Theoretical and Applied Genetics 45, 47–51 (1974)

On the Evolution of *Vicia faba* L.

JOSÉ I. CUBERO

Instituto Nacional de Investigaciones Agrarias, Centro Regional de Andalucia, Cordoba (Spain)

Summary. Diallel crosses between seven inbred lines obtained from different botanical groups including the two known subspecies of *V. faba* permitted study of the genetics of seventeen quantitative characteristics; there were very few significant reciprocal differences, and in all cases but one they were only weakly dependent on genotype. These results accord very well with those obtained from a study on population distances among thirty unselected populations of *V. faba*; many of these lie very close, forming a strong nucleus, which carries the maximum of potentialities of the species and from which different populations branch. Nevertheless differentiation occurs: the genetic system which regulates seed length shows overdominance in the positive sense in some lines, but partial or complete dominance in the negative sense in the rest of the studied lines. Interpretations suggesting that *V. faba* has suffered very little intraspecific differentiation are substantiated by the studies showing the presence of a partial incompatibility system; this is stronger in the Central European populations studied, weak (to various degrees) in the Spanish ones and absent in at least one population of the *paucijuga* group.

Vicia faba is known to have been cultivated from the early Neolithic. It can be said that it has been known from the beginning of Agriculture. It is logical to suppose that the use of *Vicia faba* as a cultivated species began in the Near East, following the Neolithic culture as it spread across the inhabited world (Cole, 1970). This does not mean that the plant was unknown in other regions, particularly in the Mediterranean countries. Philological studies (Hanelt 1972a) show that its names in the Indoeuropean languages have the same root (*ba*), except in the Greek (*kyamos*); this is an interesting exception because of the proximity of Greece to the Near East. Possibly the primitive Greeks found a people who knew the bean and named it because it would be useful (Acheens were present at Micenes towards 1800 BC; at this time, the culture of beans must have been known in Greece because of its proximity to the Near East); the Hebrew root is *pa*, very close to the Indoeuropean one and, perhaps, to the original and unknown word used by an unknown people to name the beans. The Arabic word (*ful*) is a similar case to the Greek one: it could have come from a people who knew the plant before the culture. Three different roots (Greek, Hebrew, Arabic) in a relatively small region: is it possible to deduce that the plant was known by different peoples even if only one of them began to cultivate it?

We can suppose that there were different routes radiating from the Near East (Fig. 1). The first could be the European one: across Anatolia and perhaps included in the Troyan interchange with Europe (particularly with the Vinca culture), the culture of beans had to pass to Greece, the Illyric coast (perhaps also to the Danubian regions) and to Italy. From the mediterranean regions it could pass to the rest of Europe.

Fig. 1. Expansion of the culture

A second route could also begin at the Delta, go towards the West, along the Mediterranean coast, to the Mogreb and the Iberic Peninsula (Cole, 1970).

The third way could begin at the Nile Delta (Low Egypt and Mesopotamy was the same thing from the point of view of culture; see, for example, Pirenne 1963), following the Great River and finishing at Abisinia.

The fourth and last route could begin in Mesopotamy again, but this time would go toward the East carried by the Indoeuropeans of the Indoiranian group. This culture raised India.

The existence of a fifth way from Mesopotamy across the Caucaso to the Pontic peoples is doubtful.

I think that this dispersion must have been more indirect than direct, that is, that primitive peoples transmitted knowledge about the culture and not the seeds directly, even allowing for some transmission of grains from hand to hand. In the first place, the basic vegetable material originally cultivated had to be the wild plants of the considered species. This

Fig. 2. Distribution of *V. faba* L. (from Hanelt 1972, modified)

can explain the actual absence of wild plants of *V. faba*: all these were immediately converted into cultivated ones (the problem is different when a cluster of species is considered, such as *Triticum* sp.). On the other hand, Fig. 2 shows that *minor* populations accumulated in India (with *paucijuga* also) and Abisinia, while at the same time *major* populations accumulated more and more to the western limit of the species habitat, and so were on both sides of the Mediterranean Sea. If we think that the archaeological remnants (Hanelt, 1972) would *actually* be classified as belonging to the *minor* group, it is impossible that primitive men transported *major* or *minor* seeds, because they did not exist as botanical entities. I shall try to prove in this work that they must exist as genetical ones: I do not think that in ancient times either *major, equina* or *minor* existed in that actual form, but that there must have been populations with different evolutionary potentialities. Natural migrations, previous to the cultural ones, must be the main explanation of the actual geographical distribution. I maintain that it must be more important than the human (that is, cultural) transmission; if it was the opposite, the two Mediterranean sides would present different spectra of botanical forms.

It can be argued against this idea that *equina* and *major* were artificially obtained (*major* appears in archaeological remains of the 10th century; Hanelt 1972) and then transmitted. First, Figure 2 shows a very natural separation of forms: evidently, man has played a role in the transmission; for example, in modern times some *major* varieties have been introduced in England and France. But it is difficult to explain Fig. 2 this way. Secondly, if we admit this argument (that is, the artificial transmission of some forms), it would be necessary to explain why in the western Mediterranean an accumulation of some forms (lentils, beans, chickpeas for example) with big seeds is registered in contrast to the small-seeded forms of the same species on the other side of the old Thetis sea (western regions of India). It seems that, at least for the *Vicieae* genera, a "genetic natural migration" happened. Environmental conditions and independence of recessives had to play an important role, even if archaeologically we can not distinguish between one population with the potential to become *major* or *equina* and another to stay as *minor* or to become *paucijuga*. Man has acted to accelerate the morphological differentiation process.

I have studied the problem from different points of view: distances between populations (Cubero, 1973a), studies on quantitative inheritance (Cubero 1970a, 1973b), relations between morphological characteristics and studies on the reproductive system of this species (Cubero 1970b). I think that it is convenient to recapitulate before going on.

A Recapitulation of Methods and Materials

I have used in the study sixty-seven populations: Thirty-eight *major*, nine *equina*, eighteen *minor* and two *paucijuga*. Seven pure lines with at least five self-pollinations were used to study the inheritance of quantitative characteristics; Hayman's (1954) diallel analysis was followed. In principle it was intended to make the analysis using eight pure lines, but one of them was eliminated because of its lack of adaptability to Spanish conditions.

Populations were classified according to the seed weight and number of leaflets per leaf. The first character is closely related to the main taxonomic characteristic of Muratova (1931), that is, the thickness/length ratio of the seed, whose suitability as a taxonomic index has been discussed (Cubero, 1973). Two formal classes were considered for *paucijuga* (P_1 and P_2) and three for *major* (M_1, M_2 and M_3). The weight intervals were: P_1: less than 0,30 grams/seed; P_2: 0,31 – 0,40; *minor*: 0,41 – 0,60; *equina*: 0,61 – 1,10; M_1: 1,11 – 1,40; M_2: 1,41 – 1,70 and M_3 more than 1,71 grams/seed.

From the total, thirty unselected populations (little unconscious selection has actually occurred over all kinds of populations; our term "unselected" refers here to this circumstance), were taken out and the distances between them (in Mahalanobi's sense) were calculated (Rao 1952).

Results and Discussion

Fig. 3 shows the between-groups graphic relations according to four characters previously studied (Cubero, 1970 a, b). It can be seen that the *paucijuga* and *minor* are opposed groups in all cases but one. In three graphs the straight line connecting the two representative points goes through the *major-equina* conjoint. *Equina* shows a central position in all the graphs, and the three *major* subgroups always lie together, and are closer to *equina* than the other group. The two *paucijuga* subpopulations are generally very close to one another.

It is curious that only one graph (Fig. 3f) seems to show a linear connection between our taxonomic character (seed weight) and the number of ovules per ovary: a straight line joins *paucijuga, minor, equina* and *major*, in that order. The other figures show no connections of this kind at all.

Three possibilities can be deduced from these figures: 1) The primitive group is *paucijuga*, from which, by two divergent routes, arise *minor* on one side and *equina* and *major* on the other. 2) The primitive group is *minor*, with *paucijuga* originating on one side and *equina* and *major* on the other. 3) A primitive group, possibly classified archaeologically as *minor* but genetically richer (at least than the actual *minor*), evolves giving a strong nucleus formed by *equina* and *major*; *minor*, and perhaps *paucijuga*, would be relicts, or the end of the series. I suggest this third explanation.

It is necessary to assert that I do not maintain that *equina* and *major* are the most primitive as botanical types but that their genetical systems are those with the maximum possibilities, giving the necessary variability to evolve and form new morphological forms.

In previous work (Cubero, 1973a), I have shown that this is possibly so. Using the population distances between thirty populations taken from the total (see Methods and Materials), I have defined a Central Nucleus of Evolution which includes most *equina* and some *major* populations. It is possible that some *major* populations of the Nucleus become more differentiated, arising from an undifferentiated group formed by the *equina* and the lesser *major*, but it is not possible to decide this at the moment.

An interesting consequence is that, even if the existence of such a Central Nucleus is taken as subjective, that is, as a function of the number of variates and of the populations considered, the relative distances between extreme populations showed that some *major* were farther from one another than each was from *paucijuga*, which has the category of subspecies in Muratova's taxonomy. This gives rise to strong doubts about the classic Taxonomy; it is possible that, at least in this species, a stem-like structure exists, which grows and originates specialized branches. This stem seems not to be geography-dependent: distances to the Central Nucleus were, in general, independent of geographical situation; *major* populations from close situations can be very far apart taxonomically and vice versa (Cubero 1973a).

But the Central Nucleus can not be a calculus artifice. We have made a similar study on *Cicer arietinum* (not published data) and the graphic picture does not suggest a growing stem, but a rugby ball. The same technique that detects a Nucleus in the first case fails in the second.

Such a Nucleus suggests a high degree of undifferentiation in *Vicia faba.* If we apply inversely the argument that the greater the differentiation the greater the differences between reciprocals, we have that the less the differentiation the less the reciprocal differences. Using this idea, I have analyzed a 7×7 diallel cross (Cubero, 1973b), which was very heterogeneous from the point of view of the origin of parental lines: two Spanish *major*, two *minor* and one *equina* of Central-European origin and two Indian *paucijuga*. Table 1 contains the results of the seventeen studied characteristics, only in connection with our problem. Only five characteristics showed reciprocal differences: two at the $1^0/_{00}$ level, two at the

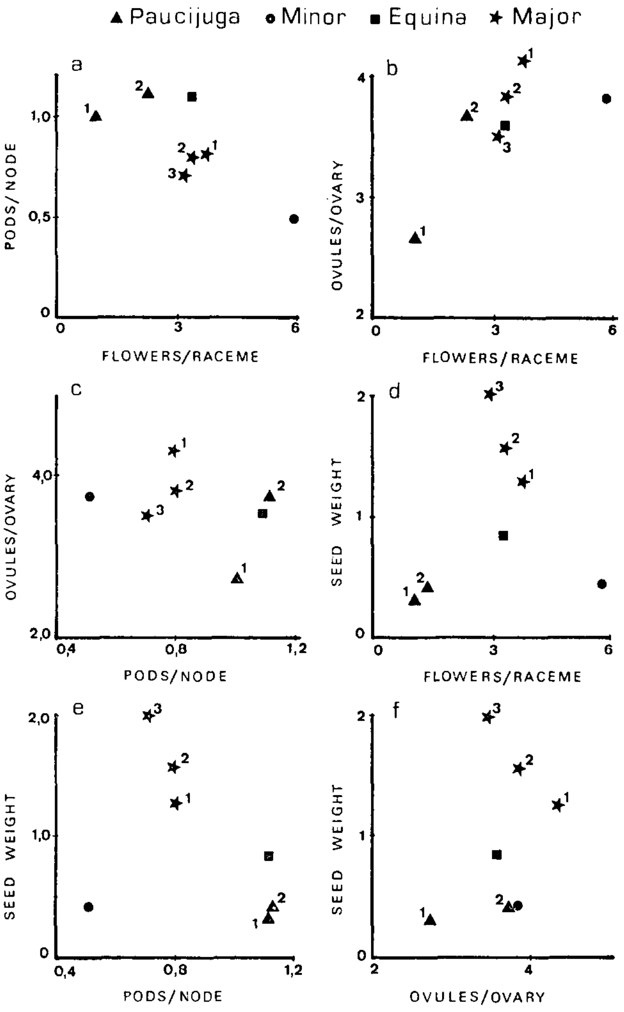

Fig. 3. Relationships between botanical groups

Table 1. *Significance of reciprocal differences (from Cubero, 1973b)*

Characteristic	Level of Sig. (1)	Characteristic	Level of Sig. (1)
Plant height	*** (g)	Pods/node	ns
Rachis length	ns	Ovules/ovary	* (g)
Leaflets/leaf	ns	Seeds/pod	ns
Leaflet width	ns	Pod width	ns
Leaflet $\frac{\text{width}}{\text{length}}$	ns	Seed length	** (a)
Total weight/plant	** (g)	Seed $\frac{\text{thickness}}{\text{length}}$	** (a)
Seeds/plant	(*) (g)	Seed weight	ns
		Days to blossom	ns
Flowers/raceme	*** (g)	Days to maturity	ns

(1) *** $< 1^0/_{00}$; ** $< 1\%$; * $< 5\%$; (*) $< 10\%$; ns: not significant
g: genotype dependent; a: genotype independent

1% and one at the 5% level. Even if we add another characteristic, number of seeds per plant, both because of its strong correlation with the total weight per plant and its near significance at the 5% level, we have only six characteristics, one third of which present a low level of significance. If we consider that the analyses were carried out with parental lines that include the whole variation range of the species, it must be concluded that the differentiation is not great but very small.

But it exists and it can be demonstrated by means of three different kinds of result.

Table 2. *Reciprocal differences: parental effects (1) (from Cubero, 1973b)*
Parental line (considered as female)

Characteristic	164	165	166	168	169	171	172
Plant height	A	A	D	D	A	D	D
Weight/plant	A	A	D	D	A	—	D
Seeds/plant	A	A	D	D	—	—	D
Flowers/raceme	A	A	D	D	—	D	D
Ovules/ovary	A	A	D	D	A	—	D
Seed $\frac{\text{thickness}}{\text{length}}$	D	A	—	A	—	D	D

(1) A: to augment the F_1 value: D: to diminish it; —: no effect. Accession number 164 and 165: *major*; 166 and 168: *minor*; 169 *equina*; 171 and 172: *paucijuga*

First, a more detailed analysis of the reciprocal differences (Table 2) showed that the *equina* and *major* cytoplasms uniformly increase the F_1 value of the studied characteristics; the opposite effect is presented by *minor* and *paucijuga*. There are two exceptions to this rule, both presented by seed thickness/length; this was the only character showing a very strong environmental influence in the reciprocal differences.

Second, the *equina* and *minor* lines used show different behaviour from the other parental lines in connection with the quantitative inheritance of four characteristics. We can analyze the four small 3 × 3 subdiallel tables and compare the results with those of one 4 × 4 diallel cross previously analyzed (this one was only performed with Central-European lines; Cubero 1970a). The results can be seen in Table 3, and it is evident that the Central-European lines differ from the rest of the parental lines in the genetical systems controlling plant height, the number of flowers per raceme, seed length and seed weight; in these two last cases, even the dominance sense changes. It is clear that the Central-European lines are specialized in some senses. It is logical to suppose that in not very sunny countries (compared to the Mediterranean ones) height must be an important adaptive characteristic, and from here, the overdominance is detected; it is also logical that in plants which are not strongly branched (the Central-European used in this work), to have a great number of flowers must improve fitness. It is more difficult to discuss the overdominance in the positive sense presented by seed length and weight; if we compare these results with the negative dominance of these characteristics in the *major* studied (Cubero, 1973b), perhaps the most probable mean is that an optimum seed size must exist, in such a way that the amount of reserve substances in each seed and the necessity of producing a great number of seeds must be in equilibrium.

Thirdly, the incompatibility. The species has a partial incompatibility system (Cubero 1970b), very strong in some populations but very weak in others. It does not exist in one line of *paucijuga* at least, which is functionally autogamous. In some Spanish populations it is not difficult to breed to obtain cultivars with a very weak incompatibility system, getting a high degree of self compatibility. This is not easy to do in Central-European populations, at least under our conditions. Table 4 shows these results: the two *paucijuga* lines (171 and 172) considered as female parents show a very high degree of intercompatibility, while the 168 and 169 lines show a very low degree. As male parents, all lines show similar percentages. It is curious to notice the different behaviour of the *paucijuga* lines considered either as female or as male parents. It might be supposed that the generally weak incompatibility system (strong in the Central-European lines) is very reduced, even nil, in *paucijuga*, perhaps because of the partial lack of function of the incompatibility genes of the style.

Briefly, intraspecific differentiation exists, but it is not strong enough to have cut the genetic flux

Table 3. *Characteristics that present discrepancy in the genetical systems*

Characteristics	7 × 7 Diallel cross (1)				4 × 4 Diallel cross (2) (centroeuropean lines)	
	All lines	Dominance sense	Centroeuropean lines	Dominance sense	system	Dominance sense
Plant height	partial dominance	positive	overdominance	positive	overdominance	positive
Flowers/raceme	partial dominance	positive	overdominance	positive	overdominance	positive
Seed length	partial dominance	negative	overdominance	positive	overdominance	positive
Seed weight	partial dominance	negative	doubtful	doubtful	overdominance	positive

(1) From Cubero 1973 b (2) From Cubero 1970 a

Table 4. *Percentage of hybridization success (fifty flowers by cross as minimum) (1)*

♀ Line	♂ 164	165	166	168	169	171	172
164	—	38,5	25,0	35,7	33,3	35,7	16,7
165	6,3	—	41,7	33,3	23,1	14,3	16,7
166	28,6	21,4	—	28,6	42,8	23,1	21,4
168	8,3	0,2	7,7	—	7,7	15,4	7,7
169	7,7	16,6	7,1	14,3	—	30,7	7,7
171	81,3	85,6	53,3	84,6	85,6	—	50,0
172	78,6	69,2	83,3	73,7	71,5	84,6	—

(1) Accession number 164 and 165: *major*; 166 and 168: *minor*; 169: *equina*; 171 and 172: *paucijuga*

between populations, even between classic subspecies. *Paucijuga* seems to evolve towards autogamy (at least towards functional autogamy, because they can be visited by pollinator insects), with strong branching, small height, small number of leaflets per leaf and very small seed size. And there is a very curious detail in the three *paucijuga* populations known to us — indehiscent pods. It is curious because at the other extreme of the habitat of *Vicia faba* this character appears in the major group, which is also at the opposite extreme of the variability range of the species; it is evident that the "indehiscent" character was in the nucleus that originated *major* and *paucijuga*. It is present in my "Central Nucleus", which is composed of dehiscent and indehiscent forms, being an indication of its genetic richness and potentiality, because in the actual *minor* group indehiscence never occurs. The *minor* group has fixed too many characters and surely represents an end of series. This is also the case for some *major* populations which have detached from the nucleus at different moments and regions in such a way that there can be more differences between them than there are when they are compared with *paucijuga*. In marginal regions, at the frontiers of the species, some particular differentiations occur: strong self-and inter-incompatibility and different genetic systems for some characteristics in connection with the rest of the species. It will be interesting to see if these particularities are also present in other border-forms; I have begun to study this matter.

Hanelt (1972b) has proposed a new Taxonomy for *Vicia faba*. He recognizes two subspecies: *minor* (the oldest one) and *faba*, the latter having two varieties, *faba* and *equina*. I think that it is more realistic than Muratova's but in all cases I am reluctant to admit two subspecies. I would prefer to speak only of four groups or varieties (in the botanical concept of this word): *paucijuga*, *minor*, *equina* and *major*. Most of the *equina* and some *major* populations form the richest groups in genetic potentiality (the Central Nucleus); *paucijuga* and *minor* (this is the botanical primitive form — botanical, not genetical) are actually ends of series, relicts or border-forms. The *major* populations not belonging to the Nucleus are derived from this in a geography independent form. Probably the extreme *major* (even the median ones) must be grateful to Man for its existence.

The possibility of inter- and self-fertility can explain both the differentiation and creation of new forms and the unity of the species from the point of view of reproduction. It seems that the intraspecific differentiation has been recent; the fact that wide crosses are easily obtained with minimal reciprocal differences is a good index of the youth of *Vicia faba*.

Literature

Cole, Sonia: The Neolithic Revolution, pg. 18. Trustees of the British Museum (Natural History), London (1970).

Cubero, J. I.: Herencia de quince caracteres cuantitativos en *Vicia faba*. Anales INIA **19** (1), 11—50 (1970a).

Cubero, J. I.: Influencia de homocigosis y heterocigosis en la fertilidad de *Vicia faba*. Tesis Doctoral. Escuela Técnica Superior de Ingenieros Agrónomos, Madrid (1970b).

Cubero, J. I.: Evolutionary trends in *Vicia faba* L. Theor. Appl. Genetics **43** (2), 59—65 (1973a)

Cubero, J. I.: Herencia de caracteres cuantitativos en *Vicia faba* L. Tesis Doctoral. Facultad de Ciencias (Biológicas) Universidad Complutense de Madrid (1973b).

Hanelt, P.: Zur Geschichte des Anbaues von *Vicia faba* und ihrer verschiedenen Formen. Die Kulturpflanze **20**, 209—223 (1972a).

Hanelt, P.: Die infraspezifische Variabilität von *Vicia faba* L. und ihrer Gliederung. Die Kulturpflanze **20**, 75—128 (1972b).

Hayman, B. I.: The theory and analysis of diallel crosses. Genetics **39**, 789—809 (1954).

Muratova, V.: Common beans (*Vicia faba* L). Suppl. 50 Bull. Appl. Bot. Genet. Plant Breed. 285 pp. (1931).

Pirenne, J.: Historia de la Civilizatión del Antiguo Egipto. Barcelona: Editorial Exito 1963.

Rao, C. R.: Advanced statistical methods in biometric research. New York: John Wiley & Sons Inc. 1952.

Received October 11, 1973

Communicated by H. Stubbe

Dr. J.-I. Cubero
Instituto Nacional de Investigaciones
Agrarias
Centro Regional de Andalucía
Apartado 240
Córdoba (Spain)