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Quantitative Inheritance and Barriers to Crossability in *Cicer arietinum* L.

A. Martinez, A. Coiduras and M.T. Moreno
Instituto Nacional de Investigaciones Agrarias, Centro Regional de Andalucia, Córdoba (Spain)

J.I. Cubero
Department of Genetics, Escuela de Ingenieros Agrónomos, Córdoba (Spain)

Summary. Three different diallel crosses were studied in *Cicer arietinum*; two of size 6 × 6, one within each of the two botanical groups 'macrosperma' and 'microsperma' of the cultivated subspecies, and one of 9 × 9 involving lines covering most of the morphological variation of chickpea. Barriers to crossability present neither a botanical nor a geographical pattern, being probably a direct consequence of interactions between genotypes. The genetic systems of twelve quantitative characters were analysed. Full dominance in a negative sense (small values dominant) is shown by leaflet length, width and shape index, rachis length, leaflet density on the rachis and pod length. Full dominance in a positive sense is shown by seeds per pod. Overdominance (in a positive sense) is evident for pods, seeds and yield per plant. Weak reciprocal differences were manifested by pod length, and pods, seeds and yield per plant. The system controlling number of leaflets per leaf is not clear. Dominance of 'primitive' over 'selected' characters seems to be the rule. As far as the environmental effects have permitted the analysis, no differences in genetic systems were observed between botanical groups.

Key words: Genetic barriers – *Cicer arietinum* – Diallel analysis

Introduction

Although *C. arietinum* L. (chickpea, pois chiche, garbanzo) is ranked third among the pulses of the world in cultivated area, little is known about it from a genetical point of view. Research on qualitative genetics and studies on evolution and systematics are rather scarce and no published data on quantitative inheritance are available, at least to our knowledge. We are studying systematically the variability within this species, looking at different aspects of its geographical distribution, as well as its qualitative genetics (in terms of morphological and biochemical characters) and quantitative genetics. In a previous paper (Moreno and Cubero 1978) we described the general pattern of variability of this species and proposed a classification in which the wild forms are grouped in the subspecies *reticulatum* (Lad.) Cubero and Moreno and the cultivated ones in subspecies *arietinum* L. In the latter, two groups were recognized, 'macrosperma' and microsperma', according to a complex of characteristics including seed, pod and leaf size. Populations belonging to the first group are characterized by large seeds, pods and leaves (rachides as well as leaflets) and those belonging to the second one by a smaller size of these organs. 'Macrosperma' is supposed to be derived in recent times from 'microsperma'.

The problem with which we are now concerned is not only to know the genetic systems controlling quantitative characters in chickpea, but also, if these systems are different in the two groups, to find the extent to which they differ. This should provide information about whether the separation of 'macrosperma' from 'microsperma' led not only to a morphological differentiation but also to genetic isolating barriers.

The reason why *C. arietinum* has not been more frequently used in genetic studies is because of the difficulty in producing hybrids. Indeed, it is substantially more difficult to produce a hybrid in chickpea than it is in peas or field beans (*Vicia faba*). Furthermore, greenhouse conditions do not fulfil chickpea requirements and it is necessary to work under field conditions to avoid a complete failure of crossing. However, in spite of these difficulties, several hybrids were obtained from which valuable conclusions can be drawn.

Material and Methods

Three different series of diallel crosses were performed, within 'microsperma' (series m̲), within 'macrosperma' (series M̲) and be-

Table 1. Characteristics of the studied lines

			Leaflet			Leaf			Pod & seed			Plant characters		
Design	Accession number	Origin	Length	Width	Shape	Leaflets/ leaf	Rachys	Leaflets density	Pod length	Seed weight	Seeds pod	Pods	Seeds	Yield
m	1282	Mexico	1.05	0.61	0.58	12.9	4.45	2.90	2.03	0.22	1.5	65	95	20
	1331	"	1.10	0.65	0.59	12.2	4.18	2.92	2.05	0.23	1.2	85	99	23
	1336	"	1.10	0.65	0.59	12.0	3.98	3.02	1.79	0.15	1.6	75	117	18
	1341	"	1.16	0.66	0.56	11.9	4.34	2.74	1.97	0.23	1.3	67	86	20
	1348	"	1.30	0.75	0.58	12.9	5.26	2.45	1.97	0.20	1.4	94	133	27
	1378	"	1.21	0.75	0.62	13.9	4.44	3.13	1.98	0.24	1.3	105	137	33
M	6	Spain	1.31	0.93	0.71	13.9	5.24	2.65	2.40	0.42	1.1	73	78	33
	16	"	1.60	1.21	0.76	13.4	5.77	2.32	2.83	0.52	1.0	44	43	22
	41	"	1.56	0.98	0.63	13.0	5.36	2.43	2.47	0.37	1.2	81	99	37
	47	"	1.44	1.06	0.74	14.0	5.69	2.46	2.46	0.41	1.1	64	72	29
	1475	"	1.36	0.87	0.64	12.9	4.30	3.00	2.26	0.30	1.1	88	96	28
	1507	"	1.49	1.08	0.72	13.0	5.03	2.58	2.35	0.42	1.0	57	56	23
S	12	Spain	1.17	0.70	0.60	12.8	4.43	2.89	2.16	0.21	1.2	88	109	23
	108	"	1.55	0.91	0.59	14.1	5.43	2.60	2.35	0.31	1.3	88	115	36
	127	"	1.77	1.05	0.59	13.3	5.36	2.48	2.23	0.44	1.1	49	52	23
	1288	Mexico	1.05	0.70	0.67	12.5	3.90	3.21	1.97	0.20	1.2	76	94	19
	1341	"	As above (see series *m*)											
	1473	India	1.15	0.70	0.61	13.8	4.12	3.35	1.85	0.13	1.7	143	240	32
	1492	Spain	1.77	1.27	0.72	13.4	5.80	2.31	2.64	0.60	1.1	60	67	40
	1550	India	1.50	0.97	0.65	14.5	5.48	2.65	2.31	0.36	0.9	54	47	17
	1569	Balcans	1.18	0.75	0.63	12.3	3.95	3.11	1.99	0.24	1.0	86	87	22

Length and width = cm, weight = grams

Table 2. Hybridization in *C. arietinum* – series m(Mexican, microsperma)

♀ ♂	1378	1341	1331	1348	1282	1336
1378	–	38	37	32	37	61
		10.5	16.2	34.4	29.7	23.0
1341	27	–	38	33	40	26
	7.4		10.5	9.1	10.0	61.5
1331	25	33	–	34	49	54
	20.0	18.2		23.5	16.3	16.7
1348	25	33	57	–	51	51
	20.0	18.2	12.3		33.3	0.0
1282	36	44	44	46	–	45
	8.3	11.4	34.1	19.6		20.0
1336	38	35	47	65	48	–
	18.4	28.6	14.9	1.5	18.8	

Upper value = number of crosses, lower value = percentage of success

Table 3. Hybridization in *C. arietinum* – series M(Spanish, macrosperma)

♀ ♂	16	1507	47	1475	41	6
16	–	100	105	70	44	71
		0.0	4.8	10.0	31.8	9.9
1507	84	–	43	106	101	92
	2.4		14.0	3.8	11.9	3.3
47	79	48	–	57	50	54
	10.3	18.8		59.7	30.0	37.0
1475	58	63	50	–	66	70
	36.2	11.1	14.0		7.6	15.7
41	45	90	49	46	–	56
	24.4	3.3	38.8	23.9		26.8
6	65	104	70	80	106	–
	9.2	3.9	20.0	18.8	3.8	

Upper value = number of crosses, lower value = percentage of success tween these groups, including lines covering most of the range of variability of the cultivated forms (series S). The sizes of the diallels were, at the beginning, 8 × 8 for the first two series and 10 × 10 for series S. Because of difficulties in producing hybrids we had to conform to 6 × 6 and 9 × 9 designs respectively, at the same time decreasing from two replications to one.

For M and m analyses the lines to be crossed were selected at random within a geographical origin, Mexican for m, Spanish for M. It was natural to choose Spanish lines as 'macrosperma' representatives but the selection of Mexican ones from 'microsperma' requires some explanation. Three reasons led us to make such a choice. First, the range of the Mexican 'microsperma' populations is around the average of the botanical group. Secondly, they were well adapted to Spanish field conditions, in contrast to such other populations as the Iranian ones. Third, they were very well represented in our collection, so that the selection could still be random. For S analysis, on the other hand, the lines to be included in the analysis were chosen in such a way as to have as much variation as possible represented in the diallel cross.

The crosses were realized during three years. It was not possible to complete two replicates because of the possibility of problems which would be caused by different ages of seeds. Five plants were used for each cross, the final average being 4.2.

m and M diallels were analysed as complete diallel crosses. S diallel was analysed as a half-diallel cross because of the great number of incompatible or almost incompatible crosses. As one of our main interests is the extent of reciprocal differences, three complete subdiallels were analysed, one 5 × 5 and two 4 × 4, including the nine parental lines. For brevity we shall only describe here the first one together with the overall 9 × 9 half-diallel, the results of the two other 4 × 4 do not add any further information.

The diallel analysis of Hayman and Jinks (Hayman 1954 a,b; Jinks 1954) has been performed, using the modification of Jones (1966) for the half-diallel analysis. In this case, the source of error has been the interplant mean square according to the model:

$$x_{ijk} = \bar{m} + g_i + p_{j(i)}$$

where x_{ijk} is the individual result, $\bar{m}$ the grand mean, g_i the effect of i^{th} genotype and $p_{j(i)}$ the effect due to the j^{th} plant within the

Table 4. Hybridization in *C. arietinum* – Series S

♀ ♂	M 108	M 1492	m 12	m 1341	M 1550	m 1473	m 1569	M 127	m 1288	
M 108	–	24	46	56	22	28	50	38	48	sp
		20.8	8.7	5.4	22.7	46.4	30.0	36.8	31.3	
M 1492	21	–	45	48	39	36	34	30	52	sp
	9.5		22.2	2.1	7.7	19.4	23.5	23.3	13.5	
m 12	57	83	–	58	37	34	51	50	61	sp
	0.0	3.6		6.9	2.7	0.0	23.5	10.0	11.5	
m 1341	51	52	42	–	32	43	19	48	58	mx
	0.0	1.9	26.2		15.6	2.3	5.3	14.6	1.7	
M 1550	35	50	57	32	–	26	26	34	37	ind
	5.7	2.0	17.5	9.4		15.2	23.1	20.6	2.7	
m 1473	32	44	35	47	37	–	43	51	51	ind
	25.0	6.8	14.3	12.8	8.1		23.3	13.7	17.7	
m 1569	47	42	33	23	53	45	–	39	39	balc
	21.3	42.9	33.3	26.1	11.3	26.7		18.0	23.1	
M 127	83	52	44	58	40	53	49	–	19	sp
	6.0	15.4	15.9	0.0	7.5	5.7	16.3		15.8	
m 1288	73	62	64	56	54	50	49	35	–	mx
	4.1	1.6	12.5	1.8	11.1	26.0	22.5	8.6		

Upper value = number of crosses, lower value = percentage of success
m = 'microsperma', M = 'macrosperma', sp = Spanish, mx = Mexican, ind = Indian, balc = Balcanic

ith genotype. Only hybrids were considered in this design as 'genotype' values in order to avoid a possible differential buffering between lines and hybrids.

Since the lines of S analysis are fixed, the conclusions are only applicable to them. It is, of course, the comparison of the S results with those obtained from the m and M series which can complete our information about the quantitative systems.

The following characters were studied: leaflet length, width and shape index (W/L), rachis length, leaflets/leaf, density of leaflets (number of leaflets per cm of rachis), pod length, seed size (weight of one seed, averaging over one hundred), seeds per pod, and pods, seeds and yield per plant. Twenty leaflets and ten leaves and pods per plant were used to take measurements. Table 1 shows characteristics of the studied lines.

Table 5. % of success in crosses between geographical groups

♀ Origin ♂	sp	mx	ind	balc
sp	14.4	10.8	18.7	23.5
mx	8.7	1.8	13.8	13.9
ind	17.6	10.6	11.8	23.2
balc	28.9	24.6	19.0	–

sp = Spanish, mx = Mexican, ind = Indian, balc = Balcanic

Results and Discussion

a) Barriers to Crossability

Tables 2-4 present, respectively, both the percentage of success in crosses, and the number of crosses realised in each one of the designs m, M and S. From Table 4 we can assess the relative success within and between both botani-

Table 6. Diallel crosses in *C. arientinum* L. W/V graph, parameters

Parameters	Leaflet length^a			Leaflet width^a			Leaflet W/L^b			Leaflets/leaf		
	m	M	S	m	M	S	m	M	S	m	M	S
D	-0.60	0.94	4.37^f	0.07	0.85	2.63^f	1.98^f	1.00^e	1.75^f	0.59^f	0.01	0.51^f
F	-0.92	0.13	1.08	0.07	-0.01	0.67^f	1.18	-0.51	0.26	0.27	-0.03	0.33^e
H$_1$	-0.03	2.42	3.76^f	-0.05	1.43	2.02^f	0.35	-0.20	1.59^e	0.19	-0.04	0.33^e
H$_2$	0.37	2.04	3.13^f	-0.04	1.28	1.66	0.52	0.00	1.53^e	0.14	-0.01	0.19
h^2	-0.14	4.20^e	0.43	-0.15	2.65^e	0.46	0.12	0.31	0.27	0.01	0.26	-0.02
D-H$_1$	-0.57	-1.48	0.61	0.12	-0.58	0.61	1.63	1.20	0.16	0.40^e	0.05	0.18
E	0.74^f	0.63^e	0.23	0.28^f	0.17	0.10	1.22^f	0.70^f	0.52^e	0.08^e	0.27^f	0.08^f

Parameters	Rachis length^d			Leaflets density^c			Pod length^a			Seed size^b		
	m	M	S	m	M	S	m	M	S	m	M	S
D	-0.30	2.54^f	2.77^f	-8.78	13.05^e	0.20^f	0.68^f	2.97^f	5.83^f	1.55^f	2.28^f	18.9^f
F	-0.57	1.65	-0.32	-1.51	13.47	0.04	0.16	1.35	2.71	0.59	-3.29^f	68.5^f
H$_1$	0.65	1.53	2.36^e	-3.31	18.03	0.39^e	0.98	0.80	4.30^e	0.78	4.10^f	55.6^f
H$_2$	0.80	1.14	2.29^f	4.33	13.45	0.29^e	0.77	0.56	3.19^e	0.73	2.94^f	45.0^f
h^2	0.16	1.05	0.02	-6.41	25.26	0.00	0.65	-0.14	0.27	0.74	-0.62	10.4^f
D-H$_1$	-0.95	1.01	0.41	-5.47	-4.98	-0.19	-0.31	2.17^e	1.54	0.77	6.38^f	-36.7^f
E	0.47^f	0.43	0.20	11.58^f	3.62	0.30	0.18^e	0.38^e	0.13	0.12	2.15^f	2.14^f

Parameters	Seeds/pod^a			Pods/plant^a			Seeds/plant^a			Weight/plant		
	m	M	S	m	M	S	m	M	S	m	M	S
D	3.37^f	0.92	4.46^e	-0.88	0.78^e	3.84^f	-0.88	1.16^e	4.18^f	-0.91	0.39	1.64^e
F	2.38^e	1.34	0.47	-1.02	0.52	3.99^f	-1.24	0.86	3.57	-1.71	0.49	1.11
H$_1$	1.96^e	2.40	5.23	4.05	3.69^f	10.31^f	3.87	3.95^f	5.77^e	1.84	4.37^e	9.06^f
H$_2$	1.29	1.58	3.75	3.74^e	3.51^f	8.79^f	3.78	3.78^f	4.73^e	2.21	4.12^a	7.76^f
h^2	0.31	-0.15	0.02	2.29	5.58^f	5.51^f	1.07	3.68^e	8.11^f	3.15	6.26^e	2.77^e
D-H$_1$	1.42^e	-1.47	-0.77	-4.93^e	-2.91^f	-6.47^f	-4.75^e	-2.79^e	-1.59	-2.74	-3.98^e	-7.42^f
E	0.50^f	0.55^e	0.50	1.53^f	0.32^e	0.76^f	1.62^f	0.30	0.73^e	2.10^f	0.44	0.77^f

Levels of significance = ^{a}Values × 10^2, ^{b}Values × 10^3, ^{c}Values × 10^4, ^{d}Values × 10^{-1}, $^e0.05 > p > 0.01$, $^f p < 0.01$

cal and geographical groups. The average success of 'macro' x 'macro' crosses is 14,9%, that of 'micro' x 'micro' is 15,8% and between groups is 13,6%. The variances are large enough to cover most of the differences among these figures. Therefore, it seems, that there is no barrier between the two groups.

Nor does geographical origin cause any barrier to crossing. Table 5 summarizes the results. It can be seen that, with the exception of one case (Balcanic x Mexican), the reciprocal differences are not important. (However, we had only one Balcanic line in the final design and the results may possibly have been biased by this fact). The lowest percentage of success was obtained within Mexican lines, and within Spanish lines the success was smaller than in Spanish x Indian crosses. In fact, the figures are rather similar, excepting within Mexican and Balcanic lines because of the reasons just mentioned.

The conclusion is that the result depends on the individual genotypes which have been crossed rather than on a botanical or geographical basis. It can be seen (Table 4) that the greater percentage of success (46,4%) was obtained in a 'macro'-'micro' cross (108 x 1472; the latter is one of the lines with the smallest seeds), a second 'micro' x 'macro' (1569 x 1492) being very similar (42,9%). On the other hand, a complete failure of crossing is shown by two 'micro' x 'macro' crosses (12 x 108 and 1341 x 108; the two lines involved in the first cross are Spanish), one 'macro' x 'micro' (127 x 1341) and one 'micro' x 'micro' (12 x 1473). Some 'macro' x 'macro' crosses also showed similar results (for example; 1550 x 1492, with 2% of success). The individual effect of genotypes stands out clearly in Tables 2 and 3, which include lines belonging, in each case, to the same geographical and botanical origin. A look at these tables, even superficial, is more useful than any detailed description.

To sum up, the very low success in crosses between lines within chickpea does not depend on geographical or botanical distinction but on the behaviour of the individual genotypes involved. This can be accounted for by the origin of 'macrosperma' populations (derived from 'microsperma' populations by selection), the strict autogamy of the species and the action of man in the spreading of cultivated forms.

b) Quantitative Genetic Systems

Table 6 shows the parameters of Jinks' analysis and Figures 1 to 12 the corresponding W/V graphs. Table 7 contains the analysis of variance (Hayman analysis) of both m and M series and, finally, Table 8 presents the same analysis for the series S, giving the results of the 9 x 9 half-diallel and of the 5 x 5 subdiallel. The Jinks and the Hayman analyses are in good agreement with each other. We will describe the analyses of the different characters by organs.

Table 7. Diallel crosses in *C. arietinum*. Analysis of variance – series m & M – mean squares

Source of variation	d.f.	Leaflet length^a		Leaflet width^a		Leaflet W/L^b		Leaflets/leaf		Rachis length		Leaflets density^c	
		m	M	m	M	m	M	m	M	m	M	m	M
a	5	0.62	4.30^e	0.29	3.23^e	3.32	4.76^e	1.24^e	0.36	9.21	43.21^e	9.57	16.72^e
b_1	1	0.48	8.18	0.01	4.93	1.45	0.14	0.10	0.73	7.54	23.25	0.05	49.09
b_2	5	0.21	1.98	0.29	0.41	1.07	0.46	0.17	0.25	2.83	10.50	1.08	10.79
b_3	9	1.34	1.12	0.27	0.56^d	1.66	0.85	0.14	0.20	4.83	8.09	21.77	5.62
b	15	0.91	1.63	0.25	0.80^e	1.44	0.68	0.14	0.25	8.54	9.90	13.43	10.24^d
c	5	0.41	0.96	0.03	2.21	0.35	0.47	2.75	0.06	3.40	5.77	7.93	5.97
d	10	0.74	0.63	0.28	0.17	1.22	0.70	0.08	0.27	4.68	4.35	11.58	3.62

Source of variation	d.f.	Pod length^a		Seeds/pod^c		Seeds/size^a		Pods/plant^a		Seeds/plant^a		Weight/plant^a	
		m	M	m	M	m	M	m	M	m	M	m	M
a	5	2.40^e	6.02^e	5.58^e	1.86^d	31.33^e	157.56^e	3.12	1.70^e	3.25	1.74^e	3.74	0.95
b_1	1	1.36	0.13	1.06	0.28	14.45	10.27	5.65	10.04	3.56	6.92	7.77	11.71
b_2	5	0.52	0.77	1.55	1.82	1.97	5.91	2.11	0.61	1.89	0.58	1.72	0.85
b_3	9	0.50	0.65	0.91	1.17	5.37^e	5.80	3.79	1.95^e	4.39	2.51^e	3.43	2.38^e
b	15	0.56^d	0.65	1.31	1.33	4.84^e	6.14	3.36	2.06^e	3.47	2.19^e	3.15	2.49^e
c	5	0.66^d	0.85	0.69	0.77	1.10	10.77	7.19^d	1.66^e	5.40	1.03^d	4.67	0.88
d	10	0.18	0.38	0.50	0.55	1.20	21.47	1.53	0.32	1.62	0.30	2.11	0.44

Levels of significance = ^{a}Values × 10^2, ^{b}Values × 10^3, ^{c}Values × 10^4, $^d0.05 > p > 0.01$, $^e p < 0.01$

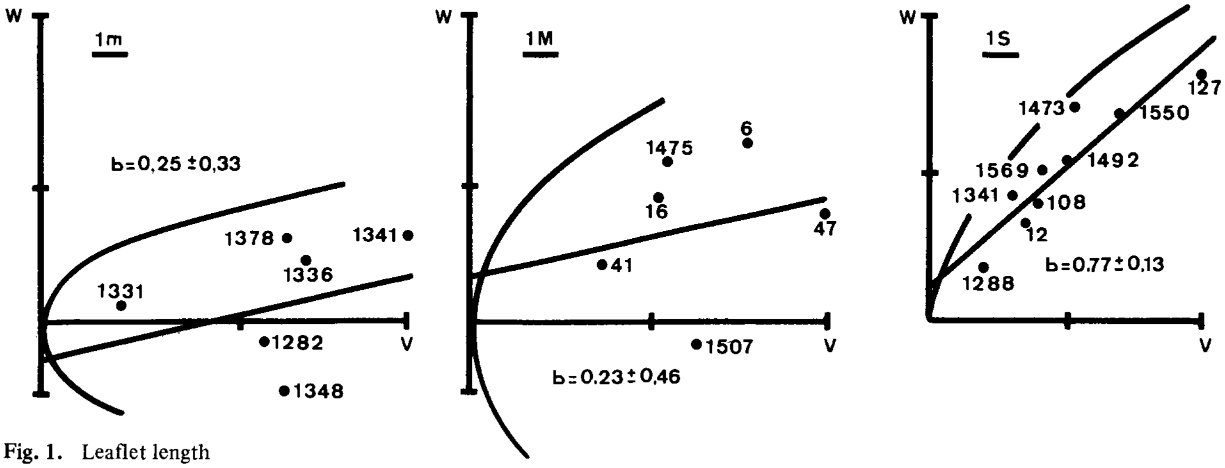

Fig. 1. Leaflet length

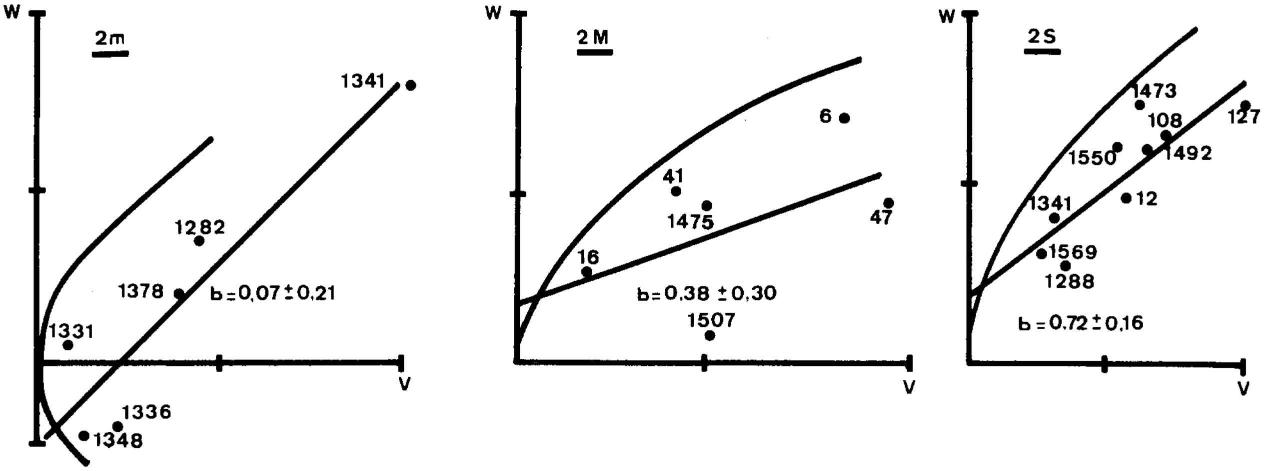

Fig. 2. Leaflet width

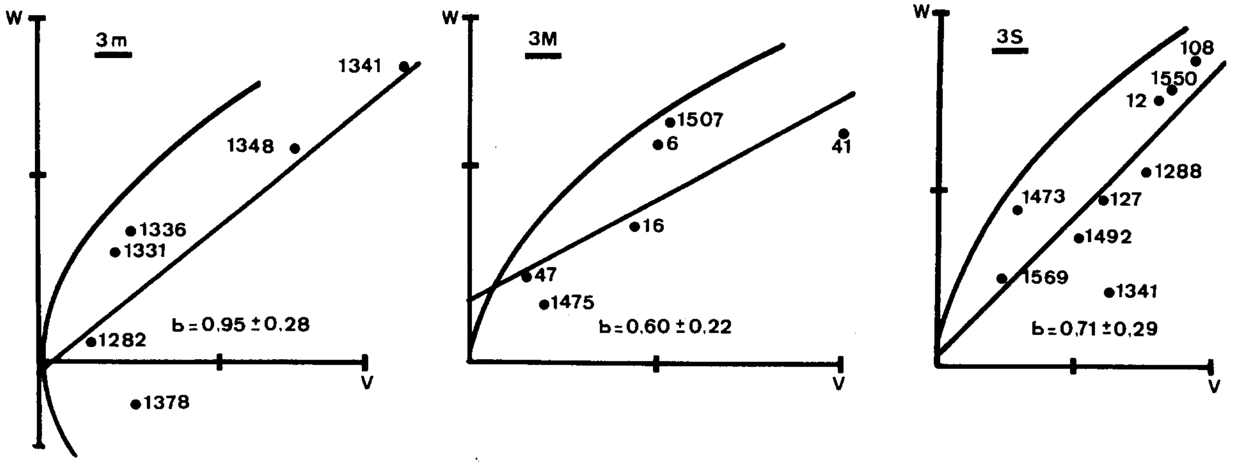

Fig. 3. Leaflet shape index

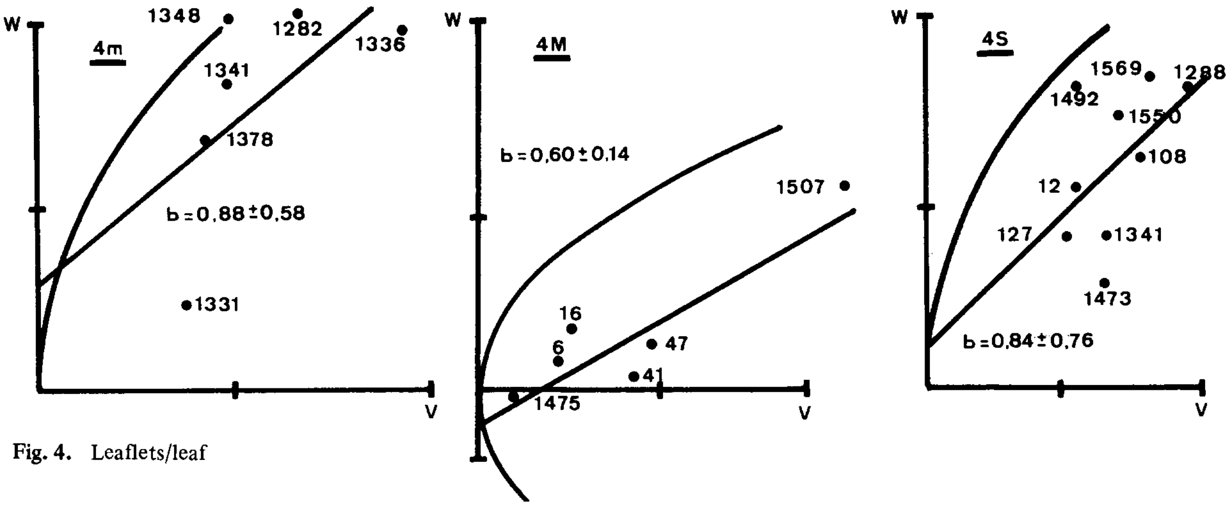

Fig. 4. Leaflets/leaf

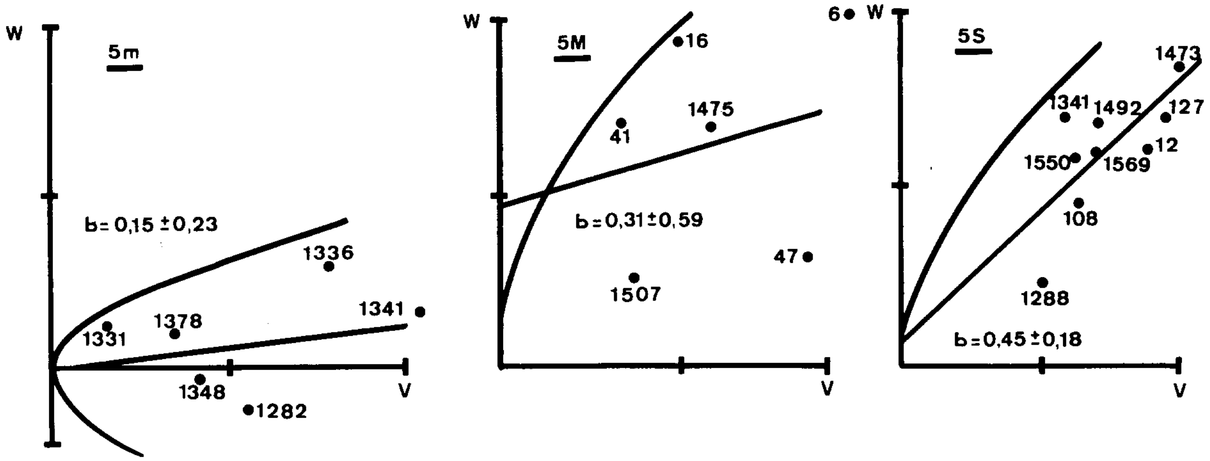

Fig. 5. Rachis length

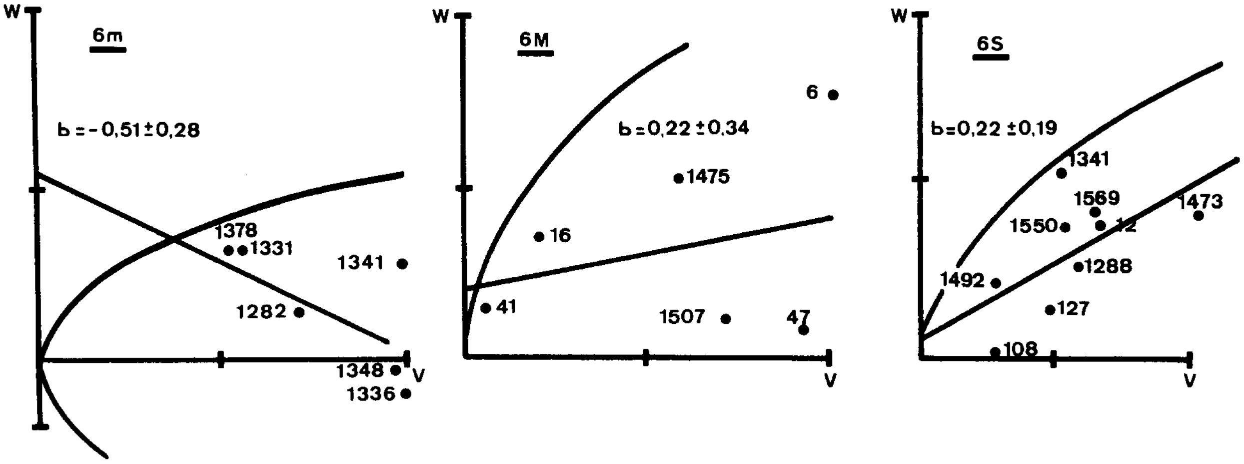

Fig. 6. Leaflets density

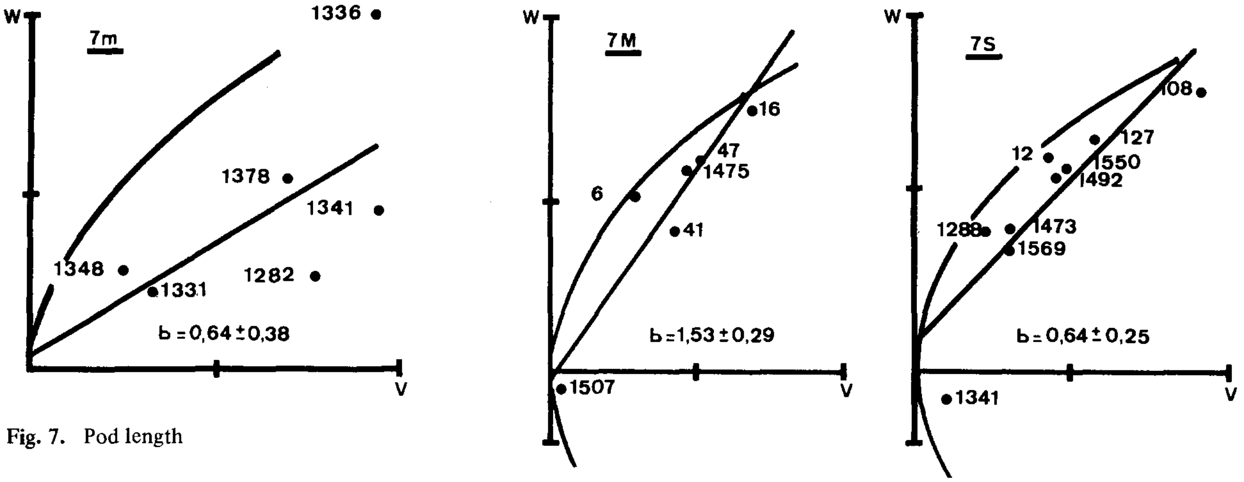

Fig. 7. Pod length

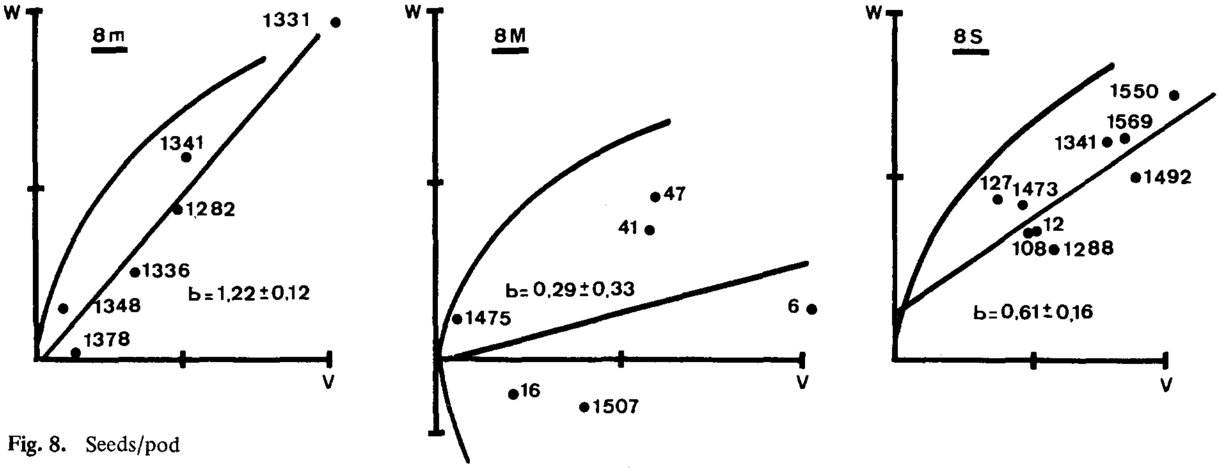

Fig. 8. Seeds/pod

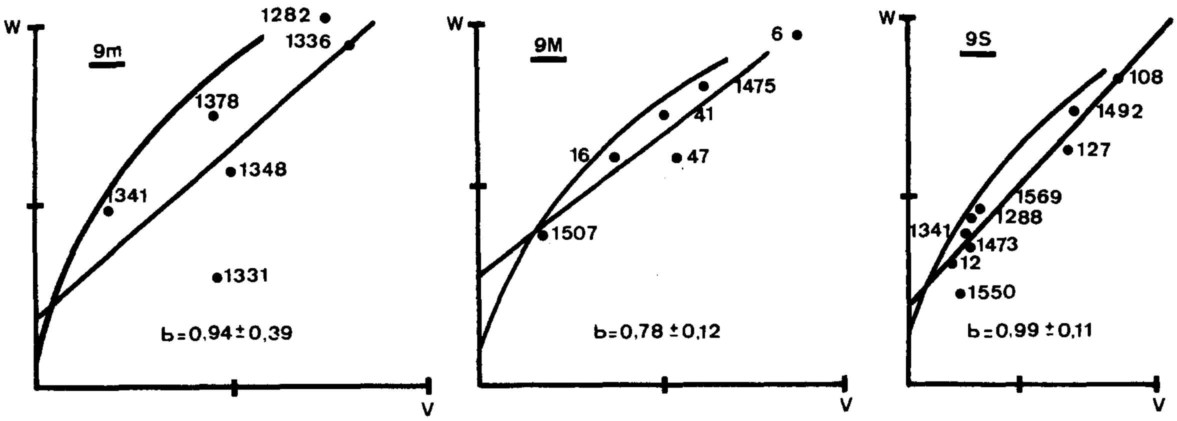

Fig. 9. Weight of one seed

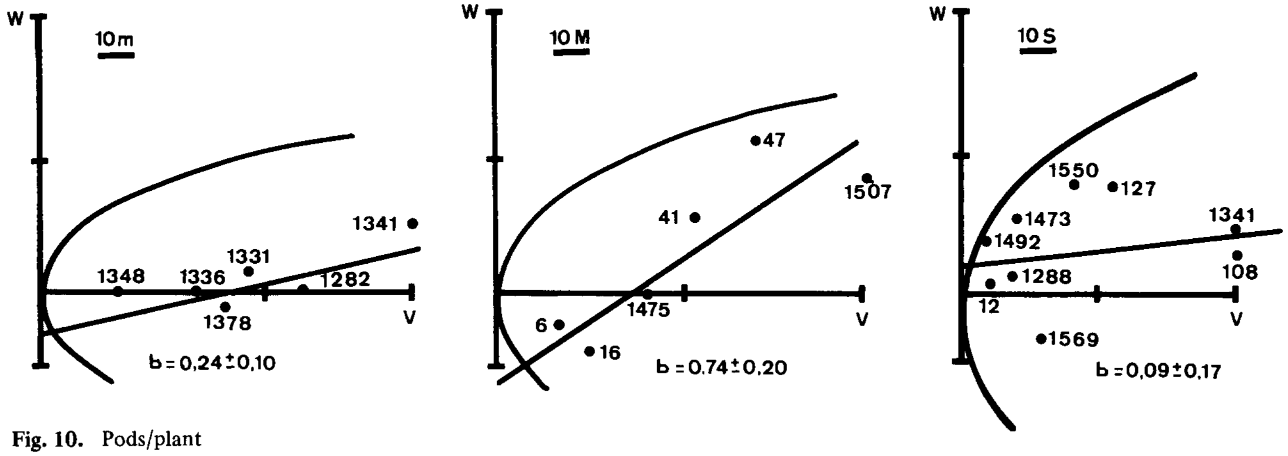

Fig. 10. Pods/plant

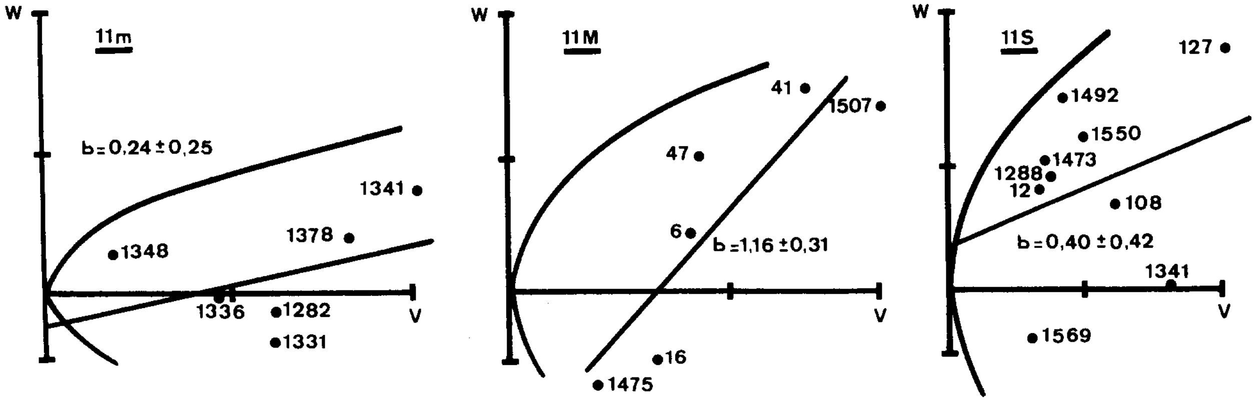

Fig. 11. Seeds/plant

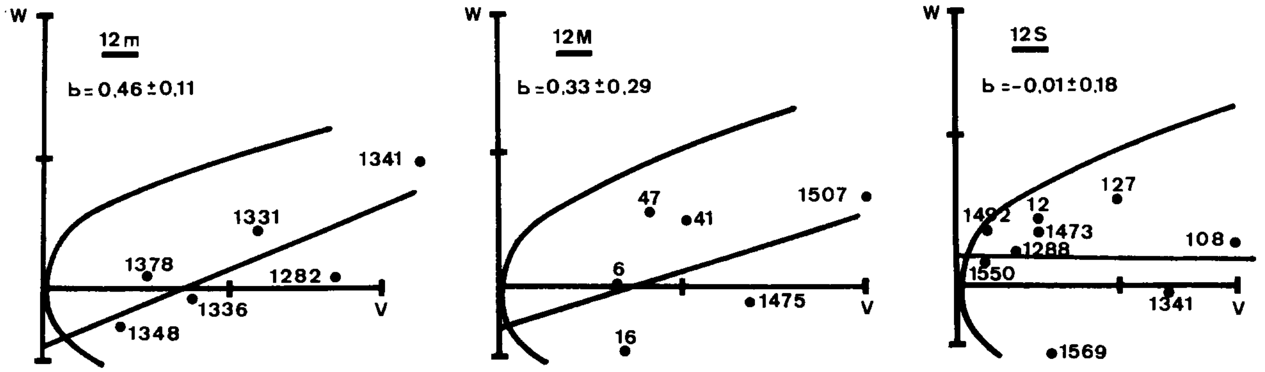

Fig. 12. Yield/plant

Table 8. Diallel crosses in *C. arietinum*. Analysis of variance series S – mean squares

Source of variation	d.f.		Leaflet length^{a}		Leaflet width^{a}		Leaflet W/A^{b}		Leaflet/leaf		Rachis length		Leaflet density^{b}	
	c	d	c	d	c	d	c	d	c	d	c	d	c	d
a	8	4	10.65^{f}	7.96^{f}	6.46^{f}	6.53^{f}	4.17^{f}	4.22^{e}	0.96^{f}	0.47	92.09^{f}	90.48^{f}	0.60^{f}	9.16^{f}
b_1	1	1	1.27	0.73	1.13	0.67	0.61	0.26	0.02	0.06	2.93	13.59	0.03	0.04
b_2	8	4	0.81	0.55	0.46^{f}	0.28	0.19	0.29	0.20^{e}	0.48	7.45^{f}	12.47	0.13^{f}	1.92
b_3	27	5	1.06^{f}	2.75	0.52^{f}	1.72	0.54^{f}	0.64	0.08	0.13	7.48^{f}	32.93^{e}	0.09^{f}	4.63^{f}
b	36	10	1.01^{f}	1.67	0.52^{f}	1.04	0.46^{f}	0.46	0.11	0.26	7.35^{f}	22.82^{e}	0.10^{f}	3.09^{f}
c	–	4	–	0.57	–	0.44	–	0.61	–	0.20	–	4.73	–	1.72
error/d	190	6	0.23	0.65	0.10	0.49	0.22	0.81	0.08	0.31	2.03	4.97	0.03	0.44

Source of variation	d.f.		Pod length^{a}		Seed size^{a}		Seeds/pod^{a}		Pods/plant^{a}		Seeds/plant^{a}		Weight/plant	
	c	d	c	d	c	d	c	d	c	d	c	d	c	d
a	8	4	11.90^{f}	16.94^{f}	3.87^{f}	3.94^{f}	14.27^{f}	15.09^{f}	4.90^{f}	1.92	5.89^{f}	3.81	4.92^{f}	2.15
b_1	1	1	0.21	0.26	0.24	0.33	0.49	5.46	13.23	0.27	19.14	3.53	7.38	0.14
b_2	8	4	0.85^{f}	1.08^{e}	0.12^{f}	0.32	1.96^{f}	1.67	2.22^{f}	2.50	1.70^{e}	2.07	1.99^{e}	3.08
b_3	27	5	0.76^{f}	0.45	0.14^{f}	0.07	1.22^{f}	3.14	2.76^{f}	2.30	1.36^{e}	0.71	2.59^{f}	1.92
b	36	10	0.77^{f}	0.68^{e}	0.14^{f}	0.19	1.36^{f}	2.78	2.96^{f}	2.18	1.93^{f}	1.54	2.59^{f}	2.20
c	–	4	–	0.75^{e}	–	0.10	–	1.24	–	8.39^{e}	–	4.19	–	6.18^{e}
error/d	190	6	0.13	0.14	0.02	0.08	0.50	1.83	0.76	1.16	0.73	1.57	0.77	0.78

Levels of significance = ^{a}Values × 10^{2}, ^{b}Values × 10^{3}, ^{c}Half-diallel 9 × 9, ^{d}Subdiallel 5 × 5, $^{e}0.05 > p > 0.01$, $^{f}p < 0.01$, ^{g}Values × 10^{4}

b1) Leaf

Analysis within groups (m and M) shows an amazing lack of significance for most of the parameters (Table 6) and sources of variation (Table 7); the exceptions are additivity and, in the case of the parameters, the environmental component. This is, perhaps, the clue; a strong environmental action over most of the characters hides the effect of the genetic systems. The sensitivity of leaf characters to environmental conditions is extreme, as has been already indicated in a previous work (Moreno and Cubero 1978).

The pattern for series S looks rather different. It is convenient to remember for the following discussion that the sub-diallel analysis will only be used to discover possible reciprocal effects. Additivity is again important but so is dominance, except for leaflets/leaf (the degree of variation of this character is very narrow). For practical purposes, we can sum up these results by saying that within botanical groups only general combining ability is important, whereas in crosses between groups specific combining ability is also important. No reciprocal effects were detected.

Inspection of the W/V graphs shows a good agreement with the Hayman-Jinks hypothesis by series S, an acceptable agreement by series m and an unacceptable one by series M. Covariance of parents and progeny has, in general, narrow limits in this series, showing that parental lines do not present a convenient degree of variability, at least for leaf characters. Series m offers a good example of the difficulties of studying some characters in isolation. Consider, for example, leaflet length (Fig. 1m): it shows a complete failure of the hypothesis; but with leaflet width (Fig. 2m) the agreement with the basic hypothesis of the diallel analysis is fairly good. Yet it has been shown (Moreno and Cubero 1978) that length and width of leaflets are, in fact, only one character: leaflet size. Then why the failure in the length case? The explanation does not seem to be difficult: the apex of the leaflet is much more exposed to an environmental inhibition of its growth than is that of the margins (our experience with *Vicia faba* points to the same conclusion). Therefore, in this case, environmental effects can be responsible for the narrow range of W values.

The results described, mainly those of series S, support the existence of complete dominance for leaflet size and shape index, rachis length and leaflet density, the sense being negative in all five cases (small and elongate leaflet, short rachis and low number of leaflets per cm of rachis being dominant). Number of leaflets is less clearly defined, but a tendency towards dominance is perceptible (Table 8 and Fig. 4S) also in a negative sense (few dominant over many). The impression of partial dominance produced by Figures 1S and 2S is counteracted by the lack of significance of (D-H_1) (Table 6).

b2) Pod and seed characters

These two characters are basic to the systematics of this species; they are strongly correlated with each other at both phenotypic and genotypic levels (Moreno and Cubero 1978). In fact we have only studied here pod length; width and thickness are so strongly correlated with the former that it would be more exact to speak about 'pod size' than about 'pod length'.

For pod length the pattern is rather similar to that described for leaf characters, that is, additivity and environmental effects for series m and M; the first one shows a small tendency towards dominance (Table 7) and also weak significant reciprocal effects. The W/V graphs support full dominance in a negative sense for this character although again the appearance of partial dominance (Fig. 7S) is challenged by the non-significance of (D-H_1) (Table 6). The high slope of the M case (Fig. 7M) is probably due to the position of Parent 1507.

Seed size clearly shows partial dominance in a negative sense in the three cases, even with the lack of significance of the dominance items (b_1, b_2, b_3 and b) in the analysis of variance of series M (Table 7). The graphs W/V support this conclusion. The significant environmental effect (Table 6) is remarkable, also in the case of pod length. Both characters showed almost no environmental influence in a previous work (Moreno and Cubero 1978); perhaps the experimental technique (use of isolated spaced plants) can account for this.

Seeds per pod exhibits an apparently contradictory pattern; in the m case, full dominance in a positive sense is the logical deduction even with a general lack of significance in the analysis of variance (Table 7). The parameters of the W/V graphs show only a weak significance (Table 6). Series M shows a complete lack of variability; the parental lines were too uniform regarding this character (in 'macrosperma', the number of seeds per pod rarely reach 1.5 as a population average). The suggestion could be that a lack of dominance is a very probable situation within 'macrosperma'. Series S shows full dominance in a positive sense; again the W/V graphs confirm this interpretation. The slope in the S case (Fig. 9S) is too low, giving the appearance of partial dominance.

b3) Plant Characters

Pods, seeds and yield per plant results are rather similar, the three characters being strongly correlated (Moreno and Cubero 1978); dominance is significant except for series M (Tables 6 and 7), where there was a negative value of (D-H_1), meaning overdominance. The sense is positive. The environmental component is strong but in this case it was expected (Moreno and Cubero 1978). Reciprocal differences have been detected in the three characters, reinforcing the idea of its existence even when the statistical significance is not always clear. The W/V graphs of series m̲ (Figs. 10 m, 11 m and 12 m) show significant regression but with the slope less than 1, probably meaning a low heritability. This is logical because of the presence of both overdominance and a high environmental effect. The graphs for series M̲ (Figs. 10 M, 11 M and 12 M) show agreement with the conclusion just mentioned, namely overdominance; in fact, the environmental effect is less in this case (Table 6). Series S̲ graphs show a surprising lack of significance for slopes; the only possible explanation is a strong environmental effect on this character accentuated by the fact that some of the lines included in this series were not completely adapted, from the point of view of yield, to Spanish conditions. The low but significant values for m̲-slopes suggest the presence of genic interactions.

It is convenient, for clarity, to summarize the genetic systems of the twelve characters studied:

Full dominance in a negative sense (small values dominant) is shown by leaflet length, width and shape index, rachis length, leaflet density and pod length. It is doubtful for leaflets/leaf.

Full dominance in a positive sense (high values dominant) is shown only by seeds per pod.

Partial dominance in a negative sense is shown only by seed size.

Overdominance in a positive sense is shown by pods, seeds and yield per plant. It is probable that genic interactions are present.

Weak reciprocal differences are shown by pod length and pods, seeds and yield per plant.

It can be seen that dominance favours characters that can be considered as 'primitive': small leaflets and leaves, small pods and grains and high number of seeds per pod. Nothing completely certain can be said about yield characters, having been highly influenced by external conditions.

The environmental effect has been remarkably strong probably due to the fact that only isolated plants, spaced 40 cm from each other, were studied; this makes them more exposed to external conditions.

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A. Martinez
A. Coiduras
M.T. Moreno
Instituto Nacional de Investigaciones Agrarias
Centro Regional de Andalucía, Apartado 240, Córdoba (Spain)

J.I. Cubero
Escuela Técnica Superior de Ingenieros Agrónomos
Departamento de Genetica, Apartado 246, Córdoba (Spain)