Damme and Van Delden 1984). These predictions have been confirmed in some studies (Krohne et al. 1980; van Damme and van Delden 1984). In *Glechoma,* however, there is no indication of increased female fecundity. On the contrary, other mechanisms must compensate for the low fecundity of females observed in natural populations (data in this study, personal observations). Here we can only briefly discuss the effect of outcrossing and the possibility of differential adult survival, and we will return to a more comprehensive discussion of the maintenance of females in *G. hederacea* in a future paper.

The restricted pollen flow influences the mating type of hermaphroditic clones (cf. Handel 1985). Fruit-set in the transplanted, hermaphroditic clone at Billebjär (57%) was similar to that in hermaphrodites at Vrams-Gunnarstorp (59%). This may suggest that hermaphroditic fruit-set at Vrams-Gunnarstorp is due primarily to selfing, which is consistent with the pattern of pollinator foraging and the spatial distribution of hermaphrodites at this site. However, we have evidence from the hand-pollination experiment that selfing does not reduce fruit-set in *G. hederacea,* and we interpret the fruit-set level of hermaphrodites in natural populations as primarily an effect of pollinator limitation. Artificial self-pollination, on the other hand, gave significantly lower seed-set per fruit in hermaphrodites than in the artificially cross-pollinated females (seed-set in artificially cross-pollinated hermaphrodites and females did not differ in an unpublished experiment). If hermaphroditic flowers are usually selfed, the obligate outcrossed progenies of female clones, may have some advantage over the progeny of hermaphroditic clones, which could compensate for the low fecundity of females.

If there is a trade-off between clonal growth and allocation to female sexual reproduction (cf. Menges 1987), the low pollination level could be compensated for by clonal growth in females. Slade and Hutchings (1987) have documented great phenotypic plasticity of growth which may enable *G. hederacea* to occupy and exploit favorable sites. If females divert their resources to clonal growth instead of seed production, they may gain some advantage over the hermaphrodites and thus escape from extinction. However, Slade and Hutchings (1989) found lower flower production and shorter half-lives for female clones than for hermaphroditic clones at two sites in England. They postulated that, in the absence of greater flowering and seed-set, self-incompatibility is crucial for the maintenance of clones of both sexes in natural populations. In southern Sweden, however, *G. hederacea* is self-compatible (M. Widén, unpublished). This raises the question if current models for maintenance of females in gynodioecious populations are valid for *G. hederacea* (cf. Gouyon and Couvet 1987).

*Acknowledgements.* We thank R. Bertin, D.G. Lloyd, L. Svensson, R. Wyatt and anonymous referees for valuable comments on earlier drafts of the manuscript. We also thank C. Weimark for assistance with the field work, and B.G. Svensson and O. Jennersten for identification of the bumblebees.

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