

CHARACTERISTICS OF INFRUCTESCENCE AND SEED YIELD IN A *PRIMULA* HYBRID ZONE

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Hybridisation between *Primula vulgaris* and *P. veris* was investigated along a southwest exposed slope in a woodland in Hungary. Parent species and hybrids were identified by colour and size of the flowers. The two morphs within each taxon showed only slight differences, but discrimination of the three taxa was unambiguous. Scape and pedicel length proved to be suitable for distinguishing hybrids from *P. veris* on the basis of inflorescence architecture. Seed yield components showed considerable differences between the two parent species: *P. veris* produced more and lighter seeds per capsule than *P. vulgaris* did. Hybrids also differed significantly from the parent species: hybrids had the fewest and heaviest seeds per capsule among the three taxa. The two parent species did not show the slightest sign of gender specialisation: fruit number per plant, fruit set, and seed number per capsule were equal in long-styled and short-styled morphs. The two morphs, however, were not equally successful in hybrids: fruit number per plant and fruit set were significantly lower in long-styled plants than in short-styled plants, although the long-styled morph with highly exerted stigmas was expected to be in more favourable situation for pollination.

Key words: gender specialisation, heterostyly, interspecific hybridisation, morphological traits, seed yield

INTRODUCTION

Plant species are generally isolated from each other by strong genetic, temporal and/or environmental barriers. In some angiosperm groups, however, interspecific hybridisation seems to be common (Stebbins 1959, Knobloch 1972, Ellstrand *et al.* 1996). In these groups the reproductive isolation is not complete for the closely related species, so they can mate and reproduce freely wherever they meet. It has been known for a long time that *Primula* species show great affinity to hybridisation (Hegi 1975). Three allied species of the genus, *P. veris* L., *P. vulgaris* Huds. and *P. elatior* (L.) Hill, form a special hybridisation circle isolated strictly from other *Primulas* (Hegi 1975). In the middle of the last century this hybridisation circle was widely investigated in terms of seed formation (Valentine 1955, Valentine and Woodell 1960, 1963, Woodell 1960, Woodell and Valentine 1961).

F₁ hybrid plants are sometimes intrinsically unfit (Arnold and Hodges 1995, Barton and Hewitt 1985, Hewitt 1988), but several examples are known where hybrids do not have any substantial fitness disadvantages (Emms and Arnold 1997, Levin and Schmidt 1985, Wang *et al.* 1997). Although F₁ hybrid seeds borne on *P. vulgaris* are not viable, germination rate of F₁ hybrid seeds borne on *P. veris* is about 14% (Valentine 1955). Some hybrid plants can survive and reach reproductive maturity, and they are able to produce viable pollen grains and to set viable seeds (Valentine 1955, Woodell 1965).

Seed yield is the product of seed number per plant (fecundity), and mean seed weight (maternal investment to the offspring), so it determines the size and quality of the offspring (Willson 1983). To determine the regulation of seed yield one needs to examine patterns of variation in yield components, and to quantify relationships among the components. In most natural plant populations all the yield components show high variability, and weak relationships can be found among them (Primack and Antonovics 1981, Pritts and Hancock 1985, Winn and Werner 1987). The high degree of flexibility allows for controlling seed production at many different points along the development of seeds.

Seed yield is of special interest in heterostylous species, where populations consist of two or three style-length morphs. *Primula* species are distylous: in long-styled flowers the stigma is in the mouth of the corolla tube and anthers are attached to the corolla tube at about middle height, while arrangement of the stigma and anthers is the opposite in short-styled flowers. Morphological differences between the flowers raise the possibility of gender specialisation, since the two morphs may have different probabilities of pollen receipt and donation (Willson 1979). Other researchers feel, however, that heterostyly is rather a means to equalise pollen receipt and donation (Horovitz 1978). This question becomes especially important in hybrid flowers, where the position of reproductive organs is likely to be changed in comparison to the parent species, whereby short-styled flowers may get into unfavourable situation for pollination.

Our investigations were performed in a hybrid zone continuously existing for more than 20 years (Nagy and Dános 1979). The hybrid zone is found along a slope in a woodland, where *Primula veris* and *P. vulgaris* grow together with their interspecific hybrids. Appearance of the hybrid plants is very diverse, but differences from the two parent species are unambiguous when they are in flower. In this work we examined some reproductive parameters (1) to document variation in morphological traits and seed yield components between the two morphs and among the three taxa; (2) to reveal the characteristics of seed yield regulation in *P. veris* and hybrids; and (3) to assess whether there is any sign of gender specialisation between the two morphs of the three taxa.

MATERIAL AND METHODS

Study organisms

Primula veris L. (cowslip) and *P. vulgaris* Huds. (primrose) are perennial herbs with large hairy leaves in a lax rosette. *P. veris* has umbel-like inflorescence with small orange flowers, while the flowers of *P. vulgaris* are solitary, large and pale yellow. The hybrids are intermediate in flower size and colour between their parents, and they have pedunculate inflorescence similar to the cowslip (Clifford 1958, Hegi 1975). Capsules are ovoid, and are enclosed in the calyx. Seeds are small with thick and hard coat.

Study site

Our study site is arranged in a woodland in the Bakony Mountain, Western Hungary. The hybrid zone is harboured on a southwest exposed slope. In the lower part of the slope there is a beech wood, in which *Fagus sylvatica* is interspersed with *Carpinus betulus*. The moist, shady wood is the habitat of *P. vulgaris* (vulgaris site). The upper part of the slope continues in a plateau, and there is a mixed oak wood there with *Quercus cerris*, *Fraxinus ornus* and *Acer campestre*. The warm, bright wood is the habitat of *P. veris* (veris site). The pure stands of parental species are connected by a steep slope of ca 85 m length containing hybrids (hybrid site).

Sampling procedure

In 2000, about 120 long-styled and 120 short-styled plants each from the three taxa were tagged when they were in flower. Taxa were considered only in their own sites, and no selection of hybrid plants was made. In *P. veris*, 97 long-styled and 96 short-styled infructescences, in hybrids 80 long-styled and 77 short-styled infructescences were found on the tagged plants. Length of scapes and number of flowers and fruits per infructescence were recorded. Plants were characterised by the length of the longest scape (as this invariably carries the most flowers) and the total number of flowers and fruits per plant. After this census 20 long-styled and 20 short-styled plants each of *P. veris* and hybrids were arbitrarily chosen to quantify seed yield. In *P. veris* a total of 181 long-styled and 190 short-styled, in hybrids a total of 135 long-styled and 161 short-styled capsules were collected.

In *P. vulgaris* the tagging method used was absolutely unsuccessful. The failure could mainly be explained by the unexpectedly low fruit set and the high degree of fruit predation, which caused the loss of tags fastened to the

pedicels. We had to choose another 200 individuals (100 long-styled and 100 short-styled) borne at least one fruit without any symptoms of damage. Morphs were determined by the remains of style on the capsule. The number of fruits per individual was counted, and one mature, undehisced and uninjured fruit per plant was collected.

Capsules were stored in small paper envelopes and air-dried in an exsiccator (30 °C, 3 months). Digitised pictures were taken on each fruit by using a dissecting microscope equipped with a colour camera (HV-C20, Hitachi, Japan). Length of the pedicels, and length and width of the fruits were recorded by an image analysis program (Image-Pro Plus 3.0, Media Cybernetics, USA). Seeds were removed from the capsules, examined under dissecting microscope, and shrivelled (obviously non-viable) seeds were rejected. The number of seeds per capsule was counted, and all seeds from each fruit were weighed as a group to the nearest 0.01 mg. Mean seed weight per capsule was estimated by dividing the total weight of all seeds per capsule by the number of seeds per capsule.

Statistical analysis

In *P. veris* and hybrids, where all the fruits were collected from each plant, mean values for pedicel length, capsule length and width, seed number per capsule, and mean seed weight were calculated per plant because of a substantial variation between plants in number of fruits (fruit number per plant varied between 2 and 11 in *P. veris*, and between 2 and 13 in hybrids). Distribution of parameters in the two morphs of the three taxa was tested by the Shapiro-Wilk's method, and if it was necessary, data were transformed by calculating $\log_{10}(x+1)$ before analyses. The two morphs within each taxon were compared by Student t-test (parametric assumptions) or by Mann-Whitney U-test (non-parametric assumptions). We used two-way ANOVAs of each parameter to test the effect of taxa and morphs. If significant differences were found for the three taxa, Student–Newman–Keuls multiple range test was used for comparing the pairs.

Variability of the parameters was characterised by coefficients of variation (CV), which was calculated as one hundred times the standard deviation divided by the mean. Relationships among parameters were analysed by calculating Pearson product-moment correlation coefficients (r , parametric assumptions) or Spearman rank correlation coefficients (R , non-parametric assumptions).

In *P. veris* and hybrids, seed yield can be divided into components as the following expression:

$$\text{SEED YIELD} = \text{INFR} \times \text{FLOW} \times \text{FRUS} \times \text{SNUM} \times \text{SWEI},$$

where INFR is the number of infructescences per plant, FLOW is the mean number of flowers per infructescence, FRUS is the fruit set, SNUM is the mean number of seeds per fruit, and SWEI is the mean seed weight. The 80 plants chosen for quantifying seed yield had only one infructescence per plant, so the expression was simplified by leaving out the infructescence number (plants with more than one infructescences were very rare in the sample: one out of 192 plants in *P. veris* and three out of 154 plants in hybrids produced two infructescences). Data were log-transformed, and variance of each component and covariance between each pair of components were calculated. The variance of log (seed yield) is equal to the sum of variances and twice the covariance obtained on log-transformed data (Mott 1966). Variance and covariance were standardised by expressing them as percentages of variance in log (seed yield). Differences between the two taxa were also examined by using a principal component analysis (STATISTICA 5.5 2000). Data were standardised by means and standard deviations before analysis.

RESULTS

Comparison of the two morphs within each taxon did not detect any difference in *P. vulgaris*, but significant differences were found between the two morphs in *P. veris* and hybrids (Table 1). In *P. veris*, short-styled plants pro-

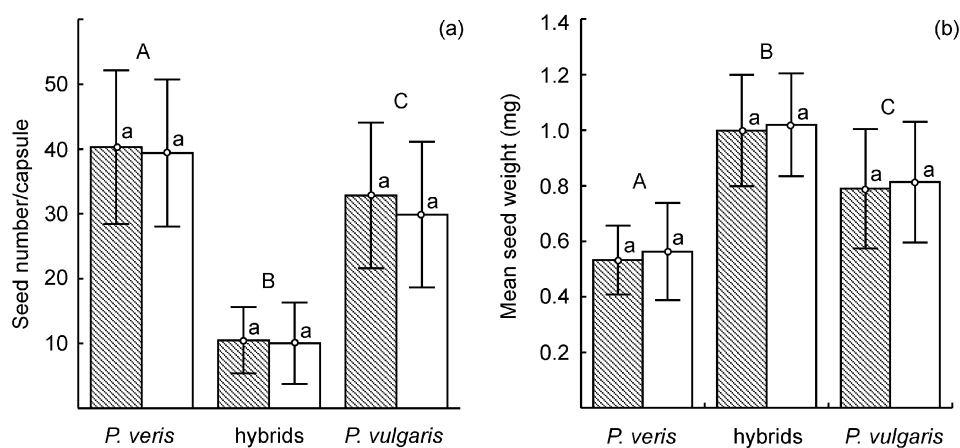


Fig. 1. Means and standard deviations of seed number per capsule (a) and mean seed weight (b) in the short-styled (hatched columns) and long-styled (open columns) morphs of the three taxa. The results of comparisons of the two morphs within each taxon are indicated by different small letters, the results of comparisons of the three taxa are indicated by different capital letters (values differ significantly at $p < 0.05$)

Table 1
Means \pm standard deviations (M \pm SD) and coefficients of variation (CV) for the parameters examined in the two morphs of the three taxa. The two morphs within each taxon were compared by Mann–Whitney U-test (fruit set in *P. veris*, fruit set, capsule width and mean seed weight in hybrids) or by Student t-test (the other parameters), and the results of comparisons are indicated by different small letter superscripts (values differ significantly at $p < 0.05$)

	<i>Primula veris</i>						Hybrids						<i>Primula vulgaris</i>								
	short-styled		long-styled		short-styled		long-styled		short-styled		long-styled		short-styled		long-styled		short-styled		long-styled		
	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	M \pm SD	CV	
Scape length (mm)	214 \pm 38a	17.6	216 \pm 40a	18.3	98 \pm 29a	29.1	97 \pm 26a	27.1	—	—	—	—	—	—	—	—	—	—	—	—	—
Pedicel length (mm)	18 \pm 3a	18.8	18 \pm 4a	23.2	21 \pm 4a	19.3	24 \pm 5a	22.1	40 \pm 13a	31.9	42 \pm 15a	35.9	—	—	—	—	—	—	—	—	—
Flower number	6.2 \pm 2.1a	33.4	5.6 \pm 2.0b	34.8	6.7 \pm 3.0a	44.5	6.5 \pm 2.9a	44.8	—	—	—	—	—	—	—	—	—	—	—	—	—
Fruit number	5.2 \pm 2.0a	38.7	4.8 \pm 1.9a	40.2	4.7 \pm 2.7a	57.9	3.9 \pm 1.7b	43.2	3.6 \pm 2.8a	77.8	4.0 \pm 2.5a	62.8	—	—	—	—	—	—	—	—	—
Fruit set	0.84 \pm 0.19a	22.6	0.85 \pm 0.18a	21.2	0.72 \pm 0.24a	33.3	0.63 \pm 0.23b	36.5	—	—	—	—	—	—	—	—	—	—	—	—	—
Capsule length (mm)	7.9 \pm 0.7a	9.2	7.8 \pm 0.9a	11.1	7.7 \pm 1.4a	18.0	7.3 \pm 1.2a	15.9	7.2 \pm 0.9a	12.3	6.9 \pm 0.9a	12.5	—	—	—	—	—	—	—	—	—
Capsule width (mm)	4.8 \pm 0.4a	7.3	5.0 \pm 0.5a	9.8	4.3 \pm 0.5a	11.2	4.4 \pm 0.7a	15.9	4.7 \pm 0.6a	12.4	4.6 \pm 0.6a	13.4	—	—	—	—	—	—	—	—	—
Seed number/capsule	40.3 \pm 11.9a	29.5	39.4 \pm 11.4a	28.9	10.5 \pm 5.1a	48.6	10.0 \pm 6.3a	63.0	32.8 \pm 11.2a	34.1	29.9 \pm 11.2a	37.5	—	—	—	—	—	—	—	—	—
Mean seed weight (mg)	0.53 \pm 0.12a	22.6	0.56 \pm 0.18a	32.1	1.0 \pm 0.2a	20.0	1.02 \pm 0.18a	18.6	0.79 \pm 0.22a	27.8	0.81 \pm 0.22a	27.2	—	—	—	—	—	—	—	—	—
Seed yield (mg)	198.1 \pm 87.7a	44.3	193.8 \pm 78.8a	40.6	85.6 \pm 56.4a	65.9	72.6 \pm 55.3a	76.2	—	—	—	—	—	—	—	—	—	—	—	—	—

duced significantly more flowers than long-styled plants. In hybrids, fruit number per plant and fruit set were significantly higher in short-styled plants than in long-styled plants. Seed number per capsule and mean seed weight did not show significant differences between the two morphs in any of the three taxa (Fig. 1).

Two-way ANOVAs testing for effects of taxa and morphs showed characteristic differences among the three taxa, whilst the morphs did not have any significant effect on the reproductive parameters examined (Table 2). Pair-wise comparison of the three taxa revealed that the two parent species differed from one another in all the parameters examined. The hybrids were clearly distinguishable from both parent species except for two parameters: hybrid plants produced similar number of fruits as *P. vulgaris* plants, and hybrids did not differ significantly from *P. veris* in capsule length. The difference between *P. veris* and hybrid plants was unambiguous on the basis of scape length and fruit set, but flower number per plant showed only a slight difference between the two taxa. Comparison of the seed yield components revealed that hybrids had the lowest number of seeds per capsule and the highest mean seed weight among the three taxa (Fig. 1).

Fruit number per plant was the most variable parameter, especially in *P. vulgaris* with coefficients of variation between 60 and 80% (Table 1). Hybrids showed higher variability for scape length, flower number per plant and fruit set than *P. veris*, and both length and width of capsules were more variable in hybrid plants than in either of the parent species. Seed number per capsule showed the highest variability in hybrid plants (especially in long-styled morph with a coefficient of variation up to 63%), whereas variability of mean seed weight was higher in both parent species than in the hybrids.

Correlation coefficients for the parameters measured in *P. veris* and hybrids are presented in Table 3. In hybrids, scape and pedicel length did not have considerable relationship with the other parameters. In *P. veris* scape length showed positive correlation with pedicel length and flower number per plant, and negative correlation with fruit set and capsule length. Pedicel length, however, was positively correlated with flower and fruit number per plant and capsule width. In hybrids significant positive correlation was detected between fruit set and seed number per capsule, but there was practically no relationship between seed number per capsule and mean seed weight. In *P. veris* seed number per capsule was totally independent from fruit set, but there was a considerable trade-off between number and size of seeds. The negative correlation between seed number per capsule and mean seed weight was also detectable in *P. vulgaris* ($r = -0.44$, $n = 200$, $p < 0.001$).

Analysis of the relative importance of each component in determining seed yield revealed that the regulation was more complex in *P. veris* than in the

Table 2

Results of two-way ANOVAs testing for effects of taxa and morphs on reproductive parameters measured. For scape length, flower number, fruit set, and seed yield, comparison of taxa is limited to *P. veris* and hybrids because of the missing data on *P. vulgaris*. * = $p < 0.05$, *** = $p < 0.001$

Dependent variable	Source	df	SS	F	P
Scape length	Taxon	1	11,763.42	1012.86	< 0.001***
	Morph	1	0.95	0.08	0.775
	Taxon × morph	1	2.29	0.20	0.657
	Error	342	3,970.62		
Pedicel length	Taxon	2	250.80	87.25	< 0.001***
	Morph	1	0.62	0.43	0.513
	Taxon × morph	2	0.28	0.10	0.906
	Error	274	391.82		
Flower number	Taxon	1	36.75	6.01	0.015*
	Morph	1	11.60	1.90	0.169
	Taxon × morph	2	4.68	0.77	0.382
	Error	342	2,089.62		
Fruit number	Taxon	2	134.28	12.51	< 0.001***
	Morph	1	7.78	1.45	0.229
	Taxon × morph	2	30.66	2.86	0.058
	Error	539	2,894.43		
Fruit set	Taxon	1	2.41	55.87	< 0.001***
	Morph	1	0.09	2.16	0.142
	Taxon × morph	1	0.21	4.83	0.029*
	Error	342	13.68		
Capsule length	Taxon	2	23.84	13.74	< 0.001***
	Morph	1	2.41	2.77	0.097
	Taxon × morph	2	0.14	0.08	0.927
	Error	274	238.38		
Capsule width	Taxon	2	6.68	9.95	< 0.001***
	Morph	1	0.24	0.72	0.396
	Taxon × morph	2	0.72	1.08	0.342
	Error	274	93.16		
Seed number/capsule	Taxon	2	19,760.44	86.28	< 0.001***
	Morph	1	84.77	0.74	0.390
	Taxon × morph	2	75.30	0.33	0.720
	Error	274	31,375.74		

Table 2 (continued)

Dependent variable	Source	df	SS	F	P
Mean seed weight	Taxon	2	4.28	50.91	< 0.001***
	Morph	1	0.03	0.62	0.434
	Taxon × morph	2	0.01	0.01	0.993
	Error	274	10.96		
Seed yield	Taxon	1	278,639.10	55.13	< 0.001***
	Morph	1	1,789.70	0.35	0.554
	Taxon × morph	1	257.90	0.05	0.822
	Error	76	384,142.00		

hybrids (Table 4). In the hybrids most variation among plants resulted from differences in flower number per plant and seed number per capsule. In *P. veris* the two most important factors were the same as in the hybrids, but considerable negative covariance was detected between seed number per capsule and mean seed weight. In contrast to the hybrids, variance of mean seed weight and covariance between flower number per plant and seed number per capsule also seemed to be important in *P. veris*.

We extended our analysis using a principal component analysis to see if *P. veris* and the hybrids could be distinguished on the basis of the reproductive

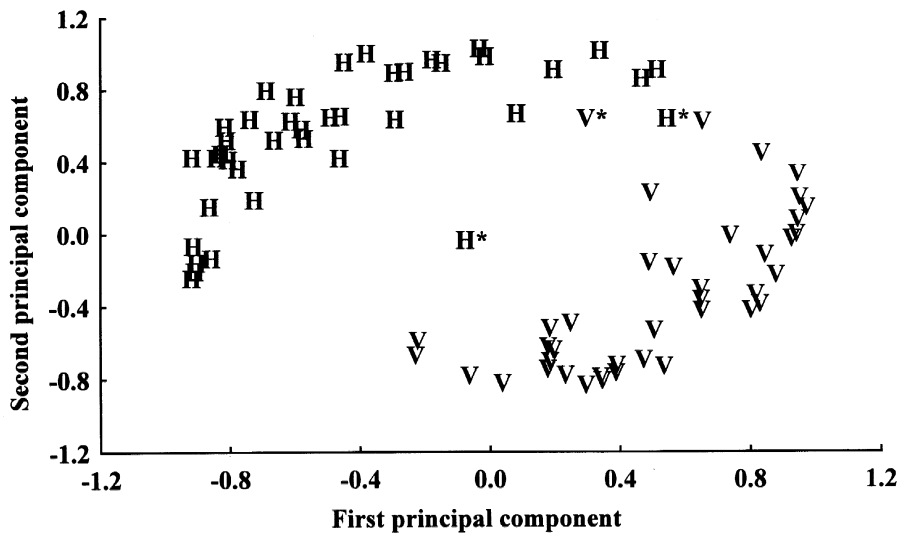


Fig. 2. Results of the principal component analysis on *P. veris* (V) and the hybrids (H). 40 individuals each from the two taxa were included in the analysis. The three individuals indicated by asterisks do not join exactly to their own groups

Table 3

Correlation coefficients for the morphological traits and seed yield components in *P. veris* (above diagonal) and hybrids (below diagonal). Spearman rank correlation coefficients were calculated for fruit set in *P. veris*, and for fruit set, capsule width and mean seed weight in hybrids, Pearson product-moment correlation coefficients were calculated for the other parameters. Asterisks denote statistical significance for the correlations: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

	Scape length	Pedicel length	Flower number	Fruit number	Fruit set	Capsule length	Capsule width	Seed number/capsule	Mean seed weight
Scape length									
Pedicel length	-0.14								
Flower number	0.33*								
Fruit number	0.29	0.31							
Fruit set	-0.29	0.24	0.93***						
Capsule length	-0.06	-0.28	-0.20	0.12					
Capsule width	-0.26	-0.01	0.04	0.10	0.18				
Seed number/capsule	-0.15	0.09	0.01	0.08	0.25	0.56***			
Mean seed weight	-0.05	0.16	-0.02	0.09	0.38*	0.67***	0.76***		
		0.05	0.10	0.07	-0.14	0.25	0.34*	0.05	
			0.49**	0.31	-0.48**	-0.40*	0.30	0.16	-0.23
			0.48**	0.45**	-0.16	-0.02	0.59***	0.27	0.17
			0.92***	0.92***	0.19	0.29	0.26	0.32	-0.14
					0.15	-0.33*	0.22	0.32	-0.17
						-0.11	-0.14	0.06	-0.01
							0.16	0.25	0.24
								0.38*	0.32
									-0.54***

Table 4

Variances of seed yield components (on diagonal) and covariances between each pair of components (below diagonal) expressed as percentage of variance in log(seed yield) in *P. veris* and hybrids. Data were log-transformed before analysis

		FN	FS	SN	SW
<i>P. veris</i>	Flower number (FN)	49.01			
	Fruit set (FS)	-7.60	6.52		
	Seed number/capsule (SN)	23.87	2.42	47.96	
	Mean seed weight (SW)	-11.54	-2.11	-42.59	34.04
Hybrids	Flower number (FN)	40.26			
	Fruit set (FS)	-4.25	4.46		
	Seed number/capsule (SN)	-6.86	10.49	45.18	
	Mean seed weight (SW)	4.11	-1.47	1.83	6.25

parameters examined. The component scores of individuals for the first two principal components were plotted against one another (Fig. 2). The two taxa comprised distinct groups, although one out of the 40 plants in *P. veris* and two out of the 40 plants in the hybrids did not join exactly to their own groups. The first principal component weighted mean seed weight, seed number per capsule, and scape length, and it explained 43% of the total variance. The second principal component explaining 23% of the total variance described flower and fruit number per plant.

DISCUSSION

Primula vulgaris and *P. veris* generally occupy strictly isolated habitats as a consequence of their different tolerance to shading (Whale 1984). This spatial isolation is thought to be a very important barrier that minimises the chance of hybridisation between the closely related species. Woodell (1965) described an example of hybridisation, where *P. veris* grew in an atypical habitat, and the two parent species were interspersed with each other. In contrast to this situation, we have carried out our investigation in a hybrid zone, where the two parent species were not in direct contact with each other, but they were connected by a slope functioning as a bridge between the two different habitats. The hybrid zone, that has stably existed for more than 20 years (Nagy and Dános 1979), occupies a unique area and holds hybrids in large mass. These facts also contradict the earlier observations, which suggested that the frequency of *P. veris* × *P. vulgaris* hybrids was rather low in the wild, and hybrid plants occurred as scattered individuals (Valentine 1955).

An investigation on the habitat preference of the *P. vulgaris* × *P. veris* hybrids in the Bakony Mountains proved that the habitat occupied by the hybrids had intermediate features between the habitats occupied by the parent species (Bauer and Cservenka 2002). In our study, the slope harbouring the hybrid zone represents a gradual transition between the pure stands of parent species. Position and width of the hybrid zone seem to be determined by environmentally dependent selection along the ecotone between the two parental sites, as it is described in the ecological selection-gradient models (Endler 1977, Moore 1977). The hybrid zone can be divided into three parts: in the lower part *P. vulgaris* coexists with hybrids, in the middle part only the hybrids grow, and in the upper part the hybrids grow together with *P. veris*. Neither parent species is able to invade the middle part of the slope, which however, seems to be favourable to their hybrids. This kind of distribution makes it probable that the structure of the hybrid zone can be explained by a special case of the ecological selection-gradient models. According to the bounded hybrid superiority model, hybrids are fitter than the parental species in the middle part of the environmental gradient, but less fit than the parental species towards the edges of or outside the hybrid zone (Moore 1977, Moore and Buchanan 1985, Moore and Price 1993).

Identification of the three taxa is unambiguous on the basis of flowers, though hybrids with flowers of intermediate colour and size resemble *P. veris*, as they both have umbel-like inflorescences (Clifford 1958, Hegi 1975). According to the examinations on scape and pedicel length, we can say that *P. veris* forms high and compact inflorescences, whilst hybrid inflorescences are low and slack. Mean flower number per inflorescence is about six in both taxa. Nevertheless, it is worth noting that there were some extremely large inflorescences among the hybrids with up to 18 flowers, while the largest inflorescences of *P. veris* had only 13 flowers. The large rhizome and the great amount of nutrients could be a possible explanation for the extremely large inflorescences of the hybrids, since garden cultivation of the three taxa showed that F₁ hybrid plants were very vigorous (Valentine 1955), and they generally outlived the parent species (Woodell 1965).

Flowers of the three taxa are sympetalous with a long and narrow corolla tube broadening out into five corolla lobes. In these tube-form flowers typical to heterostylous species the correct position of reproductive organs within the flowers is thought to influence the success of pollination (Ganders 1979, Lloyd and Webb 1992). Position of the stigma and the anthers is likely to be changed in the hybrid flowers of intermediate size. Long-styled morph with its highly exerted stigmas is expected to be advantageous for successful pollination by more likely contact with the body of pollinators, whereas concealed stigmas of short-styled flowers may get into very unfavourable situation for pollination

(Campbell *et al.* 1996, Stone and Thomson 1994). Consequently, the changes in position may increase the probability of gender specialisation in hybrids. According to our results on fruit set, fruit number per plant and seed number per capsule, in agreement with earlier observations on *P. vulgaris* (Boyd *et al.* 1990, Piper *et al.* 1986), there are no significant differences between the two morphs in reproductive success in either of the parent species. Hybrids, however, show surprising differences between the two morphs: although seed number per capsule is similar in the two morphs, but fruit number per plant and fruit set are significantly lower in long-styled plants than in short-styled plants. Although we have no explanation for this difference between the two morphs, the success of short-styled plants in reproduction proves that pollen transfer is carried out efficiently between the two morphs.

Examination of seed yield components revealed important differences among the three taxa. Fruit number per plant is similar in *P. vulgaris* and hybrids, but they both produce significantly less fruits than *P. veris*. In the hybrids seed number per capsule is about a quarter of that of *P. veris*, and about a third of that of *P. vulgaris*. The order of taxa is opposite by mean seed weight: hybrid seeds are about twice as heavy as seeds of *P. veris*, and about 1.25 times as heavy as seeds of *P. vulgaris*. It is likely that the extremely low values of capsule width in hybrids are due to the extremely low number of seeds per capsule, and this effect is not compensated by the larger weight of seeds.

The analysis of the relative importance of each component in determining seed yield revealed similar patterns in *P. veris* and the hybrids. Differences among individuals in seed yield can mainly be explained by variances of flower number per plant and seed number per capsule. In *P. veris*, however, beside these two factors variance of seed weight and covariance between flower number per plant and seed number per capsule also have an important role in regulation. In contrast to our results, a similar study on *Arum italicum* Miller showed that most variation among plants in seed yield resulted from differences in fruit set and from covariance between fruit set and seed number per fruit (Méndez 1997).

Beside the variability of seed yield components the interactions among them are also important to examine, as trade-offs between components may tend to buffer total yield (Primack and Antonovics 1981, Pritts and Hancock 1985, Marshall *et al.* 1985). Earlier studies on seed yield predicted high degree of flexibility in the process of seed development in natural plant populations (Primack and Antonovics 1981, Pritts and Hancock 1985, Winn and Werner 1987). The weak relationships among the seed yield components detected both in *P. veris* and the hybrids support this prediction. One exception was the significant positive correlation between fruit set and seed number per capsule in hybrids, which means that some hybrid individuals are more successful than

others. Since positive relationships among seed yield components generally occur if the components are positively related to plant size (Winn and Werner 1987), it would be important to reveal how seed yield components are connected to plant size in these taxa.

Trade-off between size and number of seeds is thought to be a general principle, and the model predicts a uniform size of seeds as optimal adaptation (Smith and Fretwell 1974). The negative correlation between seed number per capsule and mean seed weight is already documented in *Primula vulgaris* (Boyd *et al.* 1990), and our results confirm the accommodation to the prediction of trade-off in both parent species. In the hybrids, however, there is practically no relationship between size and number of seeds within each capsule. In contrast to all the other parameters measured, mean seed weight shows unexpectedly low variation in the hybrids. Furthermore, the hybrids have the lowest variation for this parameter among the three taxa. The lack of trade-off between size and number of seeds and the low variability of seed size make it probable that there is no resource limitation of seed weight in the partly filled capsules of the hybrids. Whether the weak fruit set and the low number of seeds per capsule in hybrids are due to little suitable pollen loads on stigmas or are the consequences of irregularities at meiosis – as it was suggested by Valentine (1955) – requires further studies.

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