The variation of F₂ progenies derived from interspecific crosses between *Phaseolus vulgaris* and *Phaseolus coccineus*

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Interspecific hybridisation within the genus *Phaseolus* represents an important source of genetic variation which can be very useful in breeding programmes based on recurrent selection. The aim of this investigation was to analyse the phenotypic variation and relationships among the most important quantitative traits in F_2 generation materials derived from crosses *P. vulgaris* x *P. coccineus*. *P. vulgaris* was used as female while *P. coccineus* as male parent. The F_2 material was composed of 825 individuals which originated from open pollination of 65 F_1 plants. The most variable quantitative trait was the number of flowers per inflorescence, which varied from 0 to 57 (CV = 45.8 %). The second was the inflorescence length which varied from 2.5 to 74 cm (CV = 39.0 %). The highest value (CV = 70.4 %) was obtained for floral colour (a qualitative trait which was transformed into a special numerical scale). The correlation analysis showed that there were close relationships among the muber of leaves, number of flowers, number of pods, number of seeds and the length of the growth period. For practical breeding, the most useful is probably the correlation between the number of inflorescences and the number of seeds per plant (r = 0.503 and 0.560) because the number of inflorescences can be easily determined at the beginning of the hybridisation period, and the number of seeds is more or less directly associated with the yield. For the final visual selection, at the end of the vegetation period, the most useful trait is the number of pods, which is highly correlated with the number of seeds (r = 0.740 and 0.916). Agricultura 2: 19-25 (2003)

Key words: interspecific hybrids; *Phaseolus vulgaris* x *P. coccineus*; hybridisation technique; phenotypic variation; phenotypic correlation coefficients

INTRODUCTION

The common bean (*Phaseolus vulgaris* L.) and the scarlet runner (*P. coccineus* L. syn. *P. multiflorus* Lam.), which belong to the family *Fabaceae*, are extremely heterogeneous species. Both of them have 2n = 22 chromosomes (Darlington and Wylie 1955, Fedorov 1969). The centre of origin is Central America (Kaplan 1965, Purseglove 1977).

These two species have many common characteristics (e.g. leaf and floral structure), however, there are also several differences (e.g. flower shape and seed size, inflorescence shape and length, hypogeal/epigeal germination, level of cross-pollination). *P. vulgaris* is characterised by relatively small flowers, while the flowers of *P. coccineus* are in general larger and more attractive for insects-pollinators. Flowers of both species are of typical legume shape and are borne on axillary inflorescences (racemes), on short pedicels. According to our observations, the inflorescences of *P. vulgaris* rarely exceed 30 cm, and are on average shorter than those of *P. coccineus* (the average inflorescence length of some varieties belonging to this species can exceed 35 cm).

P. vulgaris is predominantly autogamous while *P. coccineus* is allogamous (Frankel and Galun 1977, Escalante et al. 1997, Lapinskas 1997). The most important pollinators are bees, bumble-bees and some species of wasps. These insects are relatively heavy and with their body they press the left wing downward, causing the stigma to protrude through the opening at the end of the keel and in this way enabling the contact with pollen grains brought by the insects from other plants. When the visit is over the stigma recedes into the keel. This mechanism can also be efficiently used in artificial hybridisation (Ivančič 2002).

The varieties of both species are divided into three main groups: tall (twining), intermediate and dwarf (bushy). Each of these groups is divided into two subgroups: determinate (the main axis terminates with an inflorescence) and non-determinate (the plants are characterised by continuous growth). Dwarf or bushy types are divided further into 3 types: erect, semi-erect (sub-erect) and prostrate.

P. vulgaris appears to be much more important and is represented by thousands of varieties. Because of predominant autogamy it is relatively easy to maintain large genetic collections. Spatial or other types of isolations are in many cases not needed. The majority of varieties represent homozygous lines and are highly uniform. The traditional varieties of *P. coccineus* are in most cases phenotypically homogeneous populations. They are composed of numerous genotypes, which have more or less stable frequencies, representing the population equilibrium. For maintaining, these varieties are much more complicated because they require relatively large and well isolated plots. Reduction of the number of plants and/or the absence of insects-pollinators can cause significant inbreeding depression with very negative consequences.

In the literature, it is possible to find a lot of data associated with the inheritance because these two species have been very frequent objects of genetic studies. The first genetic studies were published at the beginning of the last century; e.g. Tschermak (1901) and Emerson (1904). The earliest studies were, in most cases, concentrated on *P. vulgaris* (probably because of its importance and similarity with the garden pea - *Pisum sativum*). Today, after one century of intense work, it is possible to find almost all crucial genetic informations and this makes the genetic breeding much more efficient. The list of the most important genes, which was published by the Genetics Committee (2003), can serve as an example.

Interspecific hybridisation between *P. vulgaris* and *P. coccineus* has been used in breeding probably for a long time and it served as an additional source of variation. It can be extremely useful in breeding for resistance against diseases. As an example is the resistance against the common bacterial blight (Singh and Munoz 1999, Welsh and Grafton 2001).

Interspecific hybrids can be found in nature, especially when the plants belonging to these two species are grown close to each other and when there are a lot of pollinating insects, especially bees and bumble-bees. The first artificial hybrids between *P. vulgaris* and *P. coccineus* were created probably at the end of the 19th century. The earliest systematic data based on observations of these hybrids were published by E. von Tschermak (1904). In 1920s, the hybridisation techniques were already well developed, enabling the detailed studies of inheritance in F1, F2 and other generations. One of the best sources of data from this period is the publication of Matsuura (1929).

In general, it is not easy to produce such hybrids (Coyne 1964, Al-Yasiri and Coyne 1966, Smartt 1970, Lapinskas 1997). Failure of a cross can occur in almost any stage and there are many different causes such as: pollen does not germinate, pollen tube does not penetrate the style, there is no fertilisation, zygote fails to develop, embryo is not normal, seed does not germinate, seedling does not grow (because of physiological disorders or there is no growth point) or the plants are sterile (they do not produce flowers or flowers are not fertile).

The investigation is associated with the breeding programme based on recurrent selection and aimed at creating varieties suitable for organic farming. One of the reasons for involving interspecific hybridisation, combined with recurrent selection, was also the possibility of creating the breeding material which would be predominantly allogamous. In this way it may be possible to replace artificial hybridisation, which is time consuming and complicated, with natural cross-fertilisation.

The aim of this investigation was to evaluate the variability and relationships among the most important morphological traits of F_2 generation materials derived from interspecific hybridisation between *P. vulgaris* and *P. coccineus*. The information about the relationships (based on correlation coefficients) will be used in the selection process in

order to replace the traits (used as selection criteria), which are extremely difficult for determination, with the traits which can be easily determined.

The investigation took place in a location near Brežice, in the south-eastern part of Slovenia.

MATERIALS AND METHODS

Breeding approach

The existing breeding programme is based on the recurrent selection approach. This approach can be defined as a systematic selection of superior individuals from a population followed by their recombination, to form a new population (a population of a new cycle). The whole process can be described with cycles, starting with the basic cycle or cycle-0. Each cycle includes three steps: development of a (new) population, evaluation of the individuals in a population and selection of the best individuals for intercrossings (to form a new, improved population). The success of such a programme depends strongly on the available genetic resources (sources of genes, genetic materials), their variation and their recombinations. It is very important that the basic cycle includes all crucial genes. Our aim was to include the genes from 3 species and this could be done step by step. At first, we created the two-species hybrids (P. vulgaris x P. coccineus) and later we added the third species by using several selected F₂ individuals as female components which were crossed with P. lunatus L.

Preparation of plant material and crossing technique

The interspecific hybridisation took place in 2000 and was based on the classical crossing technique described by Bliss (1980). To make crosses more efficient, we tried to explore several possibilities such as pollination on various periods of the day (from early morning to late evening), different ways of protection of flowers from uncontrolled pollination (isolation with small paper bags or cotton and without isolation) and treatments of stigma (with low concentrations of sucrose, honey, agar and a combination of sucrose with agar).

P. vulgaris was used as a female component (the reciprocal combinations were found to be less successful) and was represented by a mixture of 50 F_3 (25 tall and 25 dwarf) lines resulting from crosses among 12 (8 tall and 4 dwarf) local varieties from the south-eastern part of Slovenia. The materials used as males belonged to *P. coccineus* and included three tall local varieties distinguished by white, cream and red flowers. To enable continuous hybridisation throughout the growing season, the parental material was planted several times (once in every two weeks, starting on April 25 and ending on July 25). On each selected inflorescence of a female component we pollinated two or three flowers (all other flowers were carefully removed). The selected flowers were still completely closed and were 4-12 hours before they would have released pollen.

The result of this hybridisation were 94 pods, with the total number of 163 seeds. At the end of April 2001, we planted 87 seeds and obtained 65 F_1 plants which developed

more or less normal and fertile inflorescences. These plants were exposed to natural pollination (which probably included self- and cross-pollination). In mid October, they were harvested individually and seed material was labelled and stored for the following season.

At the end of April 2002, in a location near Brežice, we planted F_2 seeds (originating from 65 open - pollinated F_1 plants). At the beginning of flowering, there were 825 F_2 plants (belonging to 50 F_2 families) and these plants represented the basic population, investigated in this paper. The plants were trellised, similarly to hop.

Test of the interspecific hybrid origin of F₁ plants

The pods resulting from crossing were collected (together with labels) when they were fully ripe. The exception were young pods resulting from very late crosses which had to be collected earlier, before the first frost. These pods were collected together with about 30 cm long stem and kept for 2-3 weeks in a moderately warm room, in a cup with some water, placed close to the window (in the same way as we use to keep cut-flowers).

For testing the interspecific origin, we collected and labelled a sample of 20 seeds from each successfully crossed female parent (in all cases, this was *P. vulgaris*). In the following season (in 2001), these parental seeds were planted in a parallel row, next to the row planted with seeds resulting from crosses. Male parents were planted in a separate plot because they included only 3 genotypes (varieties). The main traits used for testing were the characteristics of germination (epigeal and hypogeal), shape and size of inflorescences, and size, shape and colour of flowers.

Analysed traits

The morpho-agronomic analysis took place in 2002, from July 15 to August 25. It included F_2 plants and their parental species. The main analysed traits were: length of the leaf petiole, length of the terminal leaflet stalk, length and width of the (left) basal leaflet, length and width of the terminal (middle) leaflet, inflorescence length, number of flowers per inflorescence, length of the floral stalk (pedicel), floral length, width and height of the *standard* petal, length of the left *wing* and floral colour.

For statistical analysis, mean values of several measurements per plant were used. The number of measurements per plant varied from less than 8 to more than 15, depending on the trait and the size of a plant. Less than 8 measurements per plant were probably not sufficient but in many cases there was no other choice (e.g. some of the dwarf plants had only 6 leaves and even less inflorescences). The measurements of leaf dimensions within plants included only fully developed leaves (the oldest two leaves, which were close to the ground, and the youngest leaves close to the tip were excluded because they were significantly different). The floral colour was at first described by words (e.g. light purple standard petals, very light purple wings and almost white keel) and then converted to a special scale using the numbers from 1 to 49. The data were statistically analysed by using SPSS 11.0.0 programme.

RESULTS AND DISCUSSION

Hybridisation technique

The average time needed for one interspecific cross (including labelling) was 2.5-3.5 min (17-24 crosses per hour). The success depended strongly on the time of the day when the pollination took place. The best option in June, July and the first decade of August was late afternoon pollination (from 4.30 to 6.30 p.m.), whereas from mid August to mid September the best results were achieved with morning pollination (from 7.00 to 9.30 a.m.).

The treatment of stigmas had some effects, although they were not always obvious. It was found that low concentration of sucrose combined with agar (15 g sucrose + 4 g agar dissolved in 1 L of water and kept in a refrigerator) had at least some positive effects. This treatment appeared to be helpful especially for late afternoon and evening crosses, probably because it enabled pollen to germinate faster and the final consequence was earlier fertilisation, when the temperatures were still optimal. The isolation (the protection from uncontrolled pollination) had a negative influence on the results.

The total number of hybridised flowers was 356 and the result was 94 pods, with the total number of 163 F_1 seeds (on average 1.73 seeds per pod), excluding the seeds which were not interspecific hybrids. Some of the seeds were characterised by abnormal embryo. Such embryos appear to be very common in interspecific crosses between *P. vulgaris* and *P. coccineus* and were also recorded by other authors (e.g. Guo et al. 1989).

The most successful were late summer crosses, which took place at the end of August and at the beginning of September. The most suitable female components were those which had been planted in mid July.

Test of the interspecific hybrid origin

The differentiation between hybrids and non-hybrids was the simplest and the most reliable at the beginning of flowering. Hybrid plants were characterised by much longer inflorescences and in most cases had much stronger axis. There were also several hybrid plants with very long and soft inflorescences which were hanging down. Flowers were also larger and in most cases widely open. There were also obvious differences in floral colour. Interspecific hybrids were characterised by colours which were unusual for *P. vulgaris* (these colours will be listed later). The problem was that some of the plants had white flowers. In such cases, we used traits associated with the size and shape of flowers and inflorescences. In general, the 'white' hybrids had larger, widely open flowers and longer inflorescences (when compared with *P. vulgaris*).

The interspecific hybrid origin could also be determined by pod and seed characteristics. They were found to be reliable, however, they could be determined relatively late, when the hybridisation period was over.

In delicate situations (e.g. when visual methods cannot be used) it may be advisable to use genetic markers or to determine the genome size differences. This approach is probably more useful for the determination of hybrids resulting from crosses *P. vulgaris* x *P. lunatus*. We found that the visual differences in these crosses are much less obvious when compared with the hybrids where the male parent is *P. coccineus*.

Phenotypic and genotypic variation

Qualitative traits

The majority of F_2 plants (76.4 %) were tall, characterised by indeterminate growth and long internodes (Fig. 1). Tall plants with terminal inflorescences were rare. There was a tremendous variation, especially in growth vigour, type of branching, resistance against diseases, stem, leaf and inflorescence shape, floral colour, and the length of the growth period.

The dwarf plants were also highly variable (Fig. 2). Some of them were extremely vigorous and could be up to 80 cm high. They could be differentiated by several characteristics such as growth type (prostrate, semi-erect or erect), number, shape and density of leaves, and number, length, shape and position of inflorescences. Some of the plants were very small, having up to 4 leaves and very few flowers. Completely sterile plants were rare (8 in total). Most of the dwarf plants were characterised by indeterminate or partly determinate growth.

The leaves of F_2 plants were in most cases very similar to the ones of the parental species. However, there were also numerous variations such as leaves with different number of

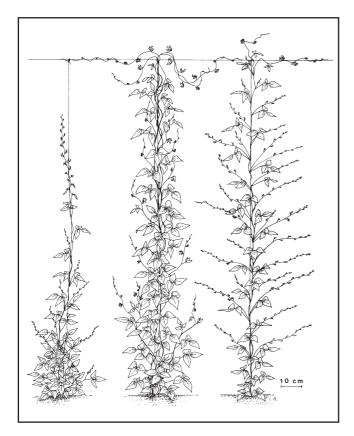


Fig. 1. Three main types of tall genotypes in F₂ generation derived from crosses *Phaseolus vulgaris* x *P. coccineus*: a plant with the terminal inflorescence (determinate growth) and two plants characterised by indeterminate growth.

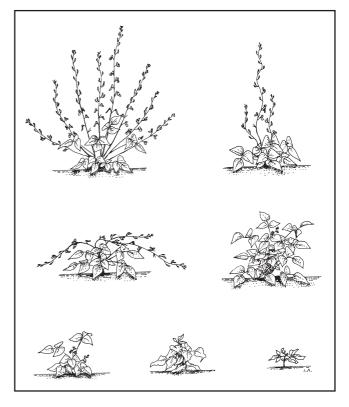


Fig. 2. Main types of dwarf genotypes (in F₂ generation derived from *crosses P. vulgaris x P. coccineus*).

leaflets (from 1 to 6), which varied in size and shape. The most unusual leaf types (e.g. fasciated leaves and leaves characterised by more than 3 leaflets) were found to be genetically 'unstable'; there were only one or few such leaves per plant.

Inflorescences (Fig. 3) were in general much longer when compared with the parental species. Most of them had semi-erect position. The most unusual were branched inflorescences and the inflorescences with extremely long (50 cm or more) axis, having flowers only at its tip.

Flowers were, on average, relatively large and soft. Regarding their size, they were larger, when compared with *P. vulgaris*, and a bit smaller, when compared with *P. coccineus* (Fig. 4). In most cases they were fully open during flowering and visited by pollinating insects such as bees, bumble bees and wasps.

One of the most obvious indicators of the genetic variation was the floral colour. As it was demonstrated by Bassett (2003), this trait can be highly variable and its inheritance is not always simple. In our F2 material, it varied from white, light yellow, dark yellow, orange, red-orange, pink, red (many variations), red-purple, light purple, light brownpurple, brown-purple and dark purple, to almost blue. The flowers of the majority of plants were characterised by red colour. The frequencies of different colours were not determined because the number of variations was very high and in many cases it was not easy to determine the differences. As an example, there were 12 different types of red colour, distributed in different ways on the standard petal, wings and the keel. The most attractive colours for insects-pollinators were yellow, yellow-orange, some variations of red (the one which is characteristic for the corolla of field poppies) and violet.

Another highly variable trait was the shape of pods

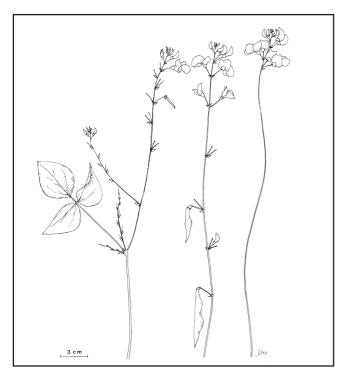


Fig. 3. The most frequent types of inflorescences (in F₂ generation derived from crosses *P. vulgaris* x *P. coccineus*).

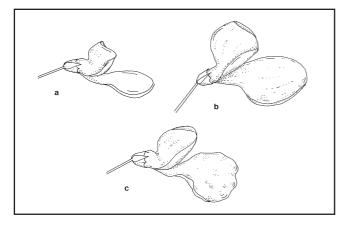


Fig. 4. Flowers of parents and F₂ individuals: a - P. vulgaris,
b - P. coccineus, c - F₂ individual.

(Fig. 5), which depended on several genetic and non genetic factors. The most important appeared to be the fertility of a plant, which probably had a strong influence on the number of seeds per pod, and the presence of efficient insectspollinators during flowering.

Quantitative traits

The most variable quantitative trait analysed in F_2 generation was the number of flowers per inflorescence (Table 1), which varied from 0 to 57 (CV = 45.8 %). The second was the inflorescence length, which varied from 3.5 to 74 cm (CV = 39.0 %). Among highly variable traits were also the length of leaf petiole (it varied from 4.6 to 19.5 cm among tall plants and from 3.3 to 18.6 cm among dwarf plants) and the length of the pedicel (floral stalk) which varied from 4.2 to 25.2 mm. The highest CV (%) value (in Table 1) was obtained for the floral colour (a qualitative trait which was transformed to a special numerical scale). The most stable were the floral dimensions

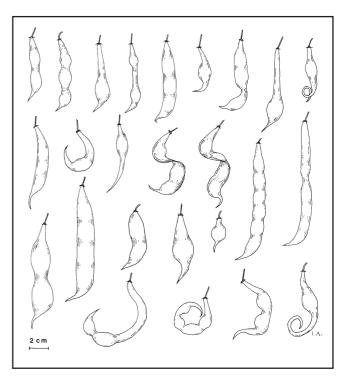


Fig. 5. Variation of pod shape within F2 progenies.

Table 1. Phenotypic variability of the most important investigated traits in F_2 generation (*Phaseolus vulgaris* x *P. coccineus*).

			Tall plants					
	Ν	Min.	Max.	Mean	S.d.	CV(%)		
L. Pet. L.	136	4.6	19.5	9.713	2.995	30.835		
T. Lfl. St. L.	136	1.7	7.2	3.312	0.885	26.721		
Bs. L. L.	136	4.1	17.2	9.157	2.061	22.507		
Bs. L. W.	136	3.7	16.3	7.186	1.813	25.230		
Term. L. L.	136	4.9	18.1	9.768	2.178	22.297		
Term. L.W.	136	4.2	14.1	8.032	1.774	22.087		
Inf. L.	136	5.5	54.5	25.626	9.973	38.918		
No. Fl./Infl.	136	0	57.0	17.490	8.015	45.826		
Fl. Ped. L.	136	6.1	22.1	13.323	3.118	23.403		
Fl. L.	136	18.5	32.0	24.538	2.302	9.381		
Std. W.	136	14.0	23.5	17.659	1.404	7.951		
Std. H.	136	10.2	19.8	14.601	1.808	12.383		
Win. L.	136	13.2	29.9	21.310	2.576	12.088		
FI. Col.	136	1	28.0	27.330	12.930	47.311		
			Dwarf plants	6				
L. Pet. L.	85	3.3	18.6	10.027	3.002	29.939		
T. Lfl. St. L.	85	1.4	5.3	2.664	0.766	28.754		
Bs. L. L.	85	5.1	15.6	8.351	1.993	23.865		
Bs. L. W.	85	3.3	13.2	6.433	1.558	24.219		
Term. L. L.	85	5.2	17.1	9.280	2.237	24.106		
Term. L.W.	85	3.9	13.6	7.188	1.652	22.983		
Inf. L.	85	3.5	74.0	32.293	12.599	39.015		
No. Fl./Infl.	85	3.0	48.0	16.180	7.370	45.550		
Fl. Ped. L.	85	4.2	25.2	15.052	4.018	26.694		
FI. L.	85	19.0	31.5	25.068	2.246	8.960		
Std. W.	85	8.1	23.4	18.287	1.825	9.980		
Std. H.	85	4.1	18.3	14.752	1.841	12.480		
Win. L.	85	16.1	27.2	21.645	2.287	10.566		
Fl. Col.	85	1.0	48.0	20.280	14.270	70.365		
L. Pet. L. – ler	L. Pet. L length of leaf petiole (cm), T. Lfl. St. L length of terminal leaflet							

L. Pet. L. – length of leaf petiole (cm), T. Lfl. St. L. – length of terminal leaflet stalk (cm), Bs. L. L. – length of left basal leaflet, Bs. L. W (cm). – width of left basal leaflet (cm), Term. L. L. – length of middle leaflet (cm), Term. L. W. – width of middle leaflet (cm), Inf. L. – inflorescence length (cm), No. FL/Infl. – number of flowers per inflorescence, Fl. Ped. L. – pedicel length (mm), Fl. L. – flower length (mm), Std. W. – standard width (mm), Std. H. – standard height (mm), Win. L. – wing length (mm), Fl. Col. – floral colour.

(length, width and height of the *standard* petals, and the length of *wings*).

For breeders, the most useful are the traits associated with fertility, such as the number of flowers, the number of pods and the number of seeds per plant (Table 2). High variation enables breeders to conduct strict selection. The most variable traits (associated with fertility), obtained on tall plants, were the number of flowers per plant, which ranged from 4 to 4032 (CV = 106.5 %), and the number of seeds, which ranged from 0 to 1168 (CV = 131.7 %). Among the

Table 2. Variation of quantitative traits associated with fertility in F₂ generation (P. vulgaris x P. coccineus).

N Min. Max. Mean S.d. CV(%)									
						CV(%)			
No. Lvs.	26	14	96	34.77	21.297	61.251			
No. Infl.	26	4	44	15.81	10.874	68.779			
N. Fl.	26	21	484	145.69	139.900	96.026			
Fl. Col.	26	1	47	21.73	18.039	83.014			
No. Pods	26	0	32	8.00	8.163	102.038			
No. Seeds	26	0	93	17.23	22.011	127.748			
Veg. Per.	26	1	8	2.38	2.192	92.101			
		all F2 plants	(P. vulgaris)	x P. coccineu	IS)				
No. Lvs.	47	14	634	137.91	121.677	88.229			
No. Infl.	47	6	318	67.53	66.177	97.996			
N. Fl.	47	4	4032	912.40	972.517	106.589			
Fl. Col.	47	1	48	27.40	12.631	46.099			
No. Pods	47	0	292	55.32	53.727	97.120			
No. Seeds	47	0	1168	187.73	247.366	131.767			
Veg. Per.	47	1	9	5.06	2.900	57.312			
		Parental an	d F2 generat	tion together					
No. Lvs.	113	14	634	88.63	92.282	104.121			
No. Infl.	113	4	318	44.02	48.639	110.493			
N. Fl.	113	4	4032	530.24	727.512	137.204			
Fl. Col.	113	1	48	25.50	16.972	66.557			
No. Pods	113	0	292	41.03	42.119	102.654			
No. Seeds	113	0	1168	159.43	198.675	124.616			
Veg. Per.	113	1	9	3.75	2.694	71.840			

No. Lvs. - number of leaves per plant, No. Infl. - number of inflorescences per plant, No. Fl. - number of flowers per plant, Fl. Col. - floral colour, No. Pods number of pods per plant, No. seeds - number of seeds per plant, Veg. Per. duration of the vegetation period

parents the most productive was a plant belonging to P. vulgaris, having 702 seeds. The maximum number of seeds determined on P. coccineus was 244.

Many of the F_2 plants were characterised by extremely long vegetation period. They were flowering until the first frost in the third decade of November. If the weather had continued to be favourable for growth the number of inflorescences, flowers and seeds would have been probably much higher. The investigation indicated that seed set was relatively very low at the beginning (in June, July and the first decade of August) and increased significantly when the weather became cooler (at the end of August). The weather was probably only one of the factors associated with the improvement of the seed set. Another very significant factor could be the plant age. Irregularities during gametogenesis of older plants were probably less frequent.

Relationships among quantitative traits

The analysis of correlation coefficients among studied traits in F_2 generation (Table 3) indicates that there were close relationships among leaf dimensions (petiole length, leaflet stalk length, basal leaflet length and width, middle leaflet length and width). The correlation coefficient ranged from 0.408 to 0.907. The highest correlation was determined between the basal and the middle leaflet length (r = 0.895-0.932). Leaf dimensions were also positively correlated with the inflorescence length, however, the correlation coefficients were in most cases lower than 0.4.

The second group of closely related traits (presented in Table 3) were floral dimensions. The highest correlation was determined between the flower length and the wing length (r = 0.876 - 0.878). Floral colour appeared to be an independent trait. However, the analysis of tall hybrids indicated that that the flowers of plants with longer inflorescences and more flowers per inflorescence were, on average, lighter (white, very light purple or light pink).

For breeders, the most interesting are the relationships among traits associated with fertility and productivity. Among the listed traits in Table 3 the most important is probably the number of flowers per inflorescence, which is highly correlated only with the inflorescence length. The inflorescence length appears to be an important factor influencing yield per plant (Campion and Servetti 1991). Longer inflorescences have more flowers and also more pods and seeds (Tables 3 and 4). Other correlation coefficients are, on average, very low.

The main indicators of fertility (and productivity) are the number of inflorescences, flowers, pods and seeds per plant. The highest correlation was established between the number of inflorescences and the number of leaves (per plant). The number of inflorescences also appear to be closely related with the number of flowers, number pods and number of seeds (Table 4).

From the physiological point of view, very important

Table 3. Phenotypic correlation coefficients among studied traits within F₂ generation (*P. vulgaris* x *P. coccineus*).

						Dwarf plants	s (N = 85)						
	L.Pet.L.	T.Lfl.Pet.L.	Bs.L.L.	Bs.L.W.	Term.L.L.	Term.L.W.	Inf.L.	No.Fl./l.	Fl.Ped.L	FI.L.	Std.W.	Std.H.	Win.L.
L.Pet.L.													
T.Lfl.Pet.L.	0.585**												
Bs.L.L.	0.354**	0.641**											
Bs.L.W.	0.348**	0.659**	0.900**										
Term.L.L.	0.375**	0.627**	0.932**	0.854**									
Term.L.W.	0.352**	0.637**	0.797**	0.886**	0.825**								
Inf.L.	0.376**	0.364**	0.438**	0.452**	0.381**	0.428**							
No.FI./I.	0.324**	0.135	0.132	0.203	0.166	0.244*	0.644**						
Fl.Ped.L.	-0.018	0.054	0.090	0.003	0.070	-0.102	0.198	0.019					
FI.L.	0.232*	0.042	0.072	0.055	0.120	0.051	-0.024	-0.011	0.177				
Std.W.	0.008	-0.100	-0.068	-0.048	-0.020	0.007	0.066	-0.013	0.067	0.392**			
Std.H.	-0.027	0.091	-0.092	-0.082	-0.128	-0.082	-0.107	0.056	0.109	0.368**	0.359**		
Win.L.	0.236*	0.103	0.086	0.087	0.128	0.056	-0.049	0.023	0.222*	0.876**	0.262*	0.361**	
FI.Col.	0.149	0.063	0.047	0.078	0.007	0.020	0.128	0.139	0.097	0.134	0.104	0.150	0.120
						Tall plants (I	N = 136)						
L.Pet.L.													
T.Lfl.Pet.L.	0.688**												
Bs.L.L.	0.535**	0.738**											
Bs.L.W.	0.474**	0.628**	0.804**										
Ferm.L.L.	0.516**	0.690**	0.895**	0.735**									
Ferm.L.W.	0.532**	0.726**	0.883**	0.832**	0.836**								
nf.L.	0.152	0.321**	0.280**	0.342**	0.377**	0.380**							
No.FI./I.	-0.081	0.012	0.069	0.125	0.100	0.166	0.656**						
FI.Ped.L.	-0.091	-0.103	0.042	0.000	0.105	0.017	0.309**	0.147					
FI.L.	-0.063	-0.110	0.010	-0.009	0.116	-0.003	0.021	-0.066	0.319**				
Std.W.	-0.019	-0.077	0.003	-0.004	0.162	0.070	0.224**	0.152	0.259**	0.444**			
Std.H.	-0.147	-0.129	-0.059	-0.057	0.037	-0.077	0.261**	0.291**	0.280**	0.451**	0.398**		
Vin.L.	-0.026	-0.079	0.051	0.013	0.132	0.028	0.086	-0.010	0.352**	0.878**	0.404**	0.413**	
FI.Col.	-0.010	-0.031	-0.139	-0.082	-0.186*	-0.193*	-0.315**	-0.382**	-0.061	0.038	-0.090	-0.158	0.065

P<0.05, ** P<0.01. L. Pet. L. – length of leaf petiole, T. Lfl. St. L. – length of terminal leaflet stalk, Bs. L. L. – length of left basal leaflet, Bs. L. W. – width of left basal leaflet, Term. L. L. – length of middle leaflet, Term. L. W. - width of middle leaflet, Inf. L. - inflorescence length, No. Fl./I. - number of flowers per inflorescence, Fl. Ped. L. - pedicel length, Fl. L. - flower length, Std. W. standard width, Std. H. - standard height, Win. L. - wing length, Fl. Col. - floral colour.

Table 4. Phenotypic correlation coefficients among the most important traits associated with fertility in F_2 generation (*P. vulgaris* x *P. coccineus*).

Dwarf plants, N = 26								
	No. Lvs.	No. Infl.	No. Fl.	Fl. Col.	No. Pods	No. Seeds		
No. Lvs.								
No. Infl.	0.930**							
No. Fl.	0.709**	0.666**						
Fl. Col.	0.282	0.218	0.375					
No. Pods	0.632**	0.666**	0.530**	0.116				
No. Seeds	0.461*	0.560**	0.400*	0.011	0.916**			
Veg. Per.	0.665**	0.659**	0.839**	0.219	0.704**	0.597**		
		Tall pl	ants, N =	47				
No. Lvs.								
No. Infl.	0.930**							
No. Fl.	0.812**	0.904**						
Fl. Col.	-0.067	-0.034	-0.042					
No. Pods	0.681**	0.709**	0.549**	0.001				
No. Seeds	0.509**	0.503**	0.409**	-0.018	0.740**			
Veg. Per.	0.251	0.202	0.212	0.018	0.243	0.309*		
* P<0.05, ** I	P<0.01.							

No. Lvs. – number of leaves per plant, No. Infl. – number of inflorescences per plant, No. Fl. – number of flowers per plant, Fl. Col. – floral colour, No Pods – number of pods per plant, No. seeds – number of seeds per plant, Veg. Per. – duration of the vegetation period.

are the relationships among the number of leaves (per plant), number of flowers, number pods, number of seeds and the length of the growth period. The number of leaves is highly correlated with the number of flowers, number of pods and number of seeds. The length of the growth period appears to have at least some influence on the rest of the traits, however, it depends on genetic material. In the first F₂ material (tall genotypes) the influence is very strong and the most probable reason was late maturity of the investigated materials.

For practical selection in heterogeneous F_2 generation materials, the most useful is a relatively high correlation between the number of inflorescences and the number of seeds per plant, (r = 0.503 and 0.560), Table 4. The first trait can be easily determined at the beginning of hybridisation period (at the beginning of flowering) while the second one is more or less directly associated with the yield. The number of seeds is also closely related with the number of flowers, however, the correlation coefficients are lower (r = 0.400 and 0.409) and it is not always simple to differentiate plants according to this trait. It is much easier to use inflorescences.

For the final visual selection, at the end of the vegetation period, the most useful trait is the number of pods. This trait is highly correlated with the number of seeds (r = 0.740and 0.916).

REFERENCES

- 1. Al-Yasiri SS, Coyne DP. Interspecific hybridisation in the genus *Phaseolus*. Crop Science. 1966; 6: 59-61.
- Bassett MJ. Inheritance of scarlet colour and vein pattern in flowers and oxblood red seedcoat colour derived from interspecific cross of common bean with scarlet runner (*Phaseolus coccineus* L.). Journal of the American Society for Horticultural Science. 2003; 128(4): 559-563.
- Bliss FA. Common bean. *In*: Hybridization of crop plants. W. R. Fehr, H. H. Hadley (eds.). Am. Soc. of Agronomy and Crop Sci. Soc. of America; Madison Wisconsin, USA. 1980; pp. 237-284.
- Campion B, Servetti E. Breeding in the runner bean (*Phaseolus coccineus* L.) for the development of dwarf lines. Journal of Genetics and Breeding. 1991; 45/3: 173-180.
- 5. Coyne DP. Species hybridisation in Phaseolus. J. Hered. 1964; 55: 5-6.

- Darlington CD, Wylie AP. Chromosome atlas of flowering plants (Second edition). George Allen and Unwin LTD; London. 1955.
- Emerson RA. Heredity of bean hybrids. Ann. Rept. Nebraska Agr. Exp. Sta. 1904; 17: 33-68.
- Escalante AM, Coello G, Eguiarte LE, Pinero D. Genetic structure and mating systems in wild and cultivated populations of *Phaseolus coccineus* and *Phaseolus vulgaris (Fabaceae)*. Am. Journal of Botany. 1994; 81(9): 1096-1103.
- Fedorov A. Chromosome numbers of flowering plants. Nauka; Leningrad. 1969. (Reprint: Koenigstein 1974).
- Frankel R, Galun E. Pollination mechanisms, reproduction and plant breeding. Monographs on Theoretical and Applied Genetics. Springer-Verlag, Berlin, Heidelberg and New York. 1977.
- Genetics Committee. List of genes *Phaseolus vulgaris* L. http://css.msu.edu/bic/geneticscommittee.html 18. 04. 2003.
- Guo M, Mok DWS, Mok MC. Isozyme banding patterns and embryo development in interspecific crosses of *Phaseolus*. J. Heredity. 1989; 80/1: 29-32.
- 13. Ivančič A. Hibridizacija pomembnejših rastlinskih vrst. Univerza v Mariboru, Fakulteta za kmetijstvo Maribor. 2002.
- Kaplan L. Archeology and domestication in American *Phaseolus* (Beans). Econ. Bot. 1965; 19: 353-368.
- Lapinskas P. The potential of *Phaseolus coccineus* and of hybrids with *P. vulgaris* as pulse crops for the U.K. Ph.D. Thesis. 1997. University of Cambridge.
- Matsuura H. A bibliographical monograph on plant genetics (Genic analysis). Tokyo Imperial University, Tokyo. 1929.
- 17. Purseglove JW. Tropical Crops Dicotyledons. Longman, London. 1977.
- Singh SP, Munoz CG. Resistance to common bacterial blight among *Phaseolus* species and common bean improvement. Crop Science. 1999; 39(1): 80-89.
- Smartt J. Interspecific hybridisation between cultivated American species of the genus *Phaseolus*. Euphytica. 1970; 19: 480-489.
- Tschermak E von. Weitere Beiträge über Verschiedenwerthigkeit der Merkmale bei Kreuzung vor Erbsen und Bohnen. Vorläufige Mittheilung. Ber. Deut. Bot. Ges. 1901; 19: 35-51.
- 21. Tschermak E von. Weitere Kreizungsstudien an Erbsen, Levkojen und Bohnen. Zts. Landw. Versuchsw. Österr. 1904; 106 pp.
- Welsh MM, Grafton KF. Resistance to common bacterial blight of bean introgressed from *Phaseolus coccineus*. Hortscience. 2001; 36(4): 750-751.

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