

Variation in floral morphology and reproductive success in *Petrocoptis grandiflora* (Caryophyllaceae)

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We examined variation in the floral morphology of *Petrocoptis grandiflora* Rothm. (Caryophyllaceae), a plant endemic to the northwest Iberian Peninsula. First, we investigated whether peduncle length, calyx length and petal-limb length influence reproductive success (as measured by seed production). Second, we investigated whether floral morphology varies with position in the inflorescence and/or among the six populations studied. Peduncle length and calyx length showed no significant relationship with seed production; however, petal-limb length was significantly and positively correlated with the number of seeds produced by the flower. All three morphometric characters, and the number of ovules per ovary, varied significantly with position in the inflorescence, but not among populations.

Key words: endemism, floral morphology, *Petrocoptis grandiflora*, reproductive success

INTRODUCTION

It is generally accepted that the evolution of entomophilous plants and their pollinators has been closely linked (Stebbins 1970), and it is thus reasonable to suppose that variation in floral morphology — specifically when the features involved affect pollinator attraction or pollen transfer — may translate into variation in plant reproductive success. Floral morphology that affects individual reproductive success may lead to evolutionary divergence and speciation; variable morphological traits that have no effect on reproductive success are unlikely to lead to evolutionary change (Herrera 1990a).

Over the last few decades, numerous authors have studied variation in floral morphology and

its effect on reproductive success. Four basic approaches have been followed. The first approach has been to investigate between-population variation in floral morphology, largely in morphometric characters (see Schlichting 1986, Herrera 1990a; references cited in both studies). The second approach has been to investigate within-population and within-plant variation under natural conditions; authors taking this approach have studied not only morphometric characters (Herrera 1990b, 1993, Johnston 1991, Andersson & Widen 1993, Johnson *et al.* 1995 and references therein) but also characters such as flower colour and type of reward (see Waser 1983 for a review; more recent work includes Galen *et al.* 1987, Galen & Newport 1987, Stanton 1987ab, Wolfe 1993). A third approach has been to assess the effects on

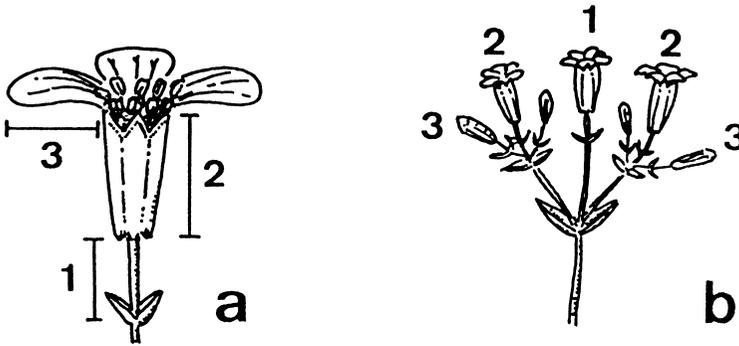


Fig 1. — a: A flower of *Petrocoptis grandiflora* Rothm. (scale 1:1), showing the three morphometric variables studied (1, peduncle length; 2, calyx length; 3, petal limb length). — b: A cymose inflorescence (dichasium) of *P. grandiflora*, showing the central flower (1), first-order lateral flowers (2), and second-order lateral flowers (3).

pollen export or seed production of either experimentally manipulated floral morphology (generally petal size; Bell 1985, Johnson *et al.* 1995) or natural among-flower variation in morphology (Campbell *et al.* 1991, Wilson 1995, Wilson & Thomson 1996). The fourth approach has been to investigate within-plant variation in floral morphology due to the effects of position in the inflorescence (i.e. architectural effects; Holtsford 1985, Thomson 1989, Diggle 1992, 1995).

In the work reported here, we investigated within-population variation in a number of characters of the flowers of *Petrocoptis grandiflora*, a plant endemic to the Iberian Peninsula. We asked how these characters are related to reproductive success as estimated on the basis of seed production. We also assessed the variability of the characters among populations and among flowers at different positions in the inflorescence. Studies of phenotypic variability and its effects on reproductive success in plants like *P. grandiflora* are of particular interest, not only because they address the immediate practical concerns of species conservation, but also because they may contribute to a better understanding of the phenomenon of endemism (see Kruckeberg & Rabinowitz 1985).

MATERIAL AND METHODS

Plant and study area

Petrocoptis grandiflora Rothm. (Caryophyllaceae) is a perennial herb, 15–30 cm high, endemic to the northwest Iberian Peninsula, where it occurs in a few populations scattered over a total area of little more than 70 km² in the western El Bierzo region of León. The purplish pink flowers are 1–1.5 cm long and arranged in dichasia. The fruit is a capsule containing 4–25 seeds, each about 1 mm long and bear-

ing a small strophiole of hairs. Pollination is by insects, largely long-tongued bees (Anthophoridae). Flowering starts in March and finishes at the beginning of June (Gutián & Sánchez 1992, Navarro *et al.* 1993).

The study was carried out in the westernmost part of El Bierzo, in six populations (Covas, Portela, Estrecho, Penarubia, Barosa and Vilardesilva) located close to the border between Galicia and León. The plants grow in cracks and on small ledges on limestone outcrops. The vegetation of the study area is typically Mediterranean, comprising a mosaic of holm oak (*Quercus rotundifolia*) woodland, thorn scrub, calcareous pasture, and previously cultivated land (abandoned about 20 years ago).

Experimental design

The first data set was collected with the aim of investigating within-population variation in floral morphology and reproductive success. In May 1992 we marked 167 flowers in one of the populations with plastic tags, numbered according to flowering order on each flower. The following flower measurements (Fig. 1a) were taken with a micrometer to the nearest 0.1 mm: (1) peduncle length (distance from the base of the most distal bract to the base of the calyx; potentially affecting the presentation of the flower to pollinators); (2) calyx length (distance from the base of the calyx to the most distal point of the calycine teeth; potentially affecting ease of access to nectar); (3) petal limb length (potentially affecting pollinator attraction and acting as a platform for certain pollinators). All the marked flowers were checked daily over a six-week period. The seed capsule was collected just prior to dehiscence. All capsules were collected within 8 weeks of marking. The number of seeds in each capsule was then determined.

The second data set was collected with the aim of investigating among-population and among-position variation in floral morphology and reproductive success. Again in May 1992, we collected 30 flowers (ten from each of the three basic positions in the inflorescence; Fig. 1b) from each of the six populations. The ten flowers from each position were from ten different plants. The flowers were immediately transferred to the laboratory for measurement of pe-

duncle length, calyx length and petal limb length as above; the number of ovules per ovary was also counted under a stereomicroscope (50×).

In both cases, sample size was deliberately minimized in view of the rarity of this species.

Data analysis

Stepwise logistic regression was used to compare morphometric variables between flowers which set fruit and flowers which did not (first data set). Relationships between female reproductive success (number of seeds per capsule) and morphometric variables were investigated with multiple regression. The influence of the factors population and position (in the inflorescence) on morphometric variables was investigated with nested analysis of variance. Relationships between variables were investigated by calculation of Spearman's rank correlation coefficients, using the data from the second sample series. Relative variabilities of the different morphometric characters were evaluated by calculation of coefficients of variation. All statistical analyses were performed with the SYSTAT package (SYSTAT 1992).

RESULTS

Of the 167 flowers marked, 111 (66.5%) set fruit, 45 (26.9%) did not, and 11 (6.6%) were eaten by herbivores (in most cases probably juvenile snails of the genus *Helix*) (see Table 1). Stepwise logistic regression shows that, of the morphometric variables considered, only petal length had a significant effect on the probability of a flower setting fruit (Wald Chi-square = 6.2, $p < 0.01$): specifically, plants with longer petals were more likely to set fruit. In addition, multiple regression analysis indicates that petal limb length is the only morphometric variable that effectively predicts the number of seeds per capsule (Table 2).

All three morphometric variables, and number of ovules per ovary, varied considerably among populations (Table 3). The most variable character was peduncle length, and the least variable calyx length (coefficients of variation 50.8% and

3.5% respectively). Nested analysis of variance, with the crossed factor population and the nested factor position, indicated that position was a significant source of variance in all four variables; population, however, was not a significant source of variance in any of the variables (Table 4). Each of the four variables was significantly and positively correlated with each of the other variables (Table 5).

DISCUSSION

Numerous studies have suggested that variation in reproductive success is related to variation in floral morphology (see Herrera 1993, and references therein). The results of the present study indicate that, in *Petrocoptis grandiflora*, flowers with larger petals are more likely to set fruit, and when they do, they produce more seeds than flowers with small petals. Similar results have been obtained in previous studies; for example, Galen (1989) and Johnson *et al.* (1995), in studies of *Polemonium viscosum* and *Campanula americana*, respectively, found positive correlations between petal size and seed set. There are two possible explanations for the positive relationships between petal size and seed production observed in the present and previous studies: (1) flowers with larger petals attract more pollinators or are more efficiently pollinated (see for example Galen & Newport 1987), and thus more of their ovules are fertilized and develop into seed; or (2) flowers with larger petals have more ovules and thus produce more seeds. One argument suggests that the first explanation is not correct for *P. grandiflora*. Supplementary pollination of *P. grandiflora* leads neither to increased fruit set nor to an increase in the number of seeds per capsule in three consecutive years (Gutián *et al.* 1994; Navarro unpublished data): this demonstrates that pollen is not a limiting resource, and that differential

Table 1. Mean \pm standard deviation (range) of the morphometric variables recorded from the 111 flowers that set fruit and the 45 flowers that did not.

	Calyx length	Petal limb length	Peduncle length
Flowers that set fruit	13.00 \pm 0.98 (10.5–15)	7.98 \pm 1.3 (4.5–11)	4.12 \pm 2.7 (0.5–13)
Flowers that did not set fruit	12.44 \pm 1.16 (9.5–14.5)	7.48 \pm 1.42 (5–9.5)	3.52 \pm 2.5 (0.5–10.5)

attraction of pollinators — even if it occurs — does not affect fertilization efficiency. Given that *P. grandiflora* flowers with large petals have more ovules (see Table 5), and given that pollen is not limiting (so that ovule-to-seed ratio is likely to be independent of ovule number), the second of the above explanations appears to be correct. High among-flower variability in the number of ovules per ovary, and correlations between number of

ovules and number of seeds, have been reported in other species (e.g., *Viola cazorlensis*; Herrera 1990b).

In the case of *Petrocoptis grandiflora*, it seems likely that the observed correlation between petal size and probability of fruit set is a reflection of the relationship between position in the inflorescence and probability of fruit set: as in many other plants with cymose inflorescences, the first-formed flowers of *P. grandiflora* inflorescences open earlier, are larger and have a higher probability of fruit set than flowers of higher-order branching axes (Gutián & Navarro 1996). First-flower dominance phenomena of this type have been attributed to preferential access by early-opening flowers to plant resources (see Stephenson 1992). In a recent review, Diggle (1995) has pointed out that covariation between the size or number of floral components and position in the

Table 2. Results of multiple regression to investigate the effects of the three morphometric variables on number of seeds per flower ($N = 111$).

Variable	Coefficient	S.E.	<i>t</i>	<i>p</i> -value
Calyx length	0.58	0.45	1.29	0.200
Petal limb length	1.10	0.37	2.99	0.003
Peduncle length	0.10	0.16	0.58	0.562

Table 3. Mean \pm S.D. (mm) of the variables studied in the six populations of *Petrocoptis grandiflora*. Basics statistics for the complete data set ($N = 180$ flowers) are also shown.

Population	Peduncle length	Calyx length	Petal limb length	Ovules/ovary
Covas	6.3 \pm 6.1	11.0 \pm 4.1	7.5 \pm 2.2	19.2 \pm 5.5
Portela	4.8 \pm 3.4	10.5 \pm 3.8	6.1 \pm 1.9	19.8 \pm 5.3
Estrecho	6.8 \pm 3.0	10.8 \pm 4.1	8.6 \pm 2.6	18.8 \pm 5.5
Peñarrubia	7.9 \pm 6.9	9.9 \pm 4.4	8.4 \pm 3.1	17.6 \pm 5.3
Barosa	1.8 \pm 1.8	10.4 \pm 3.4	9.1 \pm 12.8	16.8 \pm 4.2
Vilardesilva	13.2 \pm 6.3	10.7 \pm 3.6	8.1 \pm 1.9	18.4 \pm 4.5
All populations	7.3 \pm 5.9	11.9 \pm 1.4	8.2 \pm 1.7	19.6 \pm 2.5
Range	0.5–30.5	6.5–15	4.5–13.5	13–30
c.v.	50.8	3.5	12.2	5.4

Table 4. Results (*F*-value) of nested analysis of variance to investigate the effects of the factor population and the nested factor position (in the inflorescence) on the variables studied. *n.s.* = not significant; *** = $p < 0.001$.

Factor	Peduncle length	Calyx length	Petal limb length	Ovules/ovary
Population	1.4 <i>n.s.</i>	0.6 <i>n.s.</i>	2.0 <i>n.s.</i>	1.8 <i>n.s.</i>
Position (population)	23.9 ***	16.5 ***	27.0 ***	3.6 ***

Table 5. Spearman rank correlations between all variables studied. All correlations are positive and significant ($p < 0.001$).

	Peduncle length	Calyx length	Petal limb length	Ovules/ovary
Peduncle length	–	–	–	–
Calyx length	0.28	–	–	–
Petal limb length	0.56	0.32	–	–
Ovules/ovary	0.23	0.39	0.26	–

inflorescence may represent an 'architectural effect' rather than differences in resource availability. We thus consider — as reported by Herrera (1993) for *Viola cazorlensis* — that the selective pressures exerted by pollinators on the floral morphology of *P. grandiflora* — if they exist at all — are unlikely to be significant alongside other factors that have much more important effects on reproductive success.

Although *Petrocoptis grandiflora* is endemic to a very small area, our results indicate that there is high among-plant variability in the morphometric characters studied; this is in contrast to the assertion that 'rare' plants have low phenotypic variability (Krukeber & Rabinowitz 1985). Our data reveal that there is no significant among-population difference in any of the characters studied: this may be attributable to the existing populations being the fragmented remnants of what was once a single population. Again, this is in contrast with the results of studies of other rare plants, which reveal considerable between-population variability (see Herrera 1988, 1990a).

In conclusion, *Petrocoptis grandiflora* shows considerable variation in floral morphology. One of the morphometric characters studied, petal-limb length, is positively correlated with reproductive success as measured by seed production per flower. The observed variation in seed production may be related to position in the inflorescence or competition for resources, but cannot be attributed to among-flower variation in attractiveness to pollinators. The observed morphometric variability does not have a detectable population component.

To assess whether the pattern observed in *Petrocoptis grandiflora* is characteristic of 'rare' plants (*sensu* Rabinowitz 1981), studies of within- and among-population morphometric variation, and of the effects of such variation on reproductive success, should be performed with other endemic species. Such research can be expected to shed light on the phenomenon of rarity.

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