
FLORAL BIOMETRY, FLORAL REWARDS AND POLLEN–OVULE RATIOS IN SOME *VICIA* FROM EXTREMADURA, SPAIN

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A biometric study of the flower, floral rewards (nectar and pollen) and pollen–ovule ratios in 14 taxa of *Vicia* (Fabaceae) from Extremadura (Spain) has been evaluated. Almost all floral characteristics are directly correlated and it has been found that flower size is a good indicator of the reward production, and the pollen–ovule ratios are positively correlated to seed size. A direct correlation between pollen size (volume) and style length has likewise been observed. This may show the importance of the pollen food reserves in sustaining the growth of its pollen tube along the style.

Keywords. Fabaceae, flower size, nectar, pollen production, pollen size.

INTRODUCTION

The genus *Vicia* L. (Fabaceae) comprises 180–200 species distributed mainly in temperate zones of the Northern hemisphere and south of the extratropical American continent. The greatest diversity of species is found in the Mediterranean region and the Caucasus (Hanelt & Mettin, 1989). Approximately 35 taxa are represented in the Iberian Peninsula (Ball, 1968), of which 23 are found in Extremadura (Spain). The genus has been the subject of many taxonomic (Guinea, 1953; Kupicha, 1976; Hanelt & Mettin, 1989, and references therein) and agronomic studies; the latter have been motivated by the widespread use of taxa such as *V. faba*, *V. sativa* and others as forage crops (vide Gunn & Kluvé, 1976).

With the exception of findings reported by Gunn & Kluvé (1976), Kupicha (1976) and Hanelt & Mettin (1989), few studies have examined the reproductive biology of wild species. Earlier studies have indicated that although perennial species may reproduce by vegetative propagation, most *Vicia* species reproduce by seed (Hanelt & Mettin, 1989), with cross-pollination by Hymenoptera being the most common mechanism of reproduction (Müller, 1883). As in other species of Papilionoideae, reproduction by *Vicia* species requires a tripping mechanism, which in *Vicia* flowers is a brush type design (Delpino in Müller, 1883; Arroyo, 1981). However, in annual species of the subgenus *Cracca* (Dumort.) Peterm., and in some members of the subgenus *Vicia*, autogamy predominates over allogamy (Plitmann, 1973; Hanelt & Mettin, 1989; Zhang & Mosjidis, 1995), although the relative importance of cross-

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TABLE 1. Species of *Vicia* studied.

<i>Vicia benghalensis</i> L. (BEN)
<i>V. cracca</i> subsp. <i>tenuifolia</i> (Roth) Gaudin (TEN)
<i>V. disperma</i> DC. (DIS)
<i>V. hirsuta</i> (L.) S.F. Gray (HIR)
<i>V. lutea</i> L. subsp. <i>lutea</i> (LUT)
<i>V. lutea</i> subsp. <i>vestita</i> (Boiss.) Rouy (VES)
<i>V. sativa</i> L. subsp. <i>sativa</i> (SAT)
<i>V. sativa</i> subsp. <i>nigra</i> (L.) Ehrh. (NIG)
<i>V. parviflora</i> Cav. (PAR)
<i>V. peregrina</i> L. (PER)
<i>V. pubescens</i> (DC.) Link (PUB)
<i>V. vicioides</i> (Desf.) Coutinho (VIC)
<i>V. villosa</i> subsp. <i>eriocarpa</i> (Hausskn.) P.W. Ball (ERI)
<i>V. villosa</i> subsp. <i>varia</i> (Host) Corb. (VAR)

fertilization in these species (approximately 10% in *V. sativa*) has also been noted (Hanelt & Mettin, 1970).

This paper provides information on the floral biology of 14 wild taxa of the genus *Vicia* that form part of the Extremaduran flora. We performed a biometric study of the floral characteristics, evaluated floral rewards (nectar and pollen), and indirectly estimated the reproductive system by calculating the pollen/ovule ratio (P/O; Cruden, 1977). Specifically, we tried to answer the following questions: (1) do flowers that produce more nectar produce less pollen; (2) do smaller flowers have a lower P/O ratio than larger flowers; (3) is P/O ratio related to seed weight in this genus; and (4) is there any relation between style length and pollen grain size?

MATERIAL AND METHODS

Floral biometry

We studied 80 populations of 14 different taxa of the genus *Vicia* (see Table 1). Ten flowers were sampled from each population and were measured fresh to record the following features: flower size (total length), calyx tube, androecium tube, anther, ovary and style length.

Nectar production

We studied 30 flowers from each of 89 populations. The volume and concentration of nectar were determined in flowers of inflorescences that had previously been bagged in the field. At 24 hours after the plants were bagged, nectar was removed in the laboratory with 5 and 10 μ l micropipettes to estimate volume, and two manual refractometers (Atago models N1 and N2) were used to determine concentration.

No nectar production was found in 29 populations; this may have been because

of nectar reabsorption (Bonnier, 1878; Corbet et al., 1979). In taxa with small flowers, nectar production was sometimes too low (as seen under dissecting microscope $\times 40$) to be quantified; in these cases we assigned a volume of $0.01\mu\text{l}$.

For each flower analysed we calculated nectar weight (in mg) as the product of nectar volume, and nectar concentration as sugar density at $20^{\circ}\text{C}/100$ (see Bolten et al., in Dafni, 1992).

Pollen (P) and ovule (O) production and pollen grain size

In most taxa we used a total of 10 flower buds from three populations to estimate pollen (P) and ovule (O) number.

Ovule number was estimated by examining buds with a dissecting microscope. Pollen grain number was determined with a light microscope. When more than 2000 grains were present, counts were made with the dilution method (Cruden, 1977). When fewer than 2000 grains were found, and because there are two verticils of stamens, one external with five large anthers and the other internal with five small anthers, one anther of each verticil was counted with the help of an eyepiece grid; the two values were then multiplied by 5 and added to obtain the total production per flower.

Pollen characteristics were studied in acetolysed grains according to the method of Erdtman (1960) as modified by Hideux (1972). Measurements were taken of the polar and equatorial axes for 15 pollen grains per population. Pollen volume was calculated by the formula $\frac{4}{3} \pi a^2b$, where a is half the equatorial axis and b is half the polar axis.

The values of P and O were used to calculate the P/O ratio for each population. The data for pollen number and volume per flower were used to calculate total pollen volume per flower (in mm^3) or pollen biomass, used here as an estimate of the distribution of resources for masculine sexual function.

Statistical treatment

We calculated the correlations between variables for each population. Values which have significance at $\alpha < 0.05$ with sequential Bonferroni tests (Rice, 1989) are indicated. A series of one-way analyses of variance (ANOVA) were done to check for significant differences in pollen or ovule production, P/O ratio, and pollen volume (in data previously subjected to logarithmic transformation) between taxa with small ($< 8.75\text{mm}$ long) and large flowers ($> 13\text{mm}$ long).

Data for each population were used to find mean values for each species (Table 2). However, it should be noted that statistical analyses were done with values for populations. Mean values for given species were analysed only to determine the relation between P/O ratio and seed weight (in data previously subjected to logarithmic transformation), because the values for seed weight did not correspond to any of the populations used to study P/O.

TABLE 2. Mean values and standard deviations for variables studied in 14 taxa of the genus *Vicia* L. Numbers in parentheses are the number of populations, and numbers between hyphens are the number of flowers examined. For each species, sample sizes are the same for data in columns 1–6; 9, 10 and 13; and 11–12 (in this case the numbers between hyphens are the number of pollen grains studied). XF = Facultative xenogamy; AF = Facultative autogamy.

	Flower size (mm)	Calyx tube (mm)	Androecium tube (mm)	Anther length (mm)	Ovary length (mm)	Style length (mm)	Nectar volume (μ l)
BEN	16.92 \pm 1.48 (9) -88-	3.32 \pm 0.47	10.75 \pm 0.72	0.44 \pm 0.06	10.80 \pm 0.90	1.79 \pm 0.18	0.45 \pm 0.50 (7) -47-
TEN	14.21 \pm 1.04 (6) -61-	2.46 \pm 0.29	6.7 \pm 0.53	0.45 \pm 0.07	6.99 \pm 0.59	1.82 \pm 0.22	2.45 \pm 2.88 (4) -62-
DIS	5.38 \pm 0.45 (9) -90-	1.46 \pm 0.21	2.97 \pm 0.25	0.21 \pm 0.03	3.16 \pm 0.42	0.88 \pm 0.13	0.02 \pm 0.04 (9) -120-
HIR	3.38 \pm 0.40 (6) -60-	1.13 \pm 0.13	1.54 \pm 0.14	0.14 \pm 0.02	1.58 \pm 0.13	0.47 \pm 0.07	0.01 \pm 0.00 (5) -77-
LUT	26.34 \pm 2.25 (11) -109-	4.86 \pm 0.70	13.94 \pm 0.81	0.57 \pm 0.08	14.29 \pm 0.90	2.52 \pm 0.30	1.10 \pm 0.91 (12) -115-
VES	24.13 \pm 1.91 (2) -20-	5.24 \pm 0.37	14.13 \pm 0.57	0.59 \pm 0.08	14.30 \pm 0.68	2.42 \pm 0.19	1.41 \pm 0.84 (1) -30-
PAR	7.29 \pm 0.95 (7) -70-	1.86 \pm 0.23	5.16 \pm 0.89	0.26 \pm 0.08	5.57 \pm 0.86	1.35 \pm 0.22	0.09 \pm 0.12 (7) -154-
PER	16.05 \pm 1.70 (2) -20-	3.95 \pm 0.38	6.30 \pm 0.33	0.50 \pm 0.10	6.90 \pm 0.53	1.67 \pm 0.17	1.09 \pm 0.61 (2) -49-
PUB	3.06 \pm 0.42 (1) -10-	0.78 \pm 0.09	1.97 \pm 0.30	0.15 \pm 0.00	2.37 \pm 0.38	0.55 \pm 0.05	—
SAT	24.64 \pm 2.41 (6) -58-	6.62 \pm 0.76	11.42 \pm 0.53	0.55 \pm 0.07	11.74 \pm 0.73	2.11 \pm 0.17	1.58 \pm 1.70 (9) -90-
NIG	19.03 \pm 2.74 (10) -93-	4.79 \pm 0.52	8.30 \pm 0.85	0.40 \pm 0.09	8.81 \pm 0.94	1.56 \pm 0.23	0.63 \pm 0.69 (12) -160-
VAR	18.03 \pm 0.85 (6) -60-	3.31 \pm 0.62	10.94 \pm 0.81	0.42 \pm 0.06	11.12 \pm 0.85	1.78 \pm 0.16	1.16 \pm 1.01 (4) -33-
ERI	13.38 \pm 0.72 (2) -20-	2.89 \pm 0.40	7.9 \pm 0.41	0.39 \pm 0.03	7.75 \pm 0.51	1.54 \pm 0.07	0.39 \pm 0.50 (3) -16-
VIC	5.93 \pm 0.88 (4) -40-	1.63 \pm 0.19	1.98 \pm 0.22	0.20 \pm 0.03	1.96 \pm 0.26	0.81 \pm 0.10	0.12 \pm 0.19 (4) -70-

RESULTS

Floral biometry

The correlation matrix (Table 3) showed that most of the flower characteristics in 80 populations of the genus *Vicia* were directly correlated. In general, species with larger flowers had larger calyces, androecium tubes, anthers and ovaries, although flower size was not significantly correlated with style length. *Vicia lutea* subsp. *lutea* ($x = 26.34 \pm 2.25$) and *Vicia sativa* subsp. *sativa* ($x = 24.64 \pm 2.41$) had the largest flowers; *Vicia pubescens* ($x = 3.06 \pm 0.42$) and *Vicia hirsuta* ($x = 3.38 \pm 0.4$) had the smallest.

Nectar production

Nectar volume per flower correlated directly with flower size and calyx tube length (Table 4). The volume of nectar was largest in *V. cracca* subsp. *tenuifolia* ($x = 2.45 \pm 2.88$), and smallest in *V. hirsuta* ($x = 0.01 \pm 0.0$). However, because *V. pubescens*, which we could not study for nectar volume, had the smallest flowers of all taxa investigated, we suspect that nectar production was lowest in this species.

TABLE 2. (continued).

Sugar weight (mg)	Pollen grain no./flower (P)	Ovule number/flower (O)	Pollen volume (μm^3) ($\times 10^3$)	Total pollen volume/flower (mm^3)	Pollen-ovule ratio (P/O)	Seed mean weight (mg)
0.18 \pm 0.12 (7) -26-	7517.86 \pm 1528.78 (3) -28-	4.29 \pm 0.45	13.10 \pm 3.96 (3) -45-	0.098	1797.14 \pm 424.38 XF	60
0.38 \pm 0.39 (4) -60-	9341.38 \pm 5062.61 (3) -29-	5.62 \pm 1.16	18.82 \pm 5.67 (4) -60-	0.176	1862.17 \pm 1424.41 XF	25
0.06 \pm 0.00 (9) -1-	1472.84 \pm 256.33 (4) -40-	2.00 \pm 0.00	9.45 \pm 3.08 (3) -45-	0.014	736.47 \pm 128.19 XF	20
—	697.75 \pm 185.26 (3) -30-	2.00 \pm 0.00	7.06 \pm 2.88 (4) -54-	0.005	348.88 \pm 92.63 AF-XF	5
0.33 \pm 0.23 (12) -90-	18035.71 \pm 7144.04 (3) -28-	4.79 \pm 0.86	16.06 \pm 5.61 (3) -45-	0.290	3780.83 \pm 1466.60 XF	70
0.34 \pm 0.25 (1) -29-	18435.00 \pm 4860.79 (2) -20-	4.00 \pm 0.77	20.11 \pm 5.19 (2) -30-	0.371	4892.08 \pm 1805.64 XF	75
0.05 \pm 0.02 (7) -24-	4842.33 \pm 1896.92 (3) -29-	5.76 \pm 0.62	7.26 \pm 1.63 (3) -45-	0.035	851.52 \pm 352.3 XF	2
0.25 \pm 0.16 (2) -48-	8842.11 \pm 2112.45 (2) -19-	6.32 \pm 0.57	16.84 \pm 3.56 (2) -30-	0.149	1409.77 \pm 361.14 XF	50
—	285.16 \pm 76.92 (1) -8-	4.00 \pm 0.71	—	—	70.67 \pm 11.58 AF	2.32
0.65 \pm 0.56 (9) -70-	19423.33 \pm 6803.00 (6) -60-	8.08 \pm 1.27	21.12 \pm 4.45 (3) -45-	0.410	2416.98 \pm 781.94 XF	60
0.23 \pm 0.19 (12) -94-	10506.67 \pm 4900.80 (3) -30-	11.43 \pm 1.43	14.90 \pm 4.33 (3) -45-	0.157	909.67 \pm 389.91 XF	10
0.42 \pm 0.32 (4) -28-	12503.33 \pm 1827.29 (3) -30-	4.53 \pm 0.76	9.48 \pm 3.92 (3) -45-	0.118	2817.06 \pm 553.56 XF	30
0.14 \pm 0.10 (3) -9-	14480.00 \pm 5878.29 (2) -30-	3.83 \pm 0.64	8.34 \pm 1.98 (2) -45-	0.121	3879.67 \pm 1713.77 XF	38
0.10 \pm 0.03 (4) -12-	3417.92 \pm 422.99 (3) -30-	2.00 \pm 0.00	10.20 \pm 2.48 (3) -45-	0.035	1708.96 \pm 211.50 XF	35

We found a direct correlation between nectar volume and weight content in sugar, although there was no relation between nectar volume (or sugar concentration) and pollen grain production per flower (see Table 4).

Pollen production per flower and pollen grain size

Pollen number was greatest in *V. sativa* subsp. *sativa* ($x=19,423.33 \pm 6803$), and lowest in *V. pubescens* ($x=285.16 \pm 76.92$). This variable correlated directly with anther size and flower size (Table 5).

We also found direct correlations between pollen grain size (or volume) and pollen number per flower and total pollen volume per flower. From these relationships we infer that species with larger pollen grains also have the highest pollen yields. In fact, species with the largest flowers produced up to $12,919.10 \pm 6293.76$ pollen grains per flower, whereas those with the smallest flowers produced a mean number of only 2372.17 ± 1796.55 grains per flower (statistically significant difference, one-way ANOVA, $F=35.78$, $P<0.001$). Mean pollen grain volume in species with large flowers was $15,414.74 \pm 4182.2\mu\text{m}^3$; the corresponding value in species that produced small flowers was $7867.49 \pm 2105.06\mu\text{m}^3$ (statistically significant difference, one-way ANOVA, $F=26.75$, $P<0.001$).

TABLE 3. Correlation matrix for flower characteristics in *Vicia*. *** $P < 0.001$; * $P < 0.05$; NS not significant ($P > 0.05$). Only those coefficients marked *** are significant with sequential Bonferroni tests, at $\alpha = 0.05$. $n = 78$.

	Flower size 1	Calyx size 2	Androecium tube 3	Anther size 4	Ovary length 5	Style length 6
1	—					
2	0.90302 (***)	—				
3	0.43423 (***)	0.47452 (***)	—			
4	0.91039 (***)	0.83112 (***)	0.45953 (***)	—		
5	0.95513 (***)	0.81857 (***)	0.42437 (***)	0.90353 (***)	—	
6	0.26045 (*)	0.16698 (NS)	0.09332 (NS)	0.28424 (*)	0.25003 (*)	—

TABLE 4. Correlation matrix for nectar and flower characteristics. *** $P < 0.001$; ** $P < 0.01$; NS not significant ($P > 0.05$). All coefficients are significant with sequential Bonferroni tests, at $\alpha = 0.05$, with the exception of the correlation between 1 and 3, and 2 and 3. $n = 35-78$.

	Nectar volume 1	Sugar weight 2	Pollen grain number/flower 3	Flower size 4	Calyx tube 5
1	—				
2	0.8553 (***)	—			
3	0.2063 (NS)	0.2486 (NS)	—		
4	0.4684 (***)	0.4437 (**)	0.6904 (***)	—	
5	0.3705 (**)	0.3366 (*)	0.6923 (***)	0.9030 (***)	—

Other interesting observations were the direct correlation between pollen grain volume and style length (see Fig. 1), and the significant direct correlation between pollen number and the number of ovules per flower (Table 5).

P/O ratio

The largest mean ratios were found in taxa with the largest flowers ($P/O = 2638.68 \pm 1352.37$) and the smallest ones in species with small flowers ($P/O = 849.84 \pm 531.57$; Table 2). This difference was significant (one-way ANOVA, $F = 21.48$, $P < 0.001$; Table 5).

The P/O ratios we obtained show that most taxa ($n = 12$) behaved as facultative

TABLE 5. Correlation matrix for different flower characteristics. *** $P < 0.001$; ** $P < 0.01$; NS not significant ($P > 0.05$). Only those coefficients marked *** or ** are significant with sequential Bonferroni tests, at $\alpha = 0.05$. * $P < 0.05$, NS not significant ($P > 0.05$). $n = 29-78$.

	Pollen/ flower 1	Flower size 2	Pollen volume 3	Anther size 4	Ovules/ flower 5	P/O 6	Total pollen volume/flower 7
1	—						
2	0.6904 (***)	—					
3	0.5637 (***)	0.8567 (***)	—				
4	0.6197 (***)	0.9104 (***)	0.8518 (***)	—			
5	0.5384 (***)	0.6307 (***)	0.4555 (*)	0.5297 (**)	—		
6	0.3551 (*)	0.6541 (***)	0.4527 (*)	0.7137 (***)	0.0478 (NS)	—	
7	0.6601 (***)	0.8377 (***)	0.8420 (***)	0.8071 (***)	0.3762 (*)	0.6173 (***)	—

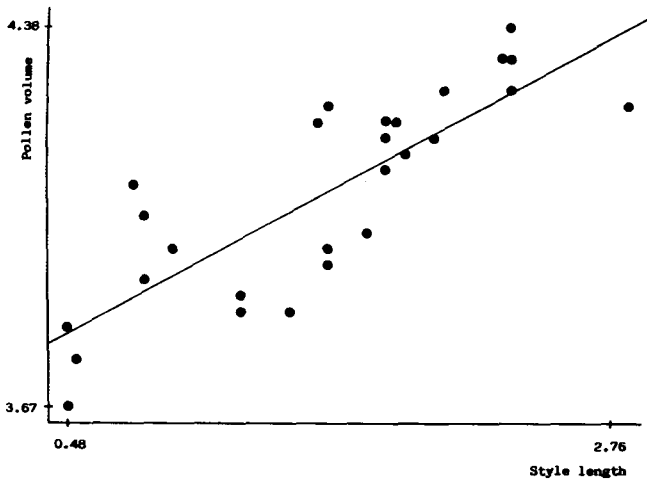


FIG. 1. Regression line for style length and pollen volume. $y = 0.26x + 3.68$; $r = 0.8254$, $P < 0.001$. $n = 27$.

xenogams, and only two (*V. hirsuta* and *V. pubescens*) acted as facultative autogams. These two species also had the smallest flowers (see Table 2).

We found that the P/O ratio correlated directly and significantly with seed weight (Fig. 2), although this finding may have been biased by sample size ($n = 14$).

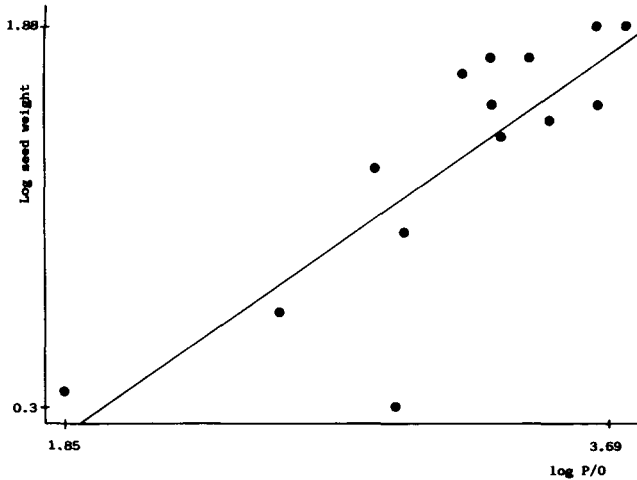


FIG. 2. Regression line for P/O ratio and seed weight. $y=0.91x+1.51$; $r=0.8222$, $P<0.001$. $n=14$.

DISCUSSION

Flower size is known to be an indicator of the potential floral rewards offered to pollinators (Opler, 1983; Herrera, 1985). In the present study, we sought evidence that confirmed this relationship in some species of the genus *Vicia*.

Larger flower size is generally associated with larger nectar production in terms of both volume and weight of sugar; this association has been reported in taxa belonging to different families (Baker & Baker, 1973; Herrera, 1985) and in species of the same family or genus (Harder & Cruzan, 1990; Guitián et al., 1993; Ortega-Olivencia & Devesa, 1993a; Petanidou & Vokov, 1993). However, environmental and other factors related to flowering dynamics also influence nectar production (see Zimmerman, 1988; Harder & Cruzan, 1990).

Species of the genus *Vicia* can produce nectar in extrafloral nectaries (e.g. *Vicia lutea* and *V. sativa*, Bonnier, 1878) which attract ants because of the protection they offer (Koptur, 1979). However, we restricted the present study to floral nectaries, and found that, in general, species with larger flowers produce larger amounts of nectar.

Earlier studies have also investigated the relationship between pollen number and flower size (e.g. tribe *Trifolieae*, Small, 1988; *Senecio*, Graumann & Gottsberger, 1988; *Scrophularia*, Ortega-Olivencia & Devesa, 1993a; *Solanum*, Mione & Anderson, 1992; *Pyrolaceae*, Knudsen & Mogens Olesen, 1993). This relationship is probably pleiotropic in origin (Primack, 1987), reflecting a link between masculine function and increasing floral size. Our data for *Vicia* species confirmed this relationship.

Some studies have shown that the trade-off between pollen number and pollen grain size is inverse (see Vonhof & Harder, 1995 for a study of legumes, and Mione & Anderson, 1992 in *Solanum*). However, in the *Vicia* species we studied, these

features were directly correlated, i.e. smaller pollen grain size was associated with small production (see also Cruden & Miller-Ward, 1981; Plitmann & Levin, 1983; Wyatt, 1984; Knudsen & Mogens Olesen, 1993). Consequently, *Vicia* species with smaller flowers usually produced smaller amounts of both nectar and pollen, and the pollen grains of these species were also smaller than in large-flowered species. In other words, the more nectariferous species were those that produced larger amounts of pollen and provided pollinators with more attractive (i.e. larger) flowers. Similarly, we found a direct correlation between pollen and ovule production, as in earlier studies (e.g. *Solanum*, Mione & Anderson, 1992; *Astragalus*, Gallardo et al., 1994).

According to Cruden (1977) most *Vicia* species investigated here can be considered xenogams or facultative xenogams, with the exception of *V. hirsuta* and *V. pubescens* (Table 2), which behaved as facultative autogams and had also the smallest flowers. This relation between flower size and breeding system has been shown in earlier studies (e.g. Lloyd, 1965; Baker, 1967; Ornduff, 1969; Gibbs et al., 1975) and that reduction in flower size may have led to a concomitant reduction in energy costs per flower (Cruden, 1977) and increased efficiency in pollen transfer (Cruden & Miller-Ward, 1981), and hence to self-pollination.

However, Zhang & Mosjidis (1995) in a paper about some species of *Vicia* reported that *V. benghalensis*, *V. lutea* and *V. sativa* were automatic self-fertilizing while *V. villosa* subsp. *varia* was cross-fertilizing. These results were based on percentage of fruit set in controlled pollination experiments but they did not show data about P/O ratios. So, either the P/O ratio is not a good indicator of outcrossing in this genus or the breeding system of those species is variable between populations.

We found that there was a significant positive correlation between mean seed weight and the pollen-ovule ratio. Charnov (1982) interpreted the correlation between the P/O ratio and the degree of outcrossing in terms of optimal resource allocation to sexual function, but because seed size is a component of effort as well as quantity, his model also predicts that species with larger seeds will have higher P/O ratios. Similar results were reported by Preston (1986) in Brassicaceae, Mione & Anderson (1992) in *Solanum*, and Uma Shaanker & Ganeshaiyah (1984) in *Phyllanthus*.

Style length in the *Vicia* species we studied correlated directly with pollen grain volume. This relationship may reflect the importance of the food reserves used by pollen grains to form the pollen tubes and migrate to the ovules. This idea was first suggested by Delpino (in Darwin, 1896), and has subsequently been corroborated by Plitmann & Levin (1983) in Polemoniaceae and Williams & Rouse (1990) in *Rhododendron*. However, this correlation does not hold for all plants (see Cruden & Lyon, 1985 and references therein, or Knudsen & Mogens Olesen, 1993 in Pyrolaceae); the lack of correlation may be explainable by the hypothesis proposed by Amici (1830), according to which the pollen tubes are also nourished via the transmission tissue of the style (see Knox, 1984; Cresti et al., 1992).

Primack (1987) predicted that, in general, species with large flowers composed of large petals would also be expected to have large sepals, filaments, anthers, ovaries,

stigmas and styles. The simplest explanation for these correlations lies in the effects of pleiotropy, possibly influenced by genes that control the increase in cell size and number in the floral parts. In *Vicia*, as in other genera, changes in the size of flower parts are accompanied by parallel changes in male (i.e. pollen number and pollen grain size) and female function (i.e. ovule number and seed size), and by changes in floral rewards (pollen or nectar). Similarly, smaller flowers and the correspondingly smaller rewards they offer to pollinators may have been associated with a change toward autogamy (see Ornduff, 1969; Arroyo, 1981; Hanelt & Mettin, 1989) in annual plants. This pattern is in fact widespread in many families found in temperate zones, such as Cistaceae (Herrera, 1992) or the section *Scrophularia* within the genus of the same name (Ortega Olivencia & Devesa, 1993b).

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APPENDIX

Vicia material studied

Between parentheses: N means population where nectar was studied; P/O, population where pollen and ovule production were studied; Tp, population where pollen size was studied; Tf, population where flower size was studied.

***Vicia benghalensis* L. (BEN)**

BADAJOZ. Near to Santa Amalia, 18 iii 1993, *G. Buzo, R. Martín & A. Ortega* 840/93 (N, Tf); Alburquerque, 26 iii 1993, *A. Ortega & S. Ramos* 841/93 (N, P/O, Tp, Tf); Badajoz, Facultad de Ciencias, 1 iv 1993, *A. Ortega & S. Ramos* 843/93 (N); Salvatierra de los Barros, 15 iv 1993, *J.A. Devesa, A. Fernández, P. Moreno & A. Ortega* 66/93 (N, P/O, Tp, Tf); Alburquerque, Sierra del Puerto del Centinela, 22 iv 1993, *A. Ortega & P. Rodríguez* 146/93 (N, Tp); From Alconera to Burguillos del Cerro, 3 vi 1993, *T. Ruiz & A. Ortega* 583/93 (N, Tf); Crossing Maguilla-Berlanga, 5 iv 1994, *A. Ortega & T. Rodríguez* 304/94 (N, Tf).

CACERES. Aliseda, 22 iv 1993, *A. Ortega & T. Rodríguez* 153/93 (N, Tf); Torrejón el Rubio, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 219/93 (N); Jaraicejo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 244/93 (N, Tf); Romangordo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 276/93 (N); Pozuelo de Zarzón, S^a de Gata, 21 v 1993, *A. Ortega & S. Ramos* 416/93 (N, P/O, Tp, Tf).

***Vicia cracca* subsp. *tenuifolia* (Roth) Gaudin (TEN)**

BADAJOZ. Tentudía, 9 vi 1993, *A. Ortega & T. Ruiz* 634/93 (N, P/O, Tf).

CACERES. Santibáñez el Alto, 21 v 1993, *A. Ortega & S. Ramos* 429/93 (N, P/O, Tp, Tf); Road Berzocana-Cañamero, 25 v 1994, *A. Ortega & T. Rodríguez* 317/94 (N, Tf); San Martín de Trevejo, 2 vi 1994, *A. Ortega & T. Rodríguez* 339/94 (N, Tf).

***Vicia disperma* DC. (DIS)**

BADAJOZ. Alburquerque, 26 iii 1993, *A. Ortega & S. Ramos* 842/93 (N, P/O); Valle de Santa Ana, 31 iii 1993, *A. Ortega & S. Ramos* 844/93 (N); Barcarrota, Río Alcarrache, 3 vi 1993, *A. Ortega & T. Ruiz* 536/93 (N, P/O, Tp, Tf).

CACERES. Montfragüe, Río Tajo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 253/93 (N, Tf); Sierra de San Pedro, Ribera del Sotillo, 22 iv 1993, *A. Ortega & T. Rodríguez* 155/93 (N, Tf); Aliseda, 22 iv 1993, *A. Ortega & T. Rodríguez* 154/93 (N, Tf); Near to Valdecañas del Tajo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 232/93 (N, Tf); Romangordo, near to National Road, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 278/93 (N, P/O, Tf); Santibáñez el Alto, 21 v 1993, *A. Ortega & S. Ramos* 425/93 (N, Tf); Road Berzocana-Cañamero, 25 v 1994, *A. Ortega & T. Rodríguez* 316/94 (N, P/O); Serrejón, 28 iv 1994, *A. Ortega & T. Rodríguez* 267/94 (N, Tf).

***Vicia hirsuta* (L.) S.F. Gray (HIR)**

BADAJOZ. Next to Monasterio de Tentudía, 16 iv 1993, *J.A. Devesa, A. Fernández, P. Moreno & A. Ortega* 67/93 (N, P/O, Tp, Tf).

CACERES. Villasbuenas de Gata, 21 v 1993, *A. Ortega & S. Ramos* 420/93 (N, Tf); From crossing Villasbuenas de Gata-Hernán Pérez to Embalse de Borbollón, 21 v 1993, *A. Ortega & S. Ramos* 423/93 (N, P/O, Tp, Tf); Santibáñez el Alto, 21 v 1993, *A. Ortega & S. Ramos* 426/93 (N, P/O, Tp, Tf); Baños de Montemayor, 9 vi 1994, *A. Ortega & T. Rodríguez* 366/94 (N, Tf); Guadalupe, 15 vi 1994, *A. Ortega & T. Rodríguez* 383/94 (N, Tf).

***Vicia lutea* L. subsp. *lutea* (LUT)**

BADAJOZ. Badajoz, Facultad de Ciencias, 2 ii 1993, *A. Ortega* 845/93 (N, P/O, Tp, Tf); From Calera de León to Tentudía, 30 iii 1993, *A. Ortega & S. Ramos* 846/93 (N, Tf); Badajoz, Arroyo de Hinojales, 15 iv 1993, *A. Ortega & S. Ramos* 847/93 (N, Tf); Valle de la Serena, 23 iv 1993, *T. Ruiz, R. Tormo, A. Gallego & F. Monge* 72/93 (N, Tf).

CACERES. Road from Aliseda to Alburquerque, 22 iv 1993, *A. Ortega & P. Rodríguez* 848/93 (N, Tf); Near to Valdecañas del Tajo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 230/93 (N, P/O, Tp, Tf); Monroy, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 258/93 (N, Tf); From crossing Villasbuenas de Gata-Hernán Pérez to Embalse de Borbollón, 21 v 1993, *A. Ortega & S. Ramos* 421/93 (N, Tf); Santibáñez el Alto, 21 v 1993, *A. Ortega & S. Ramos* 427/93 (N, Tf); Embalse de Arrocampo, Almaraz, 11 iii 1994, *A. Ortega, T. Rodríguez & S. Ramos* 49/94 (N, Tf); Plasencia, crossing to Montehermoso, 28 iv 1994, *A. Ortega & T. Rodríguez* 281/94 (N, Tf).

***Vicia lutea* subsp. *vestita* (Boiss.) Rouy (VES)**

BADAJOS. Rivera de Badajoz, Badajoz-Olivenza road, 31 v 1993, *A. Ortega* 514/93 (P/O, Tf).

CACERES. Saucedilla, 4 iv 1994, *A. Ortega & T. Rodríguez* 169/94 (N, P/O, Tp, Tf).

***Vicia sativa* L. subsp. *sativa* (SAT)**

BADAJOS. Alburquerque, 26 iii 1993, *A. Ortega, P. Rodríguez & S. Ramos* 849/93 (N, Tf); Barcarrota, 31 iii 1993, *A. Ortega, P. Rodríguez & S. Ramos* 850/93 (N, Tf); Between Alconera and La Lapa, 16 iv 1993, *J.A. Devesa, A. Fernández, P. Moreno & A. Ortega* 851/93 (N, Tf); Presa de la Peña del Aguila, Villar del Rey, 22 iv 1993, *A. Ortega & P. Rodríguez* 145/93 (N, P/O, Tf); Near to S. Francisco de Olivenza, 17 ii 1994, *A. Ortega & T. Rodríguez* 6/94 (N, P/O, Tp, Tf).

CACERES. Torrejón el Rubio, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 220/93 (N); Montfragüe, Río Tajo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 251/93 (N); Near to Romangordo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 277/93 (N); Serrejón, 11 iii 1994, *A. Ortega, T. Rodríguez & S. Ramos* 54/94 (N, P/O, Tp, Tf); Highway of Extremadura, Km 264, 24 iii 1994, *A. Ortega & T. Rodríguez* 143/94 (N, P/O, Tp, Tf).

***Vicia sativa* subsp. *nigra* (L.) Ehrh. (NIG)**

BADAJOS. Tentudía, 9 vi 1993, *A. Ortega & T. Ruiz* 633/93 (N, Tf); Alburquerque, Sierra del Puerto del Centinela, 26 iii 1993, *A. Ortega & S. Ramos* 852/93 (N); Road from Aliseda to Alburquerque, río Zapatón, 22 iv 1993, *A. Ortega & P. Rodríguez* 151/93 (N, P/O, Tp, Tf); Villar del Rey, Sierra del Puerto del Centinela, 22 iv 1993, *A. Ortega & S. Ramos* 147/93 (N, Tf).

CACERES. Sierra de San Pedro, 22 iv 1993, *A. Ortega* 149/93 (N, Tf); Near to Valdecañas del Tajo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 231/93 (N, P/O, Tp, Tf); Montfragüe, Río Tajo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 252/93 (N, Tf); Sierra de Gata, Rivera de Gata, 21 v 1993, *A. Ortega & S. Ramos* 417/93 (N, Tf); From crossing Villasbuenas de Gata-Hernán Pérez to Embalse de Borbollón, 21 v 1993, *A. Ortega & S. Ramos* 422/93 (N, Tf); Santibáñez el Alto, 21 v 1993, *A. Ortega & S. Ramos* 428/93 (N, P/O, Tp, Tf); Las Huertas, near to Valencia de Alcántara, 14 iii 1994, *A. Ortega & S. Ramos* 73/94 (N, Tf); Puerto de Tornavacas, 9 vi 1994, *A. Ortega & T. Rodríguez* 374/94 (N, Tf).

***Vicia parviflora* Cav. (PAR)**

BADAJOS. Llerena, Trasierra, 9 vi 1993, *A. Ortega & T. Ruiz* 610/93 (N, P/O, Tp, Tf); Usagre, Rivera de Usagre, 5 iv 1994, *A. Ortega & T. Rodríguez* 288/94 (N, Tf); Crossing Maguilla-Berlanga, 5 iv 1994, *A. Ortega & T. Rodríguez* 303/94 (N, Tf).

CACERES. From Villasbuenas de Gata to Hernán Pérez, 21 v 1993, *A. Ortega & S. Ramos* 419/93 (N, Tf); Santibáñez el Alto, 21 v 1993, *A. Ortega & S. Ramos* 424/93 (N,

P/O, Tp, Tf); Sierra de S. Pedro, crossing Road Badajoz-Cáceres and Aliseda, 31 v 1993, *A. Ortega* 513/93 (N, P/O, Tp, Tf); Between Valverde del Fresno and Navasfrías, 2 vi 1994, *A. Ortega & T. Rodríguez* 337/94 (N, Tf).

***Vicia peregrina* L. (PER)**

BADAJOZ. Between Zafra and Los Santos de Maimona, 16 iv 1993, *J.A. Devesa, A. Fernández, P. Moreno & A. Ortega* 57/93 (N, P/O, Tp, Tf); Villafranca de los Barros, 11 iv 1994, *A. Ortega* 215/94 (N, P/O, Tp, Tf).

***Vicia pubescens* (DC.) Link (PUB)**

BADAJOZ. Valle de Matamoros, 7 vi 1994, *A. Ortega & T. Rodríguez* 361/94 (P/O, Tf).

***Vicia vicioides* (Desf.) Coutinho (VIC)**

BADAJOZ. La Lapa, between Alconera and La Lapa, Sierra de La Lapa, 16 iv 1993, *J.A. Devesa, A. Fernández, P. Moreno & A. Ortega* 50/93 (N, P/O, Tp, Tf); Sierra de Alconera, Alconera, 17 iii 1994, *A. Ortega & T. Rodríguez* 90/94 (N, Tf); Cerro Carija, Mérida, 19 iv 1994, *T. Rodríguez* 231/94 (N, P/O, Tp, Tf).

CACERES. Valdecañas del Tajo, 11 iii 1994, *A. Ortega, T. Rodríguez & S. Ramos* 63/94 (N, P/O, Tp, Tf).

***Vicia villosa* subsp. *eriocarpa* (Hauskn.) P.W. Ball (ERI)**

BADAJOZ. Badajoz, Facultad de Económicas, 19 iii 1993, *A. Ortega* 853/93 (N, Tf); Finca de las Arenosas, 15 iv 1993, *A. Ortega & S. Ramos* 855/93 (N, P/O, Tp, Tf); Arroyo de San Gabriel, 15 iv 1993, *A. Ortega & S. Ramos* 854/93 (N, P/O, Tp).

***Vicia villosa* subsp. *varia* (Host) Corb. (VAR)**

BADAJOZ. Salvatierra de los Barros, 9 vi 1993, *A. Ortega & T. Ruiz* 607/93 (N, Tf).

CACERES. Romangordo, 7 v 1993, *A. Ortega, S. Ramos, F. Hernández, M. Rodas & P.J. Parejo* 275/93 (N, Tf); Moraleja, 21 v 1993, *A. Ortega & S. Ramos* 418/93 (N, P/O, Tp, Tf); Sierra de Gata, Torre de Don Miguel, 30 vi 1993, *A. Ortega & S. Ramos* 786/93 (N, P/O, Tp, Tf); Las Huertas, near to Valencia de Alcántara, 14 iii 1994, *A. Ortega & S. Ramos* 72/94 (N, Tf); Río Rucas, Cañamero, 25 v 1994, *A. Ortega & T. Rodríguez* 320/94 (Tf).