Inheritance of a five leaflet character arising from wild soybean (*Glycine soja* Sieb. et Zucc.) in soybeans (*G. max* (L.) Merr.)*

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Abstract The inheritance of a five leaflet mutation of soybeans originally inherited from the wild was studied using cross analysis. Six crosses were made between "Five Leaf Bean" with the five leaflet trait and other 6 lines of normal leaves. F_2 plants of 5 crosses produced major three and five leaflet leaves and also some minor four six and seven multifoliolate leaves. There were two kinds of segregation ratios for major five leaflet (including other multifoliolate leaves) and trifoliolate characters in the F_2 progeny plants. Five crosses showed a goodness of fit to a 3∶1 ratio and one cross showed a satisfactory 63∶1 ratio. The cross analysis indicated that besides the Lf_1 gene controlling five leaflets, there could be other two newly found genes governing this trait. These three genes were independently genetic, incompletely dominant and effect-duplicated.

Key words Genetic analysis; Quality character; Soybean leaf; Soybean

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1 Introduction

Commonly soybeans (*G. max*) have trifoliolate leaves most rarely with five leaflets or other multifoliolate leaves (Takahashi and Fukuyama 1919; Woodworth 1932; Fehr 1972; Fu 1986). Takahashi and Fukuyama indicated that a single major gene controls a multifoliolate character. Fehr (1972) observed a spontaneous mutational plant with multifoliolate leaves (major seven leaflets) and reported that this multifoliolate leaflet character was controlled by a dominant Lf_2 gene and a five-leaflet mutation was caused by a incompletely dominant Lf_1 gene. Fu (1986) presented a mutation with respect to multifoliolate leaves (4 to 7 leaflet) that derived from the seeds treated by γ-^{60}Co rays, whose genetic studies indicated that a pair of recessive alleles (lf_3lf_3) at a single locus lead to this mutation and the dominant allele (Lf_3) was charged with the normal trifoliolate leaves. Obviously their results were different.

Thus for in soybeans few reports with respect to the genetic control of leaflet number mutation inherited from wild soybean have been issued. In an early research work of ours we occasionally obtained plants with five leaflet leaves from a cross of F_1(cultivar 1× wild soybean)× cultivar 2. Carefully checking the parents found that the original wild parent had mere a few of five leaflet leaves. We thought this could be the source of the five leaflet character inherited to the five leaflet progeny plants that we obtained.

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The objective of this paper was to analyze the inheritance of the five- leaflet variation derived from the wild and discuss the genetic effect of the genes on control of leaflet number in soybeans.

2 Materials and Methods

The strains used were normal trifoliolate "94 - 6", "94- 12", "94- 20", line 1, line 2 and line 3 with red flowers and a five- leaflet Five Leaf Bean with white flowers in the genetic collection of the ICGR Wild Soybean. All materials contained the wild genetic background in varying degrees because in their parental progenitors the wild had ever been included. Six crosses were made between Five Leaf Bean and the other six lines in 1997. The Five Leaf Bean was used as maternal parent which has a pair of recessive alleles for white flower color and could be served as the indicator of the true and false F_1 seeds. The F_1 seeds of all crosses were planted in the experimental fields, and F_1 plants were harvested and maintained for next F_2 progeny populations in 1998. Every F_1 plant produced more F_2 seeds. The F_2 seeds from F_1 plants of 6 cross combinations were grown and formed 6 F_2 segregation populations. For F_2 plants fully expanded leaves on the main stem were studied when terminal growth of the main stem had ceased. A leaflet was counted as long as it had a distinct joint of attachment to the petiole or rachis. In the F_2 segregation populations the counts of the number of plants with different multifoliolate leaves were recorded as long as plants had one multifoliolate leaf. The plants with mixed kinds of leaflet leaves were counted independently.

3 Results

3.1 Variation in leaflet number within F_2 populations

Five Leaf Bean has five leaflet leaves sometimes with occasional normal trifoliolate leaves. The other paternal parents have normal trifoliolate leaves. The F_2 progenies produced major three and five leaflets and also an extremely small number of newly occurred four, six and seven leaflet leaves. Two cross combinations brought forth six and seven leaflets; four crosses brought forth four leaflet leaves; and one cross had only parental three and five leaflet leaves (Table 1).

The number of leaves with five leaflets per plant on which five leaflets emerged differed between the individuals by varying from 1 up to nearly all the leaves. An extremely small number of F_2 plants had five leaflet leaves on the whole plants except the basal trifoliolate leaves but most F_2 plants had a varied number. The new four leaflet leaves appeared with a lower frequency and the number of four leaflet leaves per plant on which four leaflets emerged ranged approximately from 1 to 5, sometimes together with five leaflet leaves on the same individuals.

Comparatively the frequency of plants with four leaflet leaves was higher than that of plants with other kinds of leaves (six, mixed leaves of four and five, and five and seven leaflets) in the F_2 populations. Only 4 plants were found with mere 1 - 2 leaves of six leaflets. Only two leaves with seven leaflets appeared on two plants with five leaflet leaves separately.

3.2 A major single gene behavior for the five leaflet leaves in some crosses

Six crosses were made for analysis of the inheritance of the five leaflet character. The cross combinations were Five Leaf Bean× "94- 12",× "94- 6",× "94- 20",× line 1,× line 2 and× line 3. All F_1 plants presented a five leaflet trait. In F_2 progeny populations of all the crosses two patterns of phenotype segregation for leaflet character were observed (Table1).

In the Five Leaf Bean× "94- 12" cross, we obtained one F_1 plant and it had sufficient F_2 seeds. The F_1 had only trifoliolate leaves and its selfed F_2 population had plants with three, five and six leaflet leaves, of which two plants had mixed leaves of five and four or seven leaflets. The 86

multifoliolate F_2 plants with major five leaflet leaves and 34 F_2 plants with trifoliolate leaves satisfactorily fitted a 3∶1 ratio ($p > 0.50$). This data indicated that the five leaflet character was controlled by a major single gene dominant to the recessive alleles controlling trifoliolate leaves. This allelic gene was not complete dominance over trifoliolate leaves, which expressed major five leaflets and also sometimes a minor other multifoliolates in different genetic backgrounds of some crosses (Table1).

Table 1 Segregations for F_2 plants with three and five leaflet leaves (mutifoliolate) and expected ratios in F_2 populations

Cross	Leaflets of F_1 Plants	F_2 plants	Leaflet segregation in F_2 plants							Trifoliolate∶Multifoliolate	Exp. F_2 ratio	Chi-square value	Probability
			3	4	5	6	5+4	5+7					
1× "94-12"	5	120	34		82	2	1	1		34∶86	1∶3	0.544	$0.30 < p < 0.50$
2× "94-6"	5	179	36	3	137		2	1		36∶143	1∶3	2.029	$0.10 < p < 0.20$
3× "94-20"	5	153	39	8	106					39∶114	1∶3	0.002	$0.90 < p < 0.95$
4× line 1	5	291	87	13	190		1			87∶204	1∶3	3.465	$0.05 < p < 0.10$
5× line 3	5	311	78	17	214		2			78∶233	1∶3	0.001	$0.90 < p < 0.95$
6× line 2	5	142	4	138						4∶138	1∶63	0.742	$0.50 < p < 0.70$

A similar result repeated in F_2 plants of the other four crosses. In the Five Leaf Bean× "94-6" cross, 143 multifoliolate plants including 137 five, 3 four, 2 six leaflet plants and 1 plant with five and seven leaflets to 36 trifoliolate plants fitted a good 3∶1 ratio ($P > 0.10$). In the Five Leaf Bean× "94-20" cross, 106 five leaflet and 8 four leaflet plants to 39 trifoliolate plants gave a very satisfactory fit of a 3∶1 ratio ($p > 0.90$). The F_2 plants derived from the Five Leaf Bean× line 1 cross had a segregation of 190 plants with five leaflets, 13 plants with four leaflets, 1 mixed plant with five and four leaflets and 87 trifoliolate, where multifoliolate and trifoliolate plants was a 3∶1 ratio ($p > 0.05$). In the 311 F_2 plants of Five Leaf Bean× line 1 there was a segregation of a 3∶1 ratio for major five leaflet and trifoliolate plants ($p > 0.90$).

3 Three independent genes for the five leaflets in a cross

A genetically new behavior for the five leaflet character different from the results of 3∶1 ratio above was found in the cross between Five Leaf Bean× "94-20". The F_1 plant had five leaflet leaves and the F_2 plants brought forth only normal trifoliolate and variant five leaflet leaves. There were a obvious deviation from the above 3∶1 ratio for the five leaflets and trifoliolates in the F_2 population, where 138 plants were for five leaflets and only 4 plants for trifoliolate leaves, having a goodness of fit to a 63∶1 ratio ($P > 0.90$). This result suggested that there were three genes were involved in five leaflet inheritance in this cross combination and the three genes had a dominantly duplicated effect, which, when only one of them existed, would be able to express five leaflet leaves (Table 1).

4 Discussion

The genetic analysis of five leaflets by crossing here showed that this five leaflet character inherited from wild soybean (*G. soja*) could be controlled by three major genes independently genetic incompletely dominant and effect-duplicated in the genetic backgrounds evaluated. Five leaflet character was dominant to trifoliolate character. Fehr (1972) reported a spontaneous mutation of five leaflet leaves and revealed that the five leaflet trait is controlled by a single major gene (Lf_1) partially dominant to recessive alleles controlling trifoliolate leaves. In this point our data acquired in this study were identical to Fehr's results and we sought there was the Lf_1 gene in the "Five Leaf Bean".

Our results also indicated that besides the Lf_1 gene controlling five leaflets, other two independently genetic genes newly found else could condit-

ion the five leaflet trait. The two new genes were tentatively designated as Lf_4 and Lf_5, respectively. The three genes were incompletely dominant to recessive alleles controlling trifoliolate leaves and they had a duplicated effect. When any two pairs of alleles were recessive, F_2 plants would show a segregation of a 3∶1 ratio; when three pairs of alleles in F_1 were heterozygous, F_2 plants would become a 63∶1 segregation ratio ($27Lf_1-Lf_4-Lf_5-$, $9Lf_1-Lf_4-lf_5lf_5$, $9Lf_1-lf_4lf_4Lf_5-$, $9lf_1lf_1Lf_4-Lf_5-$, $3Lf_1-lf_4lf_4lf_5lf_5$, $3lf_1lf_1Lf_4-lf_5lf_5$, $3lf_1lf_1lf_4lf_4Lf_5-$, $1lf_1lf_1lf_4lf_4lf_5lf_5$). When the three pairs of alleles were recessive, $lf_1lf_1lf_4lf_4lf_5lf_5$ plants were able to produce trifoliolate leaves.

The genes controlling five leaflets were incompletely dominant and sometimes they would produce 4~7 multifoliolate leaves in some crossing genetic backgrounds. In the Five Leaf Bean× line 3 cross, the F_2 population had only trifoliolate and five leaflet leaves which could be influenced by the existence of three dominant effect - duplicated genes to decrease the frequency of the appearance of leaves with other multifoliolates.

Cross analysis indicated that there could be heterogeneous genotypes at the three loci related to five leaflets among the Five Leaf Bean parental individuals. This reason could arise from the random selection according as phenotype in the progeny treatment, by which way the genotypes were indefinite. A white flower sister line with five leaflet leaves was obtained along with the acquisition of the Five Leaf Bean.

In domestication of soybeans from the wild into the cultivars, the allelic frequencies of many dominant traits or wild types have become low such as peroxidase activity, root fluorescence (Wang et al. 1990), Kunitz trypsin inhibitor (Kaizuma et al. 1980). The existing soybeans could be almost recessive at the loci controlling common trifoliolates and a spontaneous leaflet mutation in fields is easy to be expressed as a single gene locus. Wild soybean is the progenitor of the cultivated soybeans and would contain more original and useful characters or genes on which genetic study and breeding depends.

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来源于野生大豆的多小叶性状遗传分析

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摘要 本文通过杂交初步分析一个起源于野生大豆的多小叶性状。五叶大豆与 6 个正常大豆配制 6 个杂交组合,其中 5 个F_2分离群体产生带有主要的 3叶和 5叶,少数 4叶,个别 6叶或 7叶植株,3叶和 5叶(包括其它多小叶)表现为 3∶1分离;1 个组合仅产生带有 5叶株和 3叶,表现为 64∶1分离。遗传分析显示,除了一个已知的 Lf_1 基因控制 5叶遗传外,可能还存在另外 2 个控制 5叶的基因。5叶多小叶性状基因对正常 3叶是不完全显性的,这 3 个基因是独立遗传的,并且具有重叠效应。

关键词 遗传分析;质量性状;大豆叶片,;大豆