Analysis of a 5-parent half diallel in dried pea (Pisum sativum L). I. Seed yield heterosis

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Agronomie (1992) 12, 545-550

Plant improvement

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(Received 17 February 1992; accepted 14 May 1992)

Summary — Values of heterosis for seed yield and related traits have been calculated on F_1 hybrids of dried pea (*Pisum sativum* L), obtained in a 5-parent half diallel cross. Lines used as parents represented a good sample of the genetic variability found in Northern Europe cultivars. The experiment was performed in microplots under competitive conditions (density: 100 pl/m^2). Seed yield showed highly significant heterosis: 40% over the mid parent and 20% over the high parent respectively. Both general and specific combining ability were important. This study also concluded that heterosis was mainly expressed on branches. Heterosis for yield components was significant only for the number of pods/plant and the number of seeds/pod on the branches, but not for the number of seeds/pod on the whole plant or for dry weight/seed.

heterosis / *Pisum sativum* L / seed yield / yield component

Résumé — Analyse d'un demi-diallèle à 5 parents chez le pois. I. Hétérosis du rendement en grains. *Les valeurs d'hétérosis du rendement en grains et de caractères liés au rendement ont été calculées chez des hybrides F_1 de pois (*Pisum sativum *L), obtenus dans un croisement demi-diallèle à 5 parents. Les lignées utilisées comme parents représentaient un bon échantillon de la variabilité génétique des cultivars du Nord de l'Europe. L'expérimentation a été effectuée en micro-parcelles, en conditions de compétition (densité : 100 pl/m^2). Le rendement en grains a montré un hétérosis significatif : respectivement 40% par rapport au parent moyen et 20% par rapport au meilleur des 2 parents. Les aptitudes générale et spécifique à la combinaison étaient importantes. Cette étude a souligné le fait que le phénomène d'hétérosis s'exprimait principalement au niveau des ramifications. L'hétérosis pour les composantes du rendement était significatif seulement pour le nombre de gousses par plante et le nombre de graines par gousse sur les ramifications mais ne l'était pas pour le nombre de graines par gousse au niveau de la plante entière ni pour le poids sec du grain.*

hétérosis* / Pisum sativum *L / rendement en grains / composant du rendement

INTRODUCTION

The pea (*Pisum sativum* L) is an annual grain legume of the family Papillonaceae. Its seeds have a rather high protein content (20–25%), which is one of the reasons why increased interest in the dried pea has been shown over the last 15 years in Northern Europe with its use as cattle feed. In France, 700 000 hectares were given over to this crop in 1990.

This species is mainly self-pollinating, and breeding has therefore usually been focussed on the creation of pure lines. Recently, much interest has developed in producing F_1 hybrids, as studies on somatic embryogenesis have been initiated in France in order to produce artificial seeds. Such varieties would be valuable in an autogamous plant provided that a high hybrid value for the main characters (yield, quality) counterbalanced the increased seed production costs.

Generally, genetic studies based on full-diallel or half-diallel analysis have shown that yield and yield components are primarily controlled by additive genetic systems (Krarup and Davies, 1970; Snoad and Arthur, 1973; Srivastava *et al*, 1986; Singh and Singh, 1987). These results supported the view that the appropriate breeding approach is the development of pure lines on the basis of the parents used in each study.

On the other hand, F_1 yield heterosis has already been demonstrated by some authors. Krarup and Davies (1970) showed a 56% value of heterosis for yield based on the mid-parent comparison. Gritton (1975) found that yield heterosis based on the mid-parent averaged 55% and on the high parent 28%. Heterosis on the better parent for yield per plant ranging from 1.3 to 91.0%, was also observed by Rao and Narsinghani (1987). The value of these studies is, however, reduced by the fact that they were conducted on single-row plots, at low densities (5 to 20 plants/m^2), and sometimes on wires (Gritton, 1975).

The present study was undertaken to:

– evaluate yield heterosis under usual competitive conditions for lines representing the most common cultivars in Northern Europe;

– estimate general and specific combining abilities for yield and related characters.

MATERIAL AND METHODS

Five pea lines, Finale, Frisson, Countess, MA 814 (line derived from a Vendevil x Adela cross) representing the main cultivars used in dried pea breeding, plus a garden pea cultivar (Sylvain), were crossed by hand in 1990 in all possible combinations excluding reciprocals. The characteristics of these lines are reported in table I.

Parents and F_1 were evaluated in the fields at Estrées-Mons (latitude: 50 °N) in 1991, in a randomized block plot design including 3 replications. Plots of 1.10 m^2 were sown at a density of 100 plants/m^2 (0.10 m between rows and 0.10 m between 2 plants in a row). In the middle of each plot, there were 42 seeds of parents or F_1, surrounded by 2 rows of cultivar Solara to avoid edge effects.

Data were collected at the dry seed stage on 20 plants in the middle of each plot. Total dry weight, main stem dry weight, seed yield and number of pods both on the main stem and the branches were recorded on a single plant basis. Branch dry matter was calculated by difference. Dry weight per seed resulted from the ratio of total seed yield over the number of seeds, which was also measured for all stems.

Estimations of general and specific combining ability effects were calculated according to Griffing's (1956) model 1 method 2 analysis, through a computer program developed by Fouilloux and Chaboche (INRA Versailles) following the methodology of Schwendiman and Cateland (1976), who have related in detail all the formulae for calculation. The values of all the parents were included in the analysis. Calculations were also made with the following computer programs: Statgraphics, Lotus 123, Freelance.

RESULTS

Average parental and F_1 performances for each of the characters studied are recorded in table II. There were significant differences between parents for seeds/pod and dry weight/seed. Differences between hybrids and parents can also be seen for all characters studied.

On the average, F_1 plants showed higher values for all the variables excepting dry weight/seed (table III). F_1 progeny significantly exceeded the mid and high parent values for total dry weight/plant, seed yield/plant and number of pods/plant. Performances of the F_1's compared to both parents for each cross are represented in figure 1 for total dry weight/plant and seed yield/plant. For these characters, as for number of pods/plant, heterosis on a whole plant basis was mainly due to heterosis expressed on branches even when the main stem showed a significant positive value, as was the case for seed dry weight (table III).

Table I. Main characteristics of the 5 parents of the semi-diallel.

Genotype	*Plant type*	*Branches*	*1 000-seed weight (g)*	*Type*	*Starch*
Finale	Conventional	+++	280	Spring	Smooth
Frisson	Conventional	++	140	Winter	Smooth
Countess	Semi-leafless	+	340	Spring	Smooth
MA 814	Conventional	++	220	Winter	Smooth
Sylvain	Conventional	+++	120	Spring	Wrinkled

+ = Few branches; ++ = intermediate; +++ = many branches.

Table II. Average performance of each parent and F_1.

Genotype	*Total dry weight/ plant (g)*	*Seed yield/ plant (g)*	*Pods/plant*	*Seeds/pod*	*Dry weight/ seed (g)*
Finale	33.1 ab	18.4 abc	14.8 a	3.8 bc	0.33 h
Frisson	27.5 a	14.1 a	20.5 abc	5.2 efg	0.13 ab
Countess	36.1 abc	15.7 ab	17.1 ab	3.1 a	0.30 g
MA 814	40.0 bcd	22.2 cd	24.7 bc	4.1 bcd	0.22 de
Sylvain	27.4 a	13.7 a	21.8 abc	5.7 g	0.11 a
Finale x Frisson	35.8 abc	20.9 bcd	21.2 abc	4.5 cde	0.22 de
Finale x Countess	46.3 d	25.4 de	20.8 abc	3.6 ab	0.34 h
Finale x MA 814	44.7 cd	25.4 de	23.5 bc	4.3 bcd	0.26 f
Finale x Sylvain	34.9 abc	20.4 bcd	20.9 abc	5.1 efg	0.19 d
Frisson x Countess	42.4 bcd	21.6 cd	23.7 bc	4.0 bc	0.23 ef
Frisson x MA 814	42.1 bcd	22.2 cd	28.3 c	4.9 def	0.16 c
Frisson x Sylvain	38.4 bcd	20.7 bcd	26.7 c	5.5 fg	0.14 bc
Countess x MA 814	55.2 e	29.0 e	27.6 c	4.2 bcd	0.26 f
Countess x Sylvain	48.0 d	25.6 de	24.1 bc	4.6 cde	0.23 ef
MA 814 x Sylvain	42.7 bcd	24.1 cde	28.0 c	5.8 g	0.15 bc

Values followed by the same letter are not significantly different; multiple range test, Newman–Keuls, $\alpha = 0.05$; each hybrid is designed by the names of the parents (female x male).

Table III. Mean value of parents and F_1, mid parent (MP) and high parent (HP) heterosis.

Character	*Mean value*			*Heterosis*	
	Parents	F_1	*Std*	$F_1 - MP/MP$	$F_1 - HP/HP$
Total dry weight/plant (g):					
Main stem	17.8	19.7	2.01	0.11	–0.08
Branches	15.0	23.3	3.73	0.55*	0.31*
Total	32.8	43.1	3.65	0.31*	0.18*
Seed yield/plant (g)					
Main stem	9.5	11.2	1.28	0.18*	0.00
Branches	9.1	12.3	1.96	0.68*	0.32*
Total	16.8	23.5	2.16	0.40*	0.22*
Pods/plant:					
Main stem	10.6	11.2	0.99	0.06	–0.07*
Branches	9.1	13.3	2.56	0.45*	0.18*
Total	19.8	24.5	2.82	0.24*	0.10*
Seeds/pod:					
Main stem	4.6	4.9	0.37	0.06	–0.09*
Branches	4.1	4.5	0.32	0.07*	–0.06
Total	4.4	4.6	0.32	0.05	–0.08*
Dry weight/seed (g):					
Main stem	0.22	0.22	<0.01	0.00	–0.21*
Branches	0.22	0.22	<0.01	0.00	–0.21*
Total	0.22	0.22	<0.01	0.00	–0.21*

* Significantly different from 0 at 5% probability level (multiple range test, Newman-Keuls); Std: standard deviation.

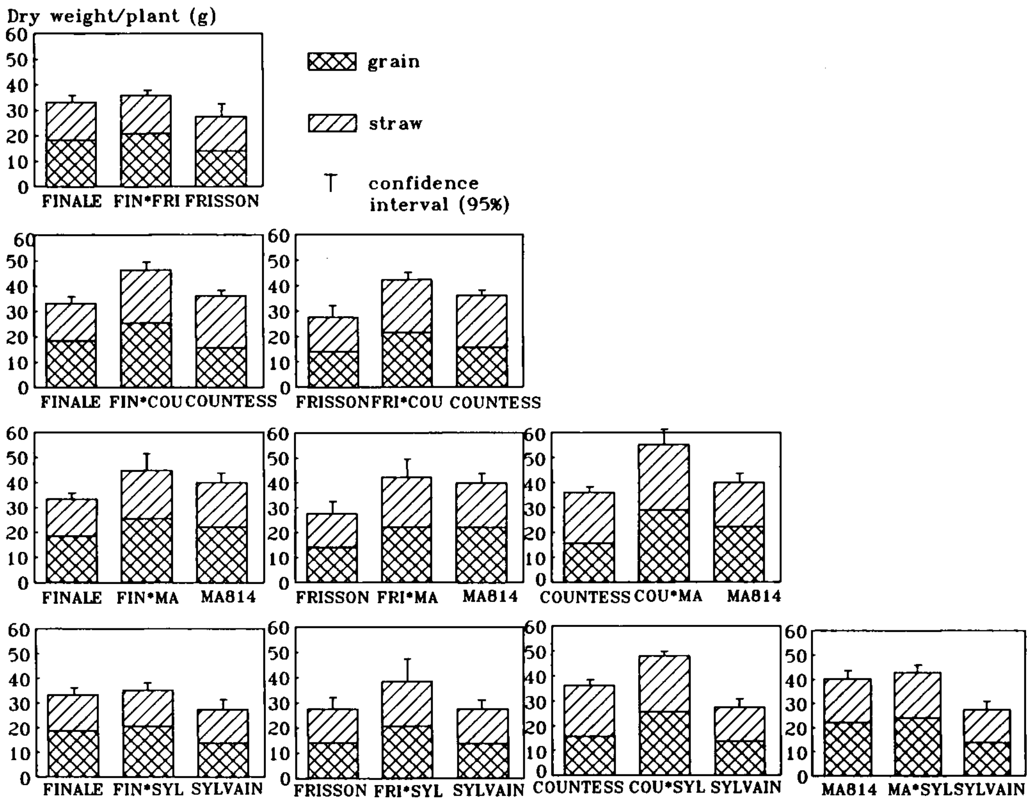

Fig 1. Dry weight/plant (grain and straw) for each cross of the semi-diallel. From the left to the right, within a frame: female parent, hybrid, male parent.

For seed yield/plant, the mean mid parent and high parent heterosis values were 40 and 22% respectively (table III). These values ranged from 25 and 2% (MP and HP heterosis, respectively), for Frisson x MA 814, to 75 and 64%, for Countess x Sylvain. The highest yielding parent (MA 814) was outyielded by its F_1 with Countess (table II).

Mean squares from the semi-diallel analysis show that general combining ability (GCA) was significant for all characters. Specific combining ability (SCA) was significant on a whole plant basis and for branches for all traits, excepting number of seeds/pod (significant only for branches) (table IV).

The GCA contributions of each parent for the characters studied is presented in table V. MA 814 and Countess were the best parents for increasing total dry weight/plant and seed dry weight/plant. Countess contributed increasing seed yield/plant on the main stem only, which is related to the very few branches formed by this genotype at usual crop densities. In contrast, MA 814 considerably increased the seed yield of branches; the contribution of this line to the yield of its progeny was explained mainly by an increase in the number of pods/plant. Frisson and

Table IV. Mean squares (MS) for general and specific combining ability effects.

Character	*MS GCA*	*MS SCA*
Total dry weight/plant (g):		
Main stem	57.32 *	2.23
Branches	19.97 *	32.46 *
Total	87.89 *	44.61 *
Seed yield/plant (g):		
Main stem	10.62 *	1.18
Branches	7.90 *	11.02 *
Total	22.31 *	18.20 *
Pods/plant:		
Main stem	8.97 *	0.56
Branches	17.18 *	6.68 *
Total	33.23 *	8.19 *
Seeds/pod		
Main stem	2.58 *	0.07
Branches	1.96 *	0.12 *
Total	2.05 *	0.07
Dry weight/seed (g):		
Main stem	0.02 *	<0.01 *
Branches	0.02 *	<0.01 *
Total	0.02 *	<0.01 *

* Significant at the 5% probability level (*F*-test).

Table V. General combining ability effects of the 5 parents of the semi-diallel.

Character	*Finale*	*Frisson*	*Countess*	*MA 814*	*Sylvain*
Total dry weight/plant (g):					
Main stem	– 1.4 *	– 1.6 *	4.5 *	1.1 *	– 2.6 *
Branches	– 0.1 *	– 1.9 *	– 0.7	2.7 *	– 0.1
Total	– 1.4 *	– 3.4 *	3.8 *	3.9 *	– 2.7 *
Seed yield/plant (g):					
Main stem	– 0.2 *	– 1.0 *	1.6 *	0.9 *	– 1.3 *
Branches	0.4	– 1.0 *	– 0.9 *	1.6 *	– 0.1
Total	0.2	– 2.0 *	0.8 *	2.5 *	– 1.4 *
Pods/plant:					
Main stem	– 1.8 *	0.4	0.8 *	1.0 *	– 0.4 *
Branches	– 1.3 *	0.1	– 1.9 *	1.8 *	1.2 *
Total	– 3.1 *	0.5	– 1.0 *	2.8 *	0.8
Seeds/pod:					
Main stem	– 0.3 *	0.2 *	– 0.7 *	0.0	0.9 *
Branches	– 0.3 *	0.3 *	– 0.7 *	0.0	0.6 *
Total	– 0.3 *	0.3 *	– 0.7 *	0.0	0.7 *
Dry weight/seed (g):					
Main stem	0.05 *	– 0.04 *	0.05 *	0.01	– 0.05 *
Branches	0.05 *	– 0.04 *	0.05 *	– 0.01 *	– 0.05 *
Total	0.05 *	– 0.04 *	0.05 *	0.01	– 0.05 *

* Significant at the 5% probability level (*F*-test).

Sylvain transmitted a higher number of seeds per pod. Finale and Countess tended to impart a higher dry weight/seed.

DISCUSSION

The inheritance of seed yield was not only additive, the variance due to SCA effects accounting for 45% of the total combining ability variance. This result is in contrast to those generally reported on this subject (Krarup and Davies, 1970; Snoad and Arthur, 1973; Srivasta *et al,* 1986; Singh and Singh, 1987). Gritton (1975), from an 8-parent full diallel analysis, found significant SCA effects for yield accounting for 17–51% of the total combining ability variance depending on year and location. Although our results apply only to the 5 lines crossed in this experiment and to a single year and location, it should be of interest to consider the SCA effect in breeding regarding heterosis for seed yield. The important SCA effects found here can be related to the fact that the 5 lines have a very different genetic background.

Heterosis was actually found to be significant for seed yield. The values reported in this study are in agreement with the values of 56 and 55% (mid parent basis) obtained respectively by Krarup and Davies (1970) and by Gritton (1975), and with the 28% value (high parent basis) reported by Gritton (1975).

Though the significant GCA effect on seed yield suggests that it would be possible to increase yield by breeding pure lines (MA 814 and Countess being the best parents), some interest should be taken in hybrids, as a significant part of the F_1's yield appears to be due to non-additive effects, at least for the parents crossed in this experiment. Hybrid varieties are, however, the fastest way to fix heterotic potential. This is also supported by the fact that the highest yielding parent (MA 814) was outyielded by one of its F_1's (Countess x MA 814).

Heterosis for yield components (on the mid parent basis) was significant only for the number of pods/plant (24%) and the number of seeds/pod on the branches (7%). These figures are consistent with the 32 and 31% presented by Krarup and Davies (1970) and by Gritton (1975) for the number of pods/plant, and with the significant 10 and 8% heterosis they also showed for seeds/pod. But in contrast to these authors significant heterosis for seeds/pod on the whole plant and for dry weight/seed were not found.

Our results also determined that heterosis was mainly expressed on branches: 68 and 32% heterosis (MP and HP basis) was found on these organs for seed yield, F_1's bearing more pods on their branches than the parents. The development of the branches appears to be a morphological factor linked to the high yielding ability of hybrids.

CONCLUSION

This study showed that GCA and SCA effects were both important for seed yield/plant and number of pods/plant.

The parents chosen for this experiment represented a good sample of lines used in dried pea cropping and breeding in Northern Europe. Though the results have to be confirmed in other years and locations, it seems reasonable to say that yield improvement of the dried pea crop can still be achieved by breeding pure lines, but that one may also progress with hybrids.

The values of heterosis found here are in agreement with those given in other papers. This result is especially significant in that it was obtained at usual crop densities (100 plants/m^2).

Further investigations have to be made on the traits related to the high yielding ability of hybrids. In this context, the presence of branches appears to be a significant factor. The study of competitiveness between plants of the same genotype for hybrids and their parents will be also possible as the plants are grown in microplots and not merely spaced on a wire.

ACKNOWLEDGMENTS

This study has been supported by the Picardie region as part of a program developed by the Biopôle Végétal. This work was carried out with the technical collaboration of M Niarquin, M Boilleau, R Devaux and JJ Stempniak.

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