Chiasma frequency and heterosis in common beans (*Phaseolus vulgaris* L.)[1] /*

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Resumen

*Se estudió extensamente la distribución de la frecuencia del chiasma en relación con la heterosis para características fundamentales, tanto morfológicas como fisiológicas, utilizando diez líneas autofecundadas de frijol común (*Phaseolus vulgaris *L.), geográficamente diversas y sus respectivas cinco líneas híbridas de la* F_1*. Las poblaciones híbridas exhibieron "chiasma heterosis" y ello fue posteriormente reflejado en una superioridad fenotípica de los híbridos respecto a cinco mediciones cuantitativas: rendimiento en granos de frijol (g/planta), materia seca total (g/planta), índice de cosecha (%), eficiencia de rendimiento en granos de frijol (g/día), y eficiencia en materia seca total producida (g/día). La heterosis genética relativa en un par de líneas híbridas (*F_1b *y* F_1c*) alcanzó una magnitud de 40 a 50% para la eficiencia de rendimiento en granos de frijol y para la eficiencia en materia seca total producida. Los resultados fueron interpretados desde el punto de vista de que la chiasma heterosis está genéticamente asociada al fenómeno global de la heterosis mediante la promoción de mayores niveles de variación genética y de ventajas heterocigóticas en los individuos híbridos. En el trabajo se discute la hipótesis de que la chiasma heterosis está gobernada por factores genéticos y es más bien debida a genes dispersos sobre los cromosomas que poseen una combinación de sobredominación e interacciones epistásicas.*

Introduction

The occurrence of chiasmata through diplotene and metaphase ensures the proper disjunction of bivalents at the first meiotic division. The chiasma is a cytological manifestation of genetical crossing over and, as such, serves as a potential marker of the degree of recombination between linked genes. Chiasma frequency differences between genotypes of various crop species have been observed (2, 8). Chiasma frequency also produces a typical attribute of quantitative traits (7) and is supposed to be governed by a polygenic mode of inheritance.

An increased chiasma frequency in hybrid populations of *Pennisetum typhoides* Rich (10) and *Gossypium hirsutum* L. (11) and its subsequent positive correlations to grain yield heterosis has been recorded.

Heterosis for chiasma frequency and quantitative traits in *Phaseolus vulgaris* has recently been demonstrated (12). The present study was an extension of our previous project at a much larger scale in *Phaseolus vulgaris* employing ten geographically diversed inbreds and their five respective hybrids to finally determine whether (a) these inbreds differ in yield and yield contributing quantitative traits including chiasma frequency; (b) whether the hybrid populations exhibit heterosis for chiasma frequency and (c) whether is there a genetic association between chiasmata frequency and key quantitative and physiological traits including those of bean yield and harvest index. The results presented here reveal the role of enhanced chiasmata in heterosis phenomenon by way of promoting higher levels of genetic variation and heterozygous advantages in hybrid individuals.

Material and methods

Seeds from fifteen genotypes of common beans (*Phaseolus vulgaris* L., 2n = 2x = 22) including inbreds and hybrids, as listed below along with their respective place of origin and common names, were grown in the yield under normal cultural conditions in a randomized block design with three replications.

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Genotype	Origin	Common	Name
P. I. 310878	USA	P 4	
P. I. 313652	USA	P 362	
12 D I 964	Venezuela	P 417	
ES 2873 I 893	Venezuela	P 428	
Jamapa I 810	Venezuela	P 459	
C 63 S 630 B	Costa Rica	P 524	
Tara	USA	P 567	
Cacahuate 72	Mexico	P 569	
Jules	USA	P 698	
PRS 7015 RSTBK	Peru	P 568	
F_1 hybrids			
P 4 x P 698	–	F_{1a}	F_{1a}
P 417 x P 569	–	F_{1b}	F_{1b}
P 362 x P 459	–	F_{1c}	F_{1c}
P 428 x P 567	–	F_{1d}	F_{1d}
P 524 x P 568	–	F_{1e}	F_{1e}

Bean seeds were planted at a density of 100 plants/m^2. Young flower buds from at least ten plants per genotype at the appropriate stage were collected at 8.30 a.m. and fixed in Carnoy's solution (6 parts absolute alcohol: 3 parts chloroform: 1 part glacial acetic acid). The squash technique for the count of chiasmata frequency in pollen mother cells (PMC's) in diplotene stage of meiosis was the same as described elsewhere (12).

A minimum of 50 plants per genotype per replication were selected for quantitative measurements. The data on the following quantitative traits: bean yield, total dry matter, and days to maturity, were recorded under normal field and laboratory conditions. Estimates for other characters were made as follows:

$$\text{harvest index} = \frac{\text{bean yield}}{\text{total dry matter}} \times 100;$$

$$\text{bean yield efficiency} = \frac{\text{bean yield}}{\text{days to maturity}};$$

and

$$\text{total dry matter efficiency} = \frac{\text{total dry matter}}{\text{days to maturity}}$$

Total dry matter was equal to weight of stem, petioles, pods and beans at maturity plus maximum leaf dry matter at post-flowering.

Results and discussion

Table 1 summarizes the estimates of mean ± standard deviation and heterosis percentage with respect to chiasma frequency in 15 genotypes including five hybrids. The inbred lines differed substantially in terms of mean chiasma frequency per PMC. The three inbred lines, viz, P 459, P 567 and P 568, however, appeared to be similar for chiasma

Table 1: Cytogenetical data obtained on frequency distribution in ten inbred lines and five hybrid lines of common beans.

Genotypes	Mean Chiasma frequency ± S. D.	Heterosis %
P 4	8.24 ± 2.11	–
P 362	9.43 ± 1.81	–
P 417	8.34 ± 1.34	–
P 428	10.24 ± 1.82	–
P 459	7.63 ± 1.25	–
P 524	6.52 ± 1.62	–
P 567	7.48 ± 1.25	–
P 569	8.24 ± 1.70	–
P 698	6.87 ± 1.90	–
P 568	7.48 ± 2.10	–
$F_{1}a$	7.82 ± 2.43	3.6
$F_{1}b$	12.56 ± 1.87	51.5
$F_{1}c$	9.87 ± 1.43	15.7
$F_{1}d$	10.43 ± 1.70	17.8
$F_{1}c$	10.32 ± 2.10	47.4

The data represent mean values ± S. D. from a range of 50-70 pollen mother cells per genotype analysed only in the diplotene stage of meiosis.

frequency as the mean values did not differ significantly. The other seven inbred lines were characterized to possess a high mean chiasmata per PMC. All the five hybrid lines (F_1a, F_1b, F_1c, F_1d, and F_1e) exhibited heterosis with regard to chiasma frequency and, among these, the two hybrid lines F_1b and F_1e showed high degree of heterosis, i.e., 51.5% and 47.4% respectively. The position distribution of chiasmata in terms of a separate count of terminal and interstitial chiasmata per PMC was not studied in these inbred and hybrid lines, as an earlier study (12) had clearly demonstrated that enhanced chiasma frequency is a result of physically spreading of the chiasmata to interstitial regions, i.e., the populations with a high mean chiasma frequency is more likely to possess simultaneously and increased number of interstitial chiasmata.

There is some consideration that chiasma frequency in a given inbred or hybrid populations may be directly related to the conservation of genetic population variability (11, 12). Many morphological and physiological traits related to bean yield in *Phaseolus vulgaris* have been reported to be controlled by oligogenes or polygenes (1, 3). To this end, six important morphological and physiological traits related to bean yield were analyzed to further elucidate whether there is a genetic association between frequency distribution of chiasmata to heterosis in hybrid populations. The data presented in Table 2 characterizes the ten inbred and five hybrid populations with regard to bean yield, total dry matter, harvest index, bean yield efficiency, and total dry matter efficiency. All five hybrid populations exhibited some degree of heterosis in these phenotypic expressions, but the two hybrids deserved special mention as they exceled approximately 25%from the mid-parental values with respect to two very important quantitative traits – bean yield and harvest index (Table 3). The hybrid line F_1a which showed relatively low chiasma frequency (Table 1) further demonstrated little heterosis for the morphological and physiological traits studied. The other hybrid F_1c was found to be highly heterotic for both bean yield efficiency and total dry matter efficiency. The results described so far establish that: 1) there is a positive genetic association between increased chiasma frequency and bean yield heterosis in hybrid populations; and 2) chiasma frequency may serve as one of the selection indices to further improve the efficiency of simultaneous selection for high yielding beans genotypes in the field.

There is strong evidence, based on ultrastructural studies of the frequency and distribution of chiasmata, that meiotic crossing over invariably occurs in the presence of the synaptonemal complex (4). Direct electron microscopic observations of chiasmata in bivalents at diplotene reveal nodule-like structures called 'SC remnants' as sites of crossing over (6). There seems to be a direct correspondence between chiasmata and SC remnants; both perhaps reflect site-specific crossing over and genetic recombinations. The interpretation of the results on heterosis for chiasma frequency and quantitative traits requires further considerations in terms of gene components

Table 2. Bean yield and key quantitative and physiological traits in ten inbreds and five hybrids lines of common beans.

Genotype	Bean yield (g/plant)	Total dry matter (g/plant)	Harvest index (%)	Days to maturity	Bean yield efficiency (g/day)	Total dry matter efficiency (g/day)
P 4	13.0	25	52	70	0.186	0.357
P 362	15.0	25	60	67	0.224	0.373
P 417	13.0	23	56	72	0.181	0.319
P 428	13.0	22	59	65	0.200	0.338
P 459	41.0	64	64	87	0.471	0.735
P 524	7.0	17	41	66	0.106	0.257
P 567	8.0	17	47	69	0.116	0.246
P 569	3.0	8	37.5	65	0.046	0.123
P 698	6.0	17	35	70	0.086	0.242
P 568	16.0	46	34.7	67	0.239	0.686
F_1a	10.2	23	44	68	0.150	0.338
F_1b	9.6	16	60	65	0.148	0.246
F_1c	31.0	50	62	60	0.516	0.833
F_1d	11.6	21	55	64	0.181	0.328
F_1e	13.9	31	45	68	0.204	0.455

The data represent mean values from observations on 150 plants per genotypes.

Table 3. Relative genetic heterosis (%) in five hybrid lines of common beans.

Hybrids	Bean yield	Total dry matter	Harvest index	Bean yield efficiency	Total dry matter efficiency
F_1a	7.3	9.52	1.2	10.3	13.0
F_1b	20.0	3.3	28.5	40.0	11.4
F_1c	10.7	12.4	–	48.7	50.4
F_1d	10.5	7.8	3.8	14.6	11.0
F_1e	20.9	–	19.0	18.6	3.5

Heterosis was calculated from the mid-parental value. The dot line indicates that there was no observable difference between F_1 hybrid value and the mid-parental value.

[dominance, overdominance or intra-allelic interaction, and epistatic interallelic (nonallelic) interactions] linked to heterosis. Diallel - cross biometrical analyses for chiasma frequency in *Pennisetum typhoides* revealed both overdominance and epistatic interactions to be associated with "chiasma heterosis" (5). The whole chromosome analysis in substituted wheat lines also indicates "chiasma heterosis" to be the result of a greater number of dispersed genes with directional dominance derived from the substituted chromosome of the parents, combined with between chromosome interaction (9). It is reasonable to postulate therefore that chiasma heterosis is controlled by genetic factors and is most likely due to dispersed genes on the chromosomes possessing combined overdominance and epistatic interactions.

Summary

Chiasmata frequency distribution in relation to heterosis for key morphological and physiological traits employing ten geographically diversed inbred lines and their five respective F_1 hybrid lines in common bean (*Phaseolus vulgaris* L.) has been extensively studied The hybrid populations exhibited "chiasma heterosis" and it was further reflected in phenotypic superiority of the hybrids with regard to five quantitative measurements: bean yield (g/plant), total dry matter (g/plant), harvest index (%), bean yield efficiency (g/day), and total dry matter efficiency (g/day). Relative genetic heterosis in a couple of hybrid lines (F_1b and F_1c) reached to a range of 40-50% for bean yield efficiency and total dry matter efficiency The results were interpreted from the point of view that chiasmata heterosis is genetically associated to overall heterosis phenomenon by way of promoting higher levels of genetic variation and heterozygous advantages in hybrid individuals. The hypothesis that chiasmata heterosis is governed by genetic factors and is most likely due to dispersed genes on the chromosomes possessing combined overdominance and epistatic interactions is discussed.

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