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Genetic components of pod shattering in soybean

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Summary

Half diallel crosses among ten pure breeding lines of soybean were made in 1997 and 1998 to study the inheritance of pod shattering in soybean. Evaluation for pod shattering among F_2 segregating populations was carried out in an oven set at 80 °C for 12 hours. Diallel analysis was carried out to estimate genetic parameters and detect presence of non allelic interaction of genes affecting pod shattering. Hayman's diallel analysis indicated significant variation of Wr + Vr and Wr − Vr over arrays, suggesting epistatic gene action. Similarly results from a joint regression coefficient over replications were significantly ($p < 0.05$) different from unity and zero, suggesting presence of non allelic interaction of genes. The intercept was positive, suggesting partial dominance for the shattering trait. Both general combining ability (GCA) and specific combining ability (SCA) effects were significant ($p < 0.05$).

Introduction

Soybean grown in tropics suffers from many production constraints which include: low seed longevity, pests and diseases, lodging and pod shattering. Seed losses of 50–100% are often associated with pod shattering in susceptible varieties and delayed harvesting after maturity (IITA, 1986), denying farmers time to plan for harvesting before pods start shattering. Shortage of labour and harvesting equipment can postpone harvesting when the farmer is otherwise prepared to harvest, leading to seed yield loss when harvesting is carried out late, particularly during dry weather conditions.

A survey conducted in Benue state, Nigeria in 1989 and 1990, found that the most important constraint to soybean production was pod shattering, and based on the results of the survey, resistance to pod shattering has been a major priority of IITA's soybean breeding program (IITA, 1992). In another survey by Sanginga et al. (1999) in the same region, resistance to pod shattering was found to be a pre-requisite for adoption of any variety by the farming communities, indicating that resistant varieties that can stand in the field for relatively longer periods after maturity without shattering must be developed.

Being a relatively new crop, most of the soybean varieties grown in the tropics are a direct introduction from other regions where soybean has been grown for decades. Breeding programs for improvement of soybean are also still in their infancy stage. Significant effects of G × E interactions on pod shattering in soybean was reported by Akpan (1988), Bailey et al. (1997) and Tukamuhabwa (2000), thus, varieties which are resistant in other parts of the world may succumb to pod shattering once they are introduced in the tropics. Such environmental effects could be the explanation for the prevalence of pod shattering varieties in the tropics.

Several genetic studies have been conducted to understand the genetic control of pod shattering in soybeans. Caviness (1969) found no significant variation between crosses involving domesticated cultivars and wild types in terms of shattering, however, Misra et al. (1980) observed a wide range of variation for shattering habit after treatment with gamma rays with the treated plants having a higher frequency of plants with delayed shattering. Tsuchiya (1986) observed no significant differences among sources of resistance from

Japan, USA, China and Thailand in conferring resistance to soybean shattering, indicating that the genetic control of pod shattering in soybean is simple and similar in all germplasm. Average broad sense heritability (h^2_b) estimate of shattering in soybean was put at 90% by Caviness (1969), 93% by Tsuchiya (1987), 98.84% by Tiwari & Bhatnagar (1991) and 92% by Bailey et al. (1997) indicating that the character is highly heritable. However, heritability in the narrow sense (h^2_n) has not been reported in literature, though it is the most useful parameter in designing breeding techniques.

Caviness (1969) and Tsuchiya & Sunada (1980) found susceptibility to soybean pod shattering to be partially dominant. Analysis of pod shattering in F_1 populations by Tiwari & Bhatnagar (1992) revealed contradictory observations where some crosses showed susceptibility being dominant while other crosses showed partial dominance for resistance. In the same study, significant ($p < 0.05$) general combining ability and specific combining ability were observed. However, the additive gene action was predominant in the expression of the trait over dominance effect. They recommended further studies including F_2 progenies since the observations made were based on F_1 hybrids. Bailey et al. (1997) showed that pod shattering was somewhat influenced by epistasis.

Observations to explain genetic components of pod shattering in soybean were made by Tiwari & Bhatnagar (1992), Saxe et al. (1996) and Bailey et al. (1997). However, there has not been an adequate attempt to partition the total variability of pod shattering in soybean, into different genetic components although this is an important prerequisite for determination of h^2_n and designing of an effective breeding program. In order to understand the type of gene action and the magnitude of additive and non additive genetic effects in control of the shattering trait, use of an appropriate mating design is required (Kang, 1994).

One of the designs most commonly used for self fertilizing crop species is the diallel design (Gumisiriza, 1987; Christie & Shattuck, 1992) which enables predictions to be made at early generations which increases the efficiency of a breeding program (Dickson, 1967). Diallel design has additional benefits in that the analysis applies to all the crosses involved and permits the estimation of parameters for additive, dominance and environmental effects and allows recognition of non allelic interactions (Jinks, 1956; Matther & Jinks, 1982; Christie & Shattuck, 1992). The most satisfactory analysis for a complete set of diallel in view of these aspects is that by Hayman (1954) described by Christie et al. (1988). Gumisiriza (1987) reported that theoretical considerations suggest that the diallel cross technique is a suitable method for the investigation of genetically controlled traits and Kearsey & Pooni (1996) reported that covariance (Wr) and variance (Vr) graphical analysis is relevant where the trait in consideration displays non-additive variation.

The study reported in this paper was carried out to elucidate the type and magnitude of the gene actions affecting pod shattering and to determine h^2_n for the trait using half diallel analysis.

Materials and methods

Ten parents characterized for their resistance to shattering were used for this study. Resistant genotypes were Nam 2, Roan, Duiker, TGx 1448-2E and GC 81090-48; susceptible genotypes were AGS 292 and TGm 737P, and intermediates were Kabanyolo 1 (Kab1), Samsoy 1 and Nam 1 (Table 1).

A half diallel cross was made in seasons 1997B and 1998A (A and B refer to first and second growing rainy seasons respectively). The F_1 plants from the crosses varied from two to twelve. The problem of achieving enough F_1 seed to raise adequate plants for analysis came about due to the unpredictable cleistogamy behaviour of lines TGm 737P, AGS 292 and Duiker. F_1 crosses produced enough F_2 seed for a replicated experiment of forty five progenies and their parental lines, which were planted in a randomised complete block design experiment with three replications during season 1998B at Namulonge. The plot size was 5 × 1.2 m at a spacing of 60 x 5 cm.

Up to twenty pods from each plant were carefully detached at R8 stage (Gazzoni, 1994) when 95% of pods had attained physiological maturity and were put in paper bags (5 × 10 × 20 cm) where they equilibrated to constant moisture content for 10 days at room temperature. The pods were then oven dried at 80 °C for 12 hours. Since some plants did not produce 20 pods, percentage of pod shattering induced was recorded and determined according to a 1–5 scale used by AVRDC (1979) in which, 1 = 0% shattering, 2 = 1–10%, 3 = 11–25%, 4 = 26–50% and 5 $\geq$ 50%. The shattering phenotypes on the 1–5 scale were described as: 1 very resistant, 2 resistant, 3 moderately resistant, 4 moderately susceptible and 5 very susceptible.

The diallel analysis was carried out using Hayman's (1954) method and Griffing's (1956) method modified by Patil & Chopde (1981) using F_2 data.

Table 1. Origin, pedigree and description of shattering resistance of parental lines

Genotype	Origin	Pedigree	Days to flowering	Day to maturity	Shattering description
TG × 1448-2E	Nigeria	(TGm 1193 × TGm 618) × (TGm 618 × TGm 7)	45	112	Resistant
Nam 2	Nigeria	87d – 668	49	112	Resistant
Roan	Zimbabwe	Kudu × 196/6/22	40	94	Resistant
Duiker	Zimbabwe	Oribi (15/6/12) × (15/6/22)	41	93	Resistant
GC81090-48 Tzuzunoko	China	Forrest × Shin Shin	41	100	Resistant
Kab 1	Uganda	Mutant of Clark 63	42	95	Intermediate
Samsoy 1	Nigeria	Clemson × Malayan	52	100	Intermediate
Nam 1	Colombia	Hales × P1307 – 861	44	110	Intermediate
AGS 292	China	–	40	80	Susceptible
TGm 737P	Indonesia	Land race	47	75	Susceptible

Table 2. Analysis of variance for crosses, variances and covariances of arrays of parental lines

	Source	DF	SS	MS	F
(a) Crosses	Blocks	2	3.586	1.793	8.019*
	Crosses	54	780.129	14.447	64.616*
	Error	108	24.146	0.224	
	Total	164	807.861		
(b) Wr – Vr	Blocks	2	1.024	0.512	0.545ns
	Wr – Vr	9	359.899	39.989	42.597*
	Error	18	16.898	0.939	
	Total	29	377.822		
(c) Wr + Vr	Blocks	2	0.584	0.292	3.369ns
	Wr + Vr	9	7.413	0.824	9.502*
	Error	18	1.560	0.939	
	Total	29	9.558		

* Significant at (p <0.05); ns = Not significant.

The data were tested for homogeneity of variances using Bartlett's test (Little & Hills, 1978) and subjected to arcsine transformation (Sokal & Roholf, 1995) to homogenize variance across replications and analyzed using micro computer software developed by Christie & Shattuck (1988). Hayman's (1954) analysis was used to generate variances (Vr) and parent-offspring covariances (Wr) of arrays for estimation of genetic parameters and to detect presence of epistasis among the crosses (Hayman, 1954).

Results and discussion

The results of variation among the crosses is presented in Table 2.The variation was significant, thus giving justification for further analysis. The differences over the arrays for the (Wr – Vr) was significant as opposed to the expected constant values suggesting presence of non allelic interaction of genes. Similarly, the values of parental order of dominance (Wr + V r) were significantly different along the arrays, again suggesting presence of non allelic interaction. Mather & Jinks (1982) and Christie & Shattuck (1992) suggested that if gene action fits the additive – dominance genetic model then the values of (Wr – Vr) and (Wr +

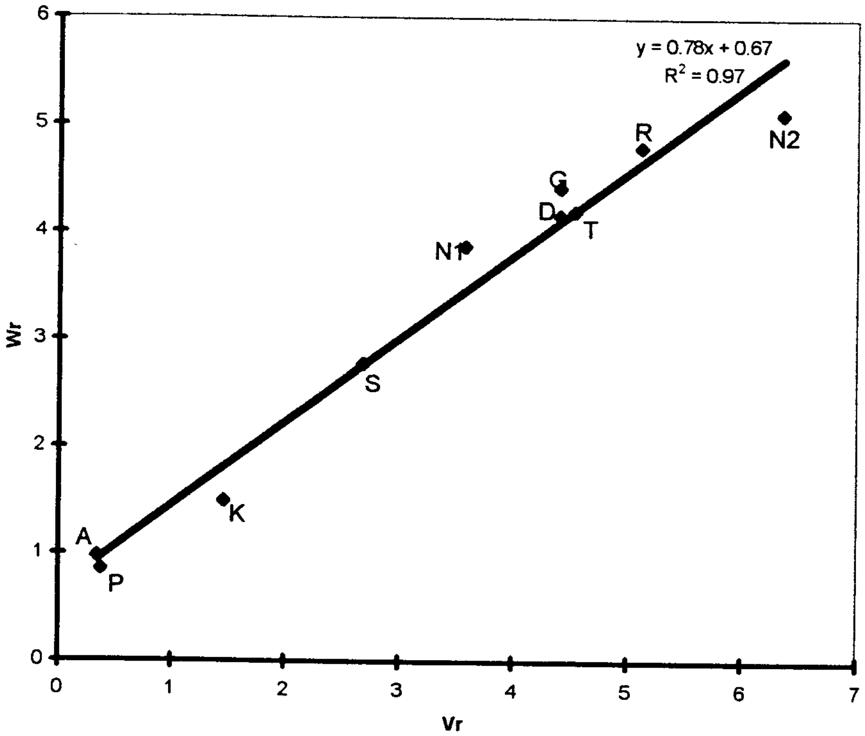

Figure 1. The relative number of dominant and recessive alleles in the ten varieties making up the parents of the diallel cross.
A = AGS 292, P = TGm 737P, K = Kabanyolo 1, S = Samsoy 1, N1 = Nam 1, D = Duiker, T = TGx 1448-2E, G = Gc81090-49E, R = Roan, N2 = Nam 2.

Vr) would be constant over the arrays and significant differences would be evidence of epistatic gene action.

The results of Wr/Vr graph demonstrating the distribution of dominant and recessive alleles among the ten soybean varieties used in the diallel cross are presented in Figure 1. The graph has a slope of 0.78 indicating failure of the additive-dominance model for the shattering trait (Jana, 1975; Chrstie et al., 1988). The varieties near the origin (AGS 292 and TGm 737P) contain dominant alleles and are susceptible while varieties Nam 2, Roan, TGx 1448-2E, Duiker and GC 81090-48 have recessive alleles and are resistant (Kearsey & Pooni, 1996). The results are in agreement with the description given to the parental lines on the basis of their resistance to pod shattering in Table 1. Varieties Samsoy 1, Nam 1 and Kab 1 are presumed to have about the same number of dominant and recessive alleles as they are presented in the middle position of the regression line. These varieties responded as intermediate when assessed for shattering (Table 1).

The results showed that the value of D was significant ($p < 0.05$), indicating that additive effects play a major role in the genetics of pod shattering in soybean (Table 3). The values of H1 and H2 were also significant ($p < 0.05$) suggesting that the effects of dominance were important. These observations from classical genetic analysis were in agreement with QTL analysis observations made by Saxe et al. (1996) and Bailey et al. (1997). The current study therefore confirms earlier observations that additive and epistatic ef-

Table 3. Genetic parameters affecting soybean shattering estimated with Hayman's (1954) method

Parameter	Value ± s.e
Error (E)	0.22 ± 0.06*
Additive effects (D)	6.21 ± 0.20*
Dominance effects(H1)	6.10 ± 0.37*
Dominance effects(H2)	5.47 ± 0.37*
Direction of gene distribution (F)	–0.54 ± 0.47ns
Average degree of dominance (H1/D)	0.98
Broad sense heritability ($h^2{}_b$)	0.97
Narrow sense heritability ($h^2{}_n$)	0.70

* Significant at $p < 0.05$.

Table 4. Variance components and narrow sense heritability estimated by Griffing's (1956) method

Source	DF	SS	MS	F
General combining ability	9	191.826	21.314	285.993*
Specific combining ability	45	68.218	1.516	20.341*
Error	108	8.049		
Additive variance ($\sigma^2{}_A$)	= 3.30;			
Dominance variance ($\sigma^2{}_D$)	= 1.44			
Narrow sense heritability ($h^2{}_n$)	= 0.69			
$\sigma^2{}_A$ (% of total variance)	= 69.60			

* Significant difference ($p < 0.05$).

fects control pod shattering in soybean. The H1 value was greater than the H2 value indicating that alleles increasing mean pod shattering (dominant alleles) were more frequent among the parents than the recessive alleles, and the average degree of dominance(H1/D) was less than 1, indicating partial dominance (Christie et al., 1992).

Both general combining ability (GCA) and specific combining ability (SCA) effects were observed to be significant ($p < 0.05$) with GCA predominant over SCA (Table 4), confirming further the overwhelming importance of additive and dominance effects. Consequently, effective selection should be possible within such a population at the F_2 generation (Patil & Chopde, 1981). The $h^2{}_b$ was 0.97 (Table 3), in the range of estimates reported in the literature (Caviness, 1969; Tsuchiya, 1987; Tiwari & Bhatnagar, 1991 and Bailey et al., 1997). The $h^2{}_n$ value of 0.70 (Tables 3 and 4) generated by the two methods confirmed that the shattering trait is highly heritable, and indicated accurate analyses.

Conclusions and recommendations

The diallel analysis techniques detected non allelic interaction for pod shattering among the crosses used and showed shattering trait to be partially dominant. Both additive and dominance effects on pod shattering were significant confirming earlier results using molecular markers. The results showed high values of $h_n{}^2$ estimates, indicating that it was possible to improve the trait by simple breeding method such as backcrossing technique. However, the germplasm used in this study had similar genetic background in respect to pod shattering as other germplasm reported in previous work. Thus classical breeding techniques that have been used in solving this problem in temperate regions can be applied in tropical areas as well. The significant non additive variance observed in this study is made up of dominance and epistatic effects (Christie & Shattuck, 1992). It is therefore recommended that further work be undertaken to partition the non additive variance into components attributable to dominance and epistasis.

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