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Reproductive biology of *Petrocoptis grandiflora* ROTHM. *(Caryophyllaceae)*, a species endemic to Northwest Iberian Peninsula

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Summary

Various aspects of the reproductive biology of *Petrocoptis grandiflora* ROTHM. *(Caryophyllaceae)* were studied, including fruit- and seed-set in response to pollination from different sources, pollen/ovule ratio, floral duration, pollinator spectrum and behaviour (including nectar robbery), and nectar characteristics and production. Fruit-set and seed production were significantly lower in autogamous and geitonogamous crosses. The pollen/ovule index value obtained is consistent with the species' xenogamous character. *P. grandiflora* is pollinated mainly by long-tongued bees *(Anthophoridae)* which characteristically demand a high-sugar nectar. Diurnal patterns of pollinator activity and nectar presentation accord with those described for other species in the Iberian peninsula. Nectar robbery did not affect fruit-set levels.

Key words: nectar, pollination, fruit-set, *Petrocoptis, Caryophyllaceae*

Introduction

Literature contains a number of taxonomic and biogeographical studies of the genus *Petrocoptis* (FERNANDEZ GONZALEZ 1984, FERNANDEZ ARECES 1989, FERNANDEZ GONZALEZ et al. 1988, FERNANDEZ CASAS 1973 and MONTSERRAT RECODER 1988). Relatively few studies have centred on the species' reproductive biology: GUITIAN & SANCHEZ (1992) locked at phenology and reproductive success, GUITIAN et al. (1992) at pollination and the effects of nectar robbery, and GARCIA et al. (1992) at floral biology.

Here, continued studies are reported of certain basic aspects of the reproductive biology of *Petrocoptis grandiflora (Caryophyllaceae)*, a species endemic to the northwest Iberian peninsula, with a highly restricted range. We have examined the effects of pollen source (same flower, same plant or different plant) on fruit-set and seed number, and have monitored patterns of nectar production and pollinator activity.

The plant

Petrocoptis grandiflora ROTHMALER is a perennial herb of 15–30 cm with opposite leaves and pentameric flowers arranged in dichasia. The purple calyx is about 10–14 mm in length, and the corolla comprises 5 bright purple petals. The flower is protandric and has 10 stamens and 5 styles. The fruit is a unilocular capsule and the seeds, of about 1 mm diameter, are smooth, black and glossy, with the strophiole composed of hairs.

The species grows almost exclusively in limestone crevices, overhangs and ledges. It occurs in small scattered populations on dolomite outcrops in the Montes Aquilianos and surrounding areas of the El Bierzo region of northwest Spain. Its total range barely exceeds 100 km^2.

Flowering commences at the beginning of March and ends in mid June. The first mature fruits appear in June. By the end of July all capsules have undergone dehiscence (GUITIAN & SANCHEZ 1992).

Study area

The study was carried out in El Bierzo (León, northwest Spain), a region surrounded on all sides by mountains, at three locations within an area of 10 km^2: Vilardesilva (650 m a.s.l.), Cobas and Estrecho (both 450 m a.s.l.). The area is characterized by a mosaic of habitats including cultivated land and small groups of houses, limestone outcrops, holm oak woodland (with *Quercus rotundifolia, Arbutus unedo* and *Quercus suber*) and Mediterranean scrub communities dominated (on siliceous soils) by *Cistus ladanifer,* or (on calciferous soils) by *Cytisus* and spiny Rosaceas. The natural vegetation of the region consists of holm oak woodland and various types of scrub community which develop following woodland disturbance (Izco et al. 1989). The populations studied were all located on limestone rockfaces.

Climate is (according to RIVAS-MARTINEZ et al. 1984) subhumid Mediterranean with a Central European tendency. Mean annual temperature in Villafranca del Bierzo (12 km from the study area and of similar altitude) is 12.3 °C. Annual precipitation is 901 mm.

Methods

Pollen source

The effect on fruit and seed production of varying the pollen source was studied using four experimental treatments as follows.

a) Reproduction in the absence of insects: bagging with mosquito netting to prevent access by insects (number of flowers, n = 42).

b) Autogamy: pollination with pollen from the same flower followed by bagging (n = 49).

c) Geitonogamy: emasculation, pollination with pollen from a different flower of the same plant, followed by bagging (n = 20).

d) Xenogamy: emasculation, pollination with pollen from another plant, followed by bagging (n = 21).

Simultaneously, 4 plants which otherwise received no treatment were monitored as controls (n = 100).

In all cases, once the necessary time had elapsed, whether or not fruit-set occurred was recorded for each flower, and if so the mean number of seeds per capsule. Mean fruit-set frequency, and overall mean number of seeds per capsule, was then calculated for each treatment.

Pollen/Ovule (P:O) ratio

Number of pollen grains was counted following preparation by the microacetolysis method (AVETISSIAN 1975), always using flower buds or closed anthers to avoid contamination. A total of 20 stamens were examined, all from different flowers. Number of ovules (in the ovaries of the flowers used for pollen grain counting) was determined with the aid of a magnifying glass.

Floral duration

A total of 106 flowers, marked before opening, were monitored daily. To determine whether floral duration varied over the flowering period, the flowers were divided in three groups corresponding to the early, mid and late flowering period, and floral duration in the three groups was compared.

Insect activity

Variations in pollinator activity throughout the day were assessed by censuses at 0800, 1100, 1400 and 1700 hours Greenwich Mean Time (GMT), recording a) the number of visits to each plant, b) whether the visitor behaved as a pollinator or a nectar robber, c) the number of flowers visited in the course of each plant visit, and d) (in the case of the two most important pollinator species) duration of each flower visit.

Daily nectar production

A total of 64 flowers were bagged (in all cases on a sunny day), and after 24 h the accumulated nectar was extracted and measured with a capillary micropipette; sugar concentration was immediately estimated with a portable refractometer. The volume and concentration data thus obtained were used to calculate the amount of sugar produced by the flower, by multiplying the nectar volume by its sugar concentration (expressed as a w/w percentage), as per PRYS-JONES & CORBET (1987).

Diurnal variation in available nectar

Available nectar was measured in 277 flowers at the same times as the insect censuses, with simultaneous recording of temperature and relative humidity.

Variations in nectar production with flower age

Available nectar was measured in flowers aged 0, 1, 2, 3, 4 and 5 days, defining day 0 as the day on which the flower opened. Flowers were bagged 24 h before they were due to be examined.

Nectar robbing

A total of 1748 flowers from the 3 populations were monitored during flowering and fruit-set, recording whether or not each flower was robbed, and whether or not it produced fruit. Field determination of whether a flower has been robbed or not is straightforward, since the robber leaves a clearly visible incision in the calyx.

Data analysis

The chi-squared test was used to compare fruit-set and nectar robbery data. Numbers of seeds per capsule and floral duration data were compared using the Kruskal-Wallis test. Nectar volume data were compared using ANOVA. Possible correlations between variables were assessed by calculation of the Spearman correlation coefficient. In all cases $p < 0.05$ was taken to be significant.

Results

Reproductive systems

The mean value obtained for the P:O index was 641.4 ± 89.6 (n = 20). Fruit-set occurred in 55 % of control plants (n = 100) and mean number of seeds per capsule was 12.6 ± 4.4. Fruit-set in plants receiving the insect exclusion, autogamy and geitonogamy treatments (Table 1) differed significantly from control ($X^2 = 3.95$, df = 1, $p < 0.05$ for insect exclusion; $X^2 = 11.89$, df = 1, $p < 0.05$ for autogamy; $X^2 = 6.15$, df = 1, $p < 0.05$ for geitonogamy); there was no such difference from control in the case of xenogamy ($X^2 = 0.67$, df = 1, p = 0.41). Number of seeds per capsule differed significantly between the different treatments (H = 26.33, df = 4, $p < 0.05$). Differences were significant with respect to control in the case of all treatments except xenogamy (H = 0.02, df = 1, p = 0.88).

Table 1. Effect of pollen source on fruit-set and seed production.

Treatment	Fruit-set	No. of seeds/capsule
Insect exclusion	26.2 % (n = 42)	x ± sd. = 6.3 ± 3.3
Autogamy	12.2 % (n = 49)	x ± sd. = 4.3 ± 2.6
Geitonogamy	10.0 % (n = 20)	x ± sd. = 7.5 ± 6.3
Xenogamy	38.1 % (n = 21)	x ± sd. = 12.2 ± 6.4
Control	55.0 % (n = 100)	x ± sd. = 12.6 ± 4.4

Floral duration

Of the flowers monitored, the first to open did so on April 11 and the last on May 24. Mean floral duration was 3.9 ± 1.6 days (n = 106). As the flowering period progressed, floral duration decreased, as is apparent from comparison of the early-, mid- and late-flowering groups shown in Table 2 (H = 27.3, df = 2, $p < 0.05$).

Table 2. Floral duration of early-, mid- and late-opening flowers: Group 1 – anthesis occurring between 11. 4. 92 and 25. 4. 92; Group 2 – anthesis occurring between 26. 4. 92 and 9. 5. 92; Group 3 – anthesis occurring between 10. 5. 92 and 24. 5. 92.

	Floral duration (days) (x ± s.d.)	N
Group 1	5.1 ± 1.7	17
Group 2	4.3 ± 1.7	44
Group 3	3.0 ± 1.0	45

Pollination

The principal pollinator was the long-tongued bee *Anthophora acervorum* (68.1 % of recorded pollination visits), followed by the dipteran *Bombylius major* (20.4 %); the remaining species recorded can be regarded as sporadic pollinators (Table 3). Hymenopterans were the most numerous group, accounting for 69.4 % of all plant

Table 3. Observations of pollinators of *P. grandiflora*.

Pollinator	No. of recorded flower vists	Percentage of total
Hymenoptera		
**Anthophoridae*		
Anthophora acervorum	160	68.1 %
**Xylocopidae*		
Xylocopa violacea	3	1.3 %
Diptera		
**Bombyliidae*		
Bombylius major	48	20.4 %
Bombylius canescens	8	3.4 %
**Syrphidae*	3	1.3 %
Lepidoptera		
**Sphingidae*		
Macroglossum stellatarum	3	1.3 %
**Pieridae*	10	4.3 %

Table 4. Mean number of flowers visited by pollinators during each plant visit.

Taxon	No. of flower visited/plant (x ± sd)	N
A. acervorum	2.8 ± 3.6	161
B. major	1.6 ± 0.9	48
B. canescens	2.0 ± 1.1	8
Pieridae	1.3 ± 0.7	10
Syrphidae	1.0 ± 0.0	3
M. stellatarum	10.4 ± 6.0	26
X. violacea	2.7 ± 0.6	6

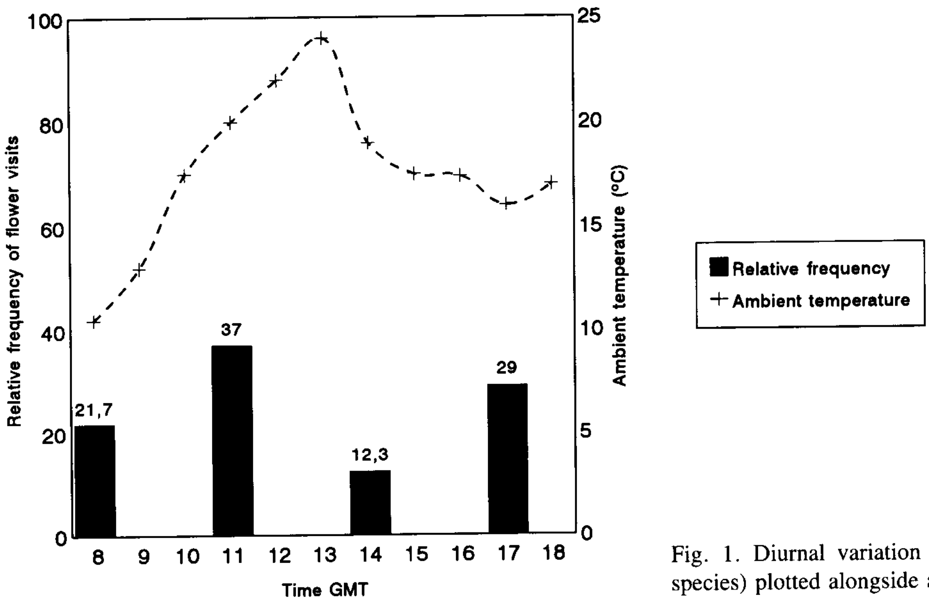

Fig. 1. Diurnal variation in frequency of pollinator visits (all species) plotted alongside ambient temperature.

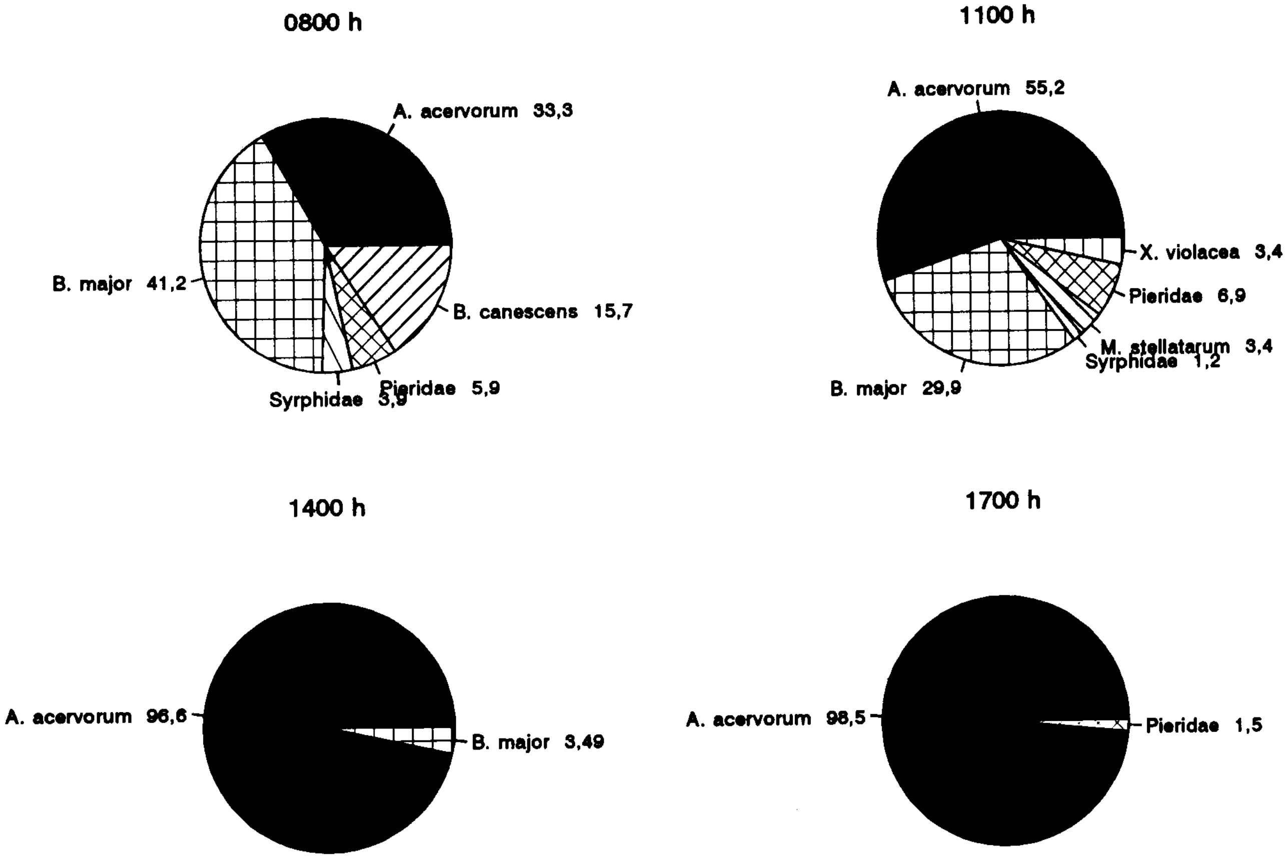

Fig. 2. Diurnal variation in relative frequency of pollinators.

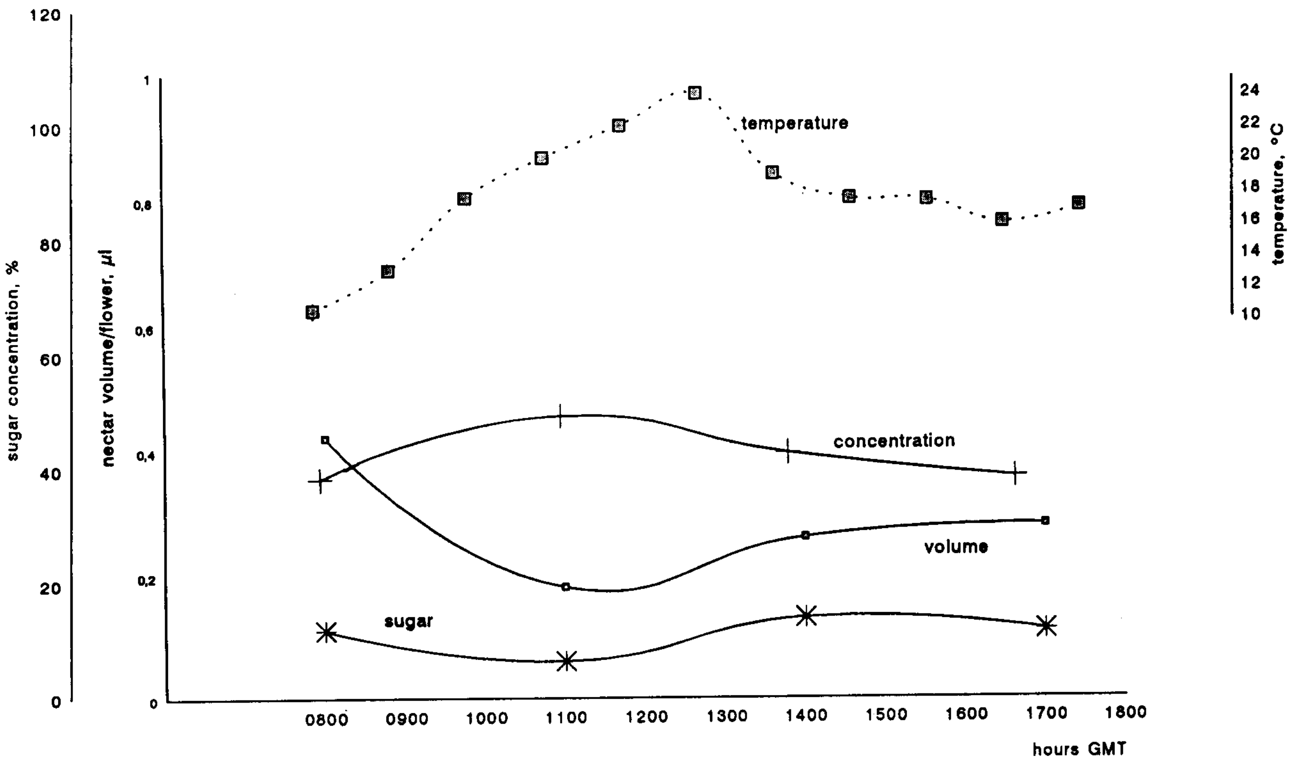

Fig. 3. Diurnal variation in available nectar volume and sugar concentration plotted alongside ambient temperature.

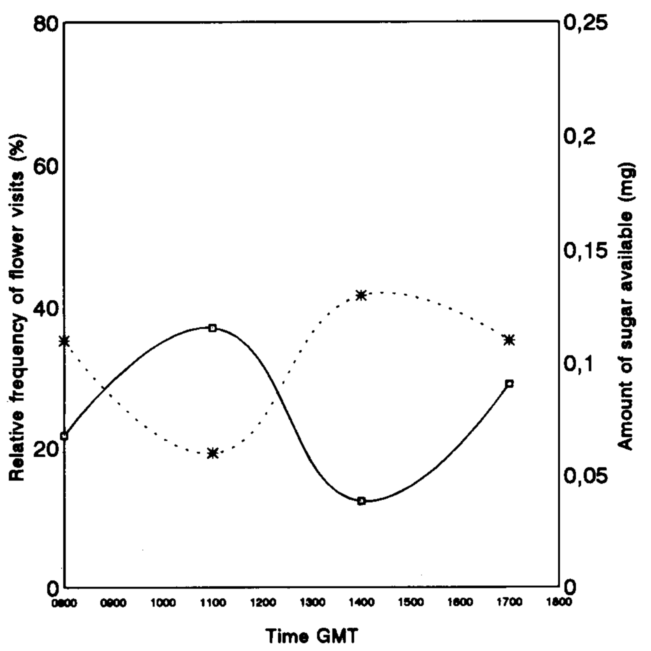

Fig. 4. Diurnal variation in amount of available sugar (dotted line) and pollinator visit frequency (unbroken line).

visits. Pollination visits occurred with maximum frequency at 1 100 h GMT (37 % of observations), and with minimum frequency at 1 400 h GMT (12.3 % of observations). On the days on which censuses were carried out, temperature increased until 1 300 h GMT and then began to drop (Fig. 1).

Although *A. acervorum* was the most frequent pollinator overall, *B. major* was the most active in the early morning (Fig. 2). The two species were active at ambient temperatures ranging from 10.5 °C to 29 °C, and only in a few isolated cases were other species observed outside this

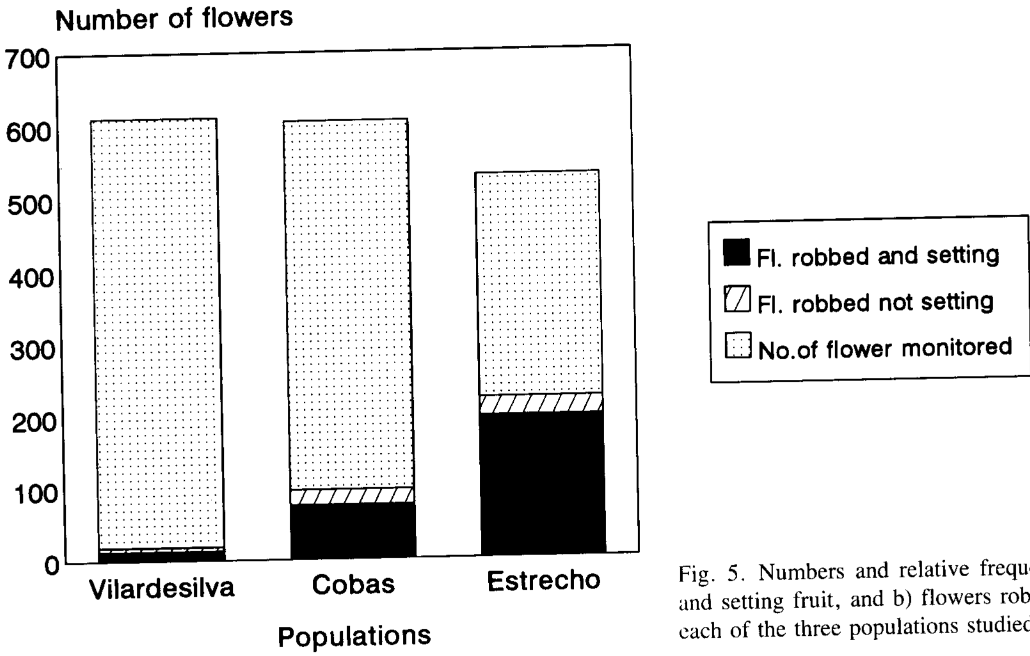

Fig. 5. Numbers and relative frequencies of a) flowers robbed and setting fruit, and b) flowers robbed and not setting fruit, in each of the three populations studied.

Table 5. Variation in availability and characteristics of *P. grandiflora* nectar with flower age (average values for one flower).

Day	Volume x ± sd (µl)	Sugar concentration x ± sd (% w/w)	Sugar content x ± sd (mg)	N
0	0	0	0	15
1	0.18 ± 0.12	41.6 ± 6.80	0.06 ± 0.04	11
2	0.31 ± 0.27	35.0 ± 3.65	0.10 ± 0.10	8
3	0.31 ± 0.18	35.53 ± 5.26	0.09 ± 0.06	15
4	0.73 ± 0.25	38.75 ± 6.58	0.24 ± 0.08	12
5	1.07 ± 0.54	32.17 ± 2.32	0.31 ± 0.17	6

Table 6. Percentages of flowers robbed and total fruit-set levels in the three *P. grandiflora* populations studied (% α = percentage of flowers robbed; % β = percentage of flowers setting fruit).

Population	% α	% β
Vilardesilva	(19) 3.10%	(328) 53.59%
Cobas	(97) 16.00%	(403) 66.50%
Estrecho	(223) 42.07%	(440) 83.01%
Total	(339) 19.39%	(1171) 66.99%

range. All visits were pollination visits except in the case of *Xylocopa violacea*, which robbed nectar. *A. acervorum* remained an average of 0.86 ± 0.34 s at each flower; this is significantly lower than *B. major* which remained an average of 4.57 ± 1.14 s ($H = 12.63$, $df = 1$, $p < 0.05$). However, there were no significant differences between the two principal pollinator species with respect to the number of flowers visited on each plant in the course of each visit ($H = 1.02$, $df = 1$, $p = 0.12$) (Table 4). It is interesting that *Macroglossum stellatarum*, which accounted for only 1.27% of total visits, visited a mean of 10.4 flowers per plant.

Nectar

The mean volume of nectar produced by the plant in 24 h was 0.5 ± 0.3 µl, and its mean sugar concentration was 41.5 ± 10.1% w/w. In both cases there was considerable between-flower variation. Analysis of variance shows that there are significant differences in the volume of nectar available at different times of day ($F = 3.13$, $df = 3$, $p < 0.05$), with greater availability in the early morning (0800 h GMT). Maximum concentration was reached at 1100 h GMT. There is a negative correlation between nectar volume and sugar concentration throughout the day ($r = -8.8$, $p < 0.17$). The increase in sugar concentration seems to be a result of the increase in ambient temperature (Fig. 3). When total amount of sugar is plotted against frequency of pollinator visits it can be seen that, in the case of all pollinator species, maximum activity coincides with minimum available nectar levels (Fig. 4). Nectar production in 24 h increases with flower age (Table 5), from zero on the day of flower opening to about 1 µl on day 5; analysis of variance shows that the differences between nectar production on the six days are significant ($F = 22.25$, $df = 5$, $p < 0.05$).

Nectar robbing

This occurred in all the populations studied, although to different extents. The mean frequency of robbery considering all populations together was 19.4% of all flower visits, with the maximum occurring in the Estrecho population and the minimum in the Vilardesilva population (Table 6). There were also significant differences between the three populations both with respect to the percentage of flowers robbed ($X^2 = 183.3$, df = 2, $p < 0.05$) and fruit-set levels ($X^2 = 21.8$, df = 2, $p < 0.05$). Analysis of the data indicates that there were no significant differences in fruit-set level between robbed and non-robbed flowers ($X^2 = 0.05$, df = 1, p = 0.49 for Vilardesilva; $X^2 = 1.4$, df = 1, p = 0.24 for Cobas; $X^2 = 0.7$, df = 1, p = 0.40 for Estrecho) (see Fig. 5).

Discussion

According to CRUDEN (1977), high P:O index values are characteristic of cross-pollinated plants (xenogams), whilst self-pollinated plants (autogams) tend to display lower values. CRUDEN & MILLER-WARD (1981) state that similar relationships are apparent with respect to characteristics such as stigma area and pollen grain size. Recently, however, a number of authors have expressed reservations about the validity of such generalizations (see MIONE & ANDERSON 1992, and references therein). The P:O index value obtained by us for *Petrocoptis grandiflora* (641.4 ± 89.6) is within the range which CRUDEN (1977) assigns to "facultative xenogams", and this is in agreement with the results of our pollen transfer experiments.

The fruit-set level (55%) differs somewhat from the value of 44.9% recorded by us in 1991 (GUITIAN & SANCHEZ 1992), although the number of seeds per capsule was very similar to that recorded previously (12.6 ± 4.4 in 1992, 14.3 ± 3.8 in 1991).

Our results show *P. grandiflora* to be a partially self-compatible species, with some limited fruit and seed production in self-pollination experiments. The results of the geitonogamous crosses are similar to those of autogamous crosses, and indicate a significant drop in fruit-set levels, and number of seeds per capsule, with respect to xenogamous crosses. In our previous study (GUITIAN & SANCHEZ 1992), however, plants from which insects were excluded by bagging did not produce fruit. This suggests that spontaneous autogamy is limited by protandry (which is generally marked in flowers of this species), and thus that such self-fertilization as occurs is generally a result of geitonogamy. This is quite conceivable, since opening of flower buds within the same inflorescence is asynchronic in *P. grandiflora*.

Xenogamic crosses achieved fruit-set and seed production levels which were not significantly different from controls from the same population; i.e. plants in which xenogamic fertilization was guaranteed by manual pollination produced the same number of fruits as plants freely exposed to pollinators. This suggests that pollinator scarcity is not a factor limiting xenogamous pollen transfer (BYERZICHUDEC 1981).

The mean floral duration recorded in 1992 (i.e. the present study) (3.9 ± 1.6 days) is almost identical to that recorded in 1991 (3.8 ± 0.42) by GUITIAN & SANCHEZ (1992). Floral duration decreases as the flowering period progresses, as has been reported for other plants (see for example MUÑOZ & DEVESA 1987).

The pollinator guild that interacts with *P. grandiflora* is dominated by the long-tongued bee *Anthophora acervorum,* which accounted for 68.1% of recorded visits. In 1991 *A. acervorum* accounted for 63% of visits (GUITIAN et al. 1992), indicating considerable constancy. Activity of this species at *P. grandiflora* flowers peaked twice, once in mid morning and once in mid afternoon (Fig. 1): this pattern is similar to that described for the genus *Anthophora* in other Mediterranean areas (HERRERA 1990). *Xylocopa violacea* showed maximum activity around midday, despite its large size (297 mg dry weight; HERRERA 1990) and the consequent apparent danger of overheting: this activity pattern has been reported by a number of authors, and can in fact be explained by the considerable thermoregulatory capacity of the members of this genus (WILMER & UNWIN 1981, WITTMAN & SCHOLZ 1989). The pierids, much smaller and requiring solar radiation for body warming, also showed peak activity around midday (PIVNICK & MCNEIL 1987).

Nectar characteristics (daily production, sugar concentration, and diurnal variation in available nectar) play a fundamental role in the plant-pollinator relationship. The flowers of *P. grandiflora* produce small quantities of highly concentrated nectar (Table 5); this is characteristic of bee-pollinated flowers (BAKER 1975, CORBET 1978, CRUDEN et al. 1983), and in agreement with previous studies of nectars consumed by long-tongued bees (BAKER & BAKER 1983, GUITIAN et al. 1992).

The quantity of nectar produced daily increases with flower age and peaks on day 4 or 5, by which time the stigma is receptive. This pattern (i.e. peak nectar production coinciding with the female phase) has been noted in many studies of protandric species (PYKE 1978, MUÑOZ & DEVESA 1987).

Various studies have indicated that nectar robbers may simultaneously act as pollinators, by coming into contact with the sexual organs of the plant during the robbery (MACIOR 1966, INOUYE 1983). In the present study, the frequency of robbery varied between the three plant populations studied. The most obvious explanation for this is variation in the local abundance of *X. violacea*; however, our observations suggest that flowering phenology also plays an important role. In the earliest-flowering population, that of Estrecho, the frequency of robbery was much higher than in the other two populations studied, in which flowering occurs considerably later. Within the Estrecho population the frequency of robbery was much higher in early-flowering plants than in late-flowering plants (i.e. plants flowering at the same time as the average for the other two populations). This suggests that nectar robbery by *X. violacea* occurs predominantly during the period when *P. grandiflora* is the only robbery-prone species in flower in this area. Once this period is past, *X. violacea* turns its attention to other species (notably *Lonicera etrusca*) which offer a more generous floral reward.

P. grandiflora is a rare species with a highly restricted distribution. In this study we have shown that pollination is sufficient and fruit-set high, and that neither is a factor limiting reproductive success. The present rarity of this species must therefore be related to other reproductive characteristics such as dispersion or germination, or to factors of a geographical, historical or other nature. In future studies we will attempt to evaluate the importance of such factors in explaining the rarity and restricted distribution of this species.

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Buchbesprechungen

Wildi, O., Orlóci, L.: **Numerical exploration of community patterns.** – The Hague: SPB Academic Publishing 1990. – 124 S., 3 Abb., 10 Tab., broschürt, DFL 40.00, US$ 24.00. – ISBN 90-5103-037-1.

Dieses Handbuch des Programmes MULVA-4 beinhaltet neben einer kurzen allgemeinen Einführung in den Problemkreis der Datenanalyse und speziell der multivariaten Statistik vorwiegend Ausführungen zu allen 21 Unterprogrammen.

Sowohl formelle Anforderungen an die Struktur der Eingangsdaten als auch die Berechnungsalgorithmen (Formeln) und Ausgabemöglichkeiten werden dargesellt. Da die beschriebene Software aus mehreren separaten Unterprogrammen besteht, werden im Buch mögliche Kombinationen für eine sinnvolle Nutzung beschrieben und prinzipielle Empfehlungen zur Organisation von Berechnungen gegeben. Konkrete Beispiele für die Anwendung der Unterprogramme erleichtern das Verständnis.

Beschrieben werden Unterprogramme zu

- Datenerfassung, Dateibearbeitung
- Initialisierung (Datenvorbereitung, Transformation)
- Datenmanipulation
- Ähnlichkeitsberechnungen
- Primären Analysen (Aufstellen von Modellen zur Datenverteilung; z. B. Rank-Algorithmus, Cluster-Verfahren, Hauptkomponentenanalyse, multiple Regression, Autokorrelation)
- Sekundären Analysen (Modellanalysen)
- Datendarstellung und -ausgabe.

Die Software wurde speziell für die Nutzung bei der Auswertung vegetationskundlicher Studien entwickelt. Sie unterstützt das Erkennen komplexer Muster der Artenzusammensetzung in Abhängigkeit von Standortmerkmalen. Erwähnenswert sind relativ gute Nutzerfreundlichkeit und die Vollständigkeit der Ausdrucke. Es ist zu hoffen, daß bei einer Weiterentwicklung dieses Programmes oder der Erstellung neuer Software zum Themenkreis zwar die Vorteile moderner Rechentechnik und Entwicklersoftware voll ausgenutzt werden, aber ebenso Bewährtes wie Vielfalt und Vollständigkeit der Ausdrucke berücksichtigt werden.

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Orlóci, L.: **Ecological programs for instructional computing on the Macintosh.** (Ecological Computations Series (ECS) 2). – The Hague: SFB Academic Publishing 1991. – 131 S., broschürt, DFL 45.00, US$ 27.00. – ISBN 90-5103-060-6.

Diese Broschüre ist das Handbuch für 45 separate Programme, die als Ergänzung zum MULVA-4 Programmpaket (Wildi & Orlóci 1990) angeboten werden.

Es werden Programme zu zahlreichen statistischen Verfahren wie auch zur Lösung informationstechnischer Aufgaben vorgestellt; z. B.:

- Übertragen der Datenstruktur, Hilfsprogramme
- Berechnen, Beschreiben und Prüfen von Verteilungen
- Varianz-, Diskriminanz- und Faktorenanalysen
- Clusteranalysen, Trendabschätzungen.

Jedes einzelne Programm wird kurz, nach einem einheitlichen 4(-5)-Punkte-Schema erläutert. Dazu gehören: Kurzbeschreibung, Bildschirm des Anfangsmenüs, Ausdruck der Eingangsdatei, Ergebnisausdruck, evtl. Grafik.

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