

Inheritance of agronomic and seed composition traits in *Glycine max* x *Glycine soja* crosses^{1,2}

Sylvia Rodríguez de Cianzio³ and Walter R. Fehr⁴

ABSTRACT

Interspecific crosses between the cultivated soybean, *Glycine max* (L.) Merr., and the wild species, *Glycine soja* Sieb. & Zucc. may be useful for broadening the genetic base of commercial cultivars. The objectives of the study were to evaluate agronomic traits of *G. max*, *G. soja* and their F₁ hybrids in tropical and temperate environments, to determine whether cytoplasmic effects were present for agronomic traits and seed composition in reciprocal crosses between the two species, and to evaluate the type of gene action that controls the inheritance of traits in interspecific crosses. Reciprocal crosses were made between 'Century' and PI326581 and between 'Amsoy 71' and PI424001. Thirty plants of each of the parents and 50 F₁ plants of each cross were grown at two environments in Puerto Rico and one in Iowa. The traits evaluated were date of stages R1 and R8, leaf size, shattering, defoliation, vining, lodging, agronomic type, plant height, 100-seed weight, percentage of seed protein and oil, and percentages of palmitic, stearic, oleic, linoleic, and linolenic acids in the oil. No significant differences were observed among environments for seven of the 11 agronomic traits evaluated in the two crosses. The relative performance among genotypes for all traits in Iowa and Puerto Rico was similar. This similarity indicates that it is possible to use tropical locations to evaluate the progeny of interspecific crosses. No significant differences between F₁ plants of reciprocal crosses were observed in the two crosses for any of the traits; thus, cytoplasmic effects were not important. The type of gene action observed differed among traits and included additive, dominance, and partial dominance.

INTRODUCTION

Interspecific crosses between *Glycine max* (L.) Merr. and *G. soja* Sieb. & Zucc. may be useful for broadening the genetic base of commercial cultivars. Harlan and De Wet (7) included the two species as part of the primary gene pool of the domesticated soybean. Both species make up the subgenus *Soja*, and have been hybridized successfully by artificial cross-pollination (6, 12, 13, 14). Partial sterility in some crosses between these two species has been reported (1, 14).

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³Associate professor, Department of Agronomy, Iowa State University, and Department of Agronomy and Soils, University of Puerto Rico, Mayagüez, P. R. 00708.

⁴Professor, Department of Agronomy, Iowa State University, Ames, IA 50011.

Tropical and temperate environments have been compared for their usefulness in selecting soybean genotypes that are adapted to the northern United States. It has been found that seed size (2, 4), protein and oil content (3), and fatty acid composition (8) can be effectively selected in tropical conditions. There is no published information, however, on the evaluation of other agronomic traits in tropical locations. The first objective of our study was to evaluate agronomic traits of *Glycine max* and *G. soja* genotypes and their F_1 hybrids in tropical and temperate environments.

The strategy for germplasm introgression from *G. soja* to *G. max* will be determined by the mode of inheritance of desirable and undesirable characters in interspecific crosses. One consideration is the presence of cytoplasmic effects, and another is the type of gene action that controls a character. Cytoplasmically-inherited traits are known to occur in *G. max*. Terao (11) described a cytoplasmically inherited mutant of *G. max*, *cyt-G1*, which controlled green cotyledon and seed coat. There have been two reports of cytoplasmic mutants of *G. max* affecting chlorophyll levels in foliage (9, 10). The only study of cytoplasmic effects in interspecific crosses of *G. max* and *G. soja* was reported by Weber (13). He studied the inheritance of seed size, maturity date, protein percentage, and iodine number of oil in a cross between the cultivar 'Dunfield' and the *G. soja* accession PI65549. The space-planted F_2 population was grown with the parents and F_1 hybrids in one location in 1940. Weber (13) did not find cytoplasmic effects for any of the four traits. A second objective of our study was to expand the evaluation of cytoplasmic effects in reciprocal crosses between *G. max* and *G. soja* to include traits not considered by Weber (13).

The type of gene action that controls some agronomic and chemical traits in interspecific crosses between *G. max* and *G. soja* has been reported (6, 12, 13, 14). Fukuda (6) reported on the inheritance of seed size in one cross of *G. max* x *G. soja*. Ting (12) studied the inheritance of pubescence tip; seed hardness, size and shape; seed coat color; defective seed coat; plant height; and growth habit in one cross. Williams (14) evaluated the inheritance of seed size, oil and protein percentage, growth habit, and maturity in 15 interspecific crosses. Additive gene action was found for seed size, growth habit, maturity date, oil percentage of the seed, and iodine number of oil (6, 12, 13, 14). Dominance of the *G. soja* parent was reported for growth habit, protein percentage, and vining (14). Partial dominance of the wild parent was found for plant height, seed size, and protein percentage (12, 13). The third objective of our study involved the evaluation of the type of gene action for 18 traits related to agronomic performance and seed composition of progeny from *G. max* x *G. soja* crosses.

MATERIALS AND METHODS

Two *G. soja* accessions from the USSR, PI326581 and PI424001, were crossed with two cultivars of *G. max* of Maturity Group II, 'Century' and 'Amsoy 71'. The two *G. soja* plant introductions were randomly selected among 20 plant introductions that produced completely fertile F₁ plants when crossed to cultivars of *G. max*⁵. Reciprocal crosses between Century and PI326581 and between Amsoy 71 and PI424001 were obtained in the greenhouse in the summer of 1980 at Ames, IA. A minimum of 50 F₁ seeds were obtained for each cross.

The parents and F₁ generation were grown at three environments in 1981. Two environments were at the Iowa State University–University of Puerto Rico Soybean Breeding Nursery at Isabela, Puerto Rico, and the third environment was at the Agronomy Research Center near Ames, Iowa. Plantings in Puerto Rico were 15 January 1981 under lighted conditions and 1 November 1981 under natural day length (unlighted). In the lighted environment, plants were exposed to continuous light for a period of 15 days after emergence, followed by 14.5-hour days until flowering was completed, then natural day length until they reached maturity. The planting date in Iowa was 29 May 1981. Thirty plants of each of the parents and 50 F₁ plants of each cross were evaluated in the three environments. In the plantings of January 1981 in Puerto Rico and May 1981 in Iowa, 80 F₂ hybrid plants were also evaluated. Plots consisted of single-plant hills sown in a grid of 1x1 m.

The traits evaluated for each plant at every environment were date of stages R1, beginning bloom, and R8, full maturity (5), leaf size, shattering, defoliation, lodging, and agronomic type. Plant height and vining were evaluated for each plant at the Iowa and Puerto Rico unlighted environments. Leaf size was recorded to the nearest mm as the average length and width of the terminal leaflet of the first three fully developed leaves on the main stem at R1. Leaf length was the distance from the petiole insertion to the tip of the leaflet, and width was measured perpendicular to length at the widest part of the terminal leaflet. Plant height in cm was measured from the soil surface to the terminal node on the main stem. On plants with no prominent main stem, leaf size and plant height were measured on the stem where the unifoliolate node was evident after the vines were separated. Shattering was rated as 1 = shattering and 2 = no shattering. Defoliation scores were 1 = complete leaf loss at maturity and 2 = no defoliation. Vining was scored as 1 = main stem prominent, 2 = intermediate, and 3 = no apparent main stem. Lodging was recorded on a scale from 1 = plant erect to 5 = plant prostrate. Agronomic type was scored on the basis of the general appear-

⁵R. G. Palmer, Iowa State University, Ames, IA. Personal communication.

ance of plants on a scale from 1 = highly desirable to 5 = undesirable. All scores were assigned to the nearest 0.1.

Seed composition and 100-seed weight were evaluated for plants of the parents and F_1 generation. Protein and oil percentage were measured with an infrared analyzer at the USDA Northern Regional Research Center, Peoria, IL. All percentages are reported on a dry-weight basis. Fatty acid composition was determined by the Department of Food Technology at Iowa State University, as outlined by Hawkins et al. (8).

Analyses of variance combined across environments were calculated independently for each of the two crosses. Environments and genotypes were considered random effects. Means of the parents, F_1 , and F_2 generations were compared by *t*-tests to assess the type of gene action controlling each trait.

RESULTS AND DISCUSSION

No significant differences were observed among environments for seven of the 11 agronomic traits evaluated in the two crosses, including lodging, defoliation, shattering, vining, agronomic type, seed weight (data not shown), and plant height (tables 1 and 2). For seed composition and fatty acid content, no significant differences among environments were observed in the two crosses (data not shown). These results indicated that the average expression of these traits for all genotypes in the three environments was similar.

The genotype x environment interaction was significant for all agronomic traits, except defoliation and shattering of both crosses, and for the agronomic type in the cross Amsoy 71 x PI424001. For the seed composition traits and fatty acids, significant genotype x environment interactions were also observed for all characters of both crosses, except for protein percentage of Century x PI326581. In spite of the significant genotype x environment interactions, the relative performance among genotypes for all traits in Iowa and Puerto Rico was similar (tables 1 and 2). These observations are in agreement with results previously reported (2, 3, 4, 8).

Significant differences between the two parents of each cross were observed for number of days to R8, lodging, shattering, vining, agronomic type, seed weight, and leaf length and width (tables 3 and 4). Amsoy 71 was also significantly different from PI424001 for number of days to R1 and defoliation. For the fatty acid and seed composition traits, significant differences between the two parents were found for the percentages of oleic and linolenic acids, and protein and oil (tables 3 and 4). In addition, Amsoy 71 differed significantly from the PI parent for the percentages of palmitic and linoleic acids.

No cytoplasmic effects were observed in the two crosses for any of the traits for which the parents differed significantly (tables 3 and 4).

TABLE 1.—Agronomic performance of Century and PI326581, and their F₁ hybrids in three environments

Genotype	Planting to		Lodging ¹	Defoliation ¹	Shattering ¹	Vining ¹	Agronomic type	Plant height	Leaf		
	R1	R8							Length	Width	
	Days				Score			cm	mm		
	<i>Iowa</i>										
Century (C)	60	129	2.0	1.0	1.0	1.0	1.5	53	83	41	
PI326581 (PI)	74	114	5.0	1.0	2.0	3.0	5.0	71	32	14	
F ₁	73	123	5.0	1.0	2.0	3.0	4.5	117	58	28	
\bar{x}	69	122	4.0	1.0	1.7	2.3	3.7	80	58	28	
	<i>Puerto Rico-Lighted</i>										
C	45	100	1.6	1.0	1.0		1.0		97	67	
PI	39	70	5.0	1.0	2.0		5.0		43	18	
F ₁	43	89	5.0	1.0	1.5		3.7		79	42	
\bar{x}	42	86	3.9	1.0	1.5		3.2		73	42	
	<i>Puerto Rico-Unlighted</i>										
C	36	94	2.1	1.0	1.0	1.0	1.5	48	90	60	
PI	38	76	5.0	1.0	2.0	3.0	5.0	69	39	18	
F ₁	40	84	4.6	1.0	2.0	3.0	4.8	104	59	32	
\bar{x}	38	85	3.9	1.0	1.7	2.3	3.8	74	63	37	
S ₈	1	1	NS	NS	NS	NS	NS	NS	1	1	

¹ Lodging: 1=plant erect to 5=plant prostrate; Defoliation: 1=complete leaf loss at maturity to 2=no defoliation; Shattering: 1=no shattering to 2=shattering; Vining: 1=main stem prominent to 3=no apparent main stem; Agronomic type: 1=highly desirable to 5=undesirable.

TABLE 2.—Agronomic performance of Amsoy 71 and PI424001, and their F₁ hybrids in three environments

Genotype	Planting to		Lodging ¹	Defoliation ¹	Shattering ¹	Vining ¹	Agronomic ¹ type	Plant height	Leaf	
	R1	R8							Length	Width
	<i>Days</i>			<i>Score</i>			<i>cm</i>	<i>mm</i>		
	<i>Iowa</i>									
Amsoy 71 (A)	56	126	1.4	1.0	1.0	1.0	2.2	49	72	34
PI424001 (PI)	41	90	4.8	2.0	2.0	3.0	5.0	46	53	18
F ₁	46	105	4.2	2.0	2.0	1.5	4.0	85	65	22
\bar{x}	48	107	3.5	1.7	1.7	1.8	3.7	60	63	25
	<i>Puerto Rico-Lighted</i>									
A	47	100	2.4	1.0	1.0		1.0		124	84
PI	40	80	5.0	2.5	2.0		5.0		67	28
F ₁	43	92	5.0	1.5	1.0		4.0		84	44
\bar{x}	43	91	4.1	1.5	1.3		3.3		92	52
	<i>Puerto Rico-Unlighted</i>									
A	40	100	1.5	1.0	1.0	1.0	1.0	52	99	62
PI	30	78	4.9	2.0	2.0	2.0	5.0	68	44	13
F ₁	32	82	4.2	2.0	2.0	3.0	4.4	63	68	34
\bar{x}	34	87	3.5	1.7	1.7	2.0	3.5	61	70	36
S _x	1	1	NS	NS	NS	NS	NS	NS	2	2

¹ Lodging: 1=plant erect to 5=plant prostrate; Defoliation: 1=complete leaf loss at maturity to 2=no defoliation; Shattering: 1=no shattering to 2=shattering; Vining: 1=main stem prominent to 3=no apparent main stem; Agronomic type: 1=highly desirable to 5=undesirable.

TABLE 3.—Mean agronomic performance, seed composition and fatty acids of Century and PI326581, and their reciprocal F_1 hybrids averaged over three environments

Genotype	Agronomic Performance										
	Planting to		Lodging ¹	Defoliation ¹	Shattering ¹	Vining ¹	Agronomic type ¹	Seed weight	Plant height	Leaf	
	R1	R8								Length	Width
	Days				Score		mg/seed	cm	mm.		
Century (C) ²	47	108** ³	1.9**	1.0	1.0**	1.0**	1.3**	212**	48	90**	56**
PI326581 (PI)	50	87	5.0	1.0	2.0	3.0	5.0	20	70	38	16
CxPI ²	51	98	4.9	1.0	1.7	3.0	4.3	51	108	68	36
PIxC	53	99	4.9	1.0	2.0	3.0	4.4	49	98	62	32
Parent \bar{x} ²	48	98	3.4**	1.0	1.5** ⁴	2.0**	3.2**	116**	59	64	36
$F_1 \bar{x}$ ²	52	98	4.9	1.0	1.8	3.0	4.4**	50**	100	65	34
	Fatty acid					Seed Composition					
	Palmitic	Stearic	Oleic	Linoleic	Linolenic	Protein		Oil			
	%										
C ²	10.8	3.9	21.7**	55.5	8.1**	42.5**		19.8**			
PI	10.9	3.9	14.8	54.8	15.5	46.1		9.0			
CxPI ²	10.5	3.8	16.5	57.2	11.8	45.3		14.7			
PIxC	10.6	3.9	16.6	57.2	11.7	45.1		15.1			
Parent \bar{x} ²	10.8	3.9	18.2	55.2	11.8	44.3*		14.4			
$F_1 \bar{x}$ ²	10.6	3.8	16.6	57.2	11.8	45.2		14.9			

¹ Lodging: 1=plant erect to 5=plant prostrate; Defoliation: 1=complete leaf loss at maturity to 2=no defoliation; Shattering: 1=no shattering to 2=shattering; Vining: 1=main stem prominent to 3=no apparent main stem; Agronomic type: 1=highly desirable to 5=undesirable.

² Significant differences between the *G. max* and *G. soja* parent based on a *t*-test. Reciprocal F_1 's were not statistically different based on a *t*-test. Means of the parents which were significantly different from the F_1 means based on a *t*-test. F_1 means significantly different from parent means were compared with the PI parent by a *t*-test.

³ Significant at the 0.01 probability level.

⁴ Significant at the 0.05 probability level.

TABLE 4.—Mean agronomic performance, seed composition and fatty acids of Amsoy 71 and PI424001, and their reciprocal F_1 hybrids averaged over three environments

Genotype	Agronomic Performance										
	Planting to		Lodging ¹	Defoliation ¹	Shattering ¹	Vining ¹	Agronomic ¹ type	Seed weight	Plant height	Leaf	
	R1	R8								Length	Width
	Days		Score				mg/sd	cm	mm		
Amsoy 71 (A) ³	48**	109**	1.8**	1.0**	1.0**	1.0**	1.4**	197**	50	98**	60*
PI424001 (PI)	37	85	4.9	2.0	2.0	2.5	5.0	33	57	55	20
AxPI ²	40	92	4.7	2.0	1.7	3.0	4.2	60	82	72	33
PIxA	41	93	4.3	1.7	1.7	2.5	4.1	60	71	73	33
Parent \bar{x} ²	42	97	3.4**	1.5	1.5**	1.8*	3.2**	115**	54	76	40
$F_1 \bar{x}$ ²	40	92	4.5	1.8	1.7	2.8	4.2**	60**	76	72	33
	Fatty acid					Seed Composition					
	Palmitic	Stearic	Oleic	Linoleic	Linolenic	Protein	Oil				
	%										
A ²	10.8**	3.8	28.0**	49.2*	8.2**	39.9*	21.3**				
PI	12.2	4.1	18.0	54.0	11.6	43.0	12.8				
AxPI ²	11.6	4.0	18.4	55.1	10.7	40.7	17.4				
PIxA	11.6	4.1	18.5	54.8	11.0	40.4	17.8				
Parent \bar{x} ²	11.5	4.0	23.0*	51.6*	9.9*	41.4	17.0				
$F_1 \bar{x}$ ²	11.6	4.0	18.4	55.0	10.8	40.6	17.6				

¹ Lodging: 1=plant erect to 5=plant prostrate; Defoliation: 1=complete leaf loss at maturity to 2=no defoliation; Shattering: 1=no shattering to 2=shattering; Vining: 1=main stem prominent to 3=no apparent main stem; Agronomic type: 1=highly desirable to 5=undesirable.

² Significant differences between the *G. max* and *G. soja* parent based on a *t*-test. Reciprocal F_1 's were not statistically different based on a *t*-test. Means of the parents which were significantly different from the F_1 means based on a *t*-test. F_1 means significantly different from parent means were compared with the PI parent by a *t*-test.

³ Significant at the 0.01 probability level.

⁴ Significant at the 0.05 probability level.

Mean values of agronomic traits, seed composition, and fatty acids of reciprocal F_1 hybrids were not significantly different from each other.

The type of gene action varied among traits and included additive, dominance, and partial dominance (tables 3 and 4). Additive gene action was found in both crosses for number of days to R8 and for leaf length and width. In the cross Amsoy 71 x PI424001, additive gene action was observed for number of days to R1. Dominance of the *G. soja* parent was observed in both crosses for lodging, shattering, and vining and for the cross Amsoy 71 x PI424001 for defoliation. Partial dominance of the wild parent was observed for agronomic type and seed weight for both crosses. No statistically significant differences were observed between the means of the F_1 and F_2 generations (data not shown). However, for lodging, shattering, and vining where dominance gene action was observed in the F_1 generation, the mean values in the F_2 generation were smaller than for the F_1 .

For seed composition traits, both crosses exhibited additive gene action for the percentage of oil (tables 3 and 4). Differences between crosses were observed in the mode of inheritance of the other chemical traits studied. In the cross Century x PI326581, additive gene action was observed for the percentage of oleic and of linolenic acids in the oil, and dominance of the *G. soja* parent was observed for protein percentage. In the cross Amsoy 71 x PI424001, dominance of the wild parent was observed for the percentages of oleic and linolenic acids, and additive gene action was observed for protein percentage. In the latter cross, additive gene action was found for the percentage of palmitic acid and dominance for the percentage of linoleic acid.

The results of our study indicated that it is possible to use tropical environments to evaluate for agronomic traits of genotypes of *G. max* and *G. soja* and their F_1 hybrids. The relative performance among genotypes within environments was similar, suggesting that the statistical significance of the genotype x environment interaction was the result of changes in the magnitude of differences among genotypes, rather than changes in the relative ranking of the genotypes across environments.

The mean agronomic performance, seed composition, and fatty acids in the oil of reciprocal F_1 's indicated that cytoplasmic effects were not important in interspecific crosses between *G. max* and *G. soja*. These observations agree with the report of Weber (13) who did not find any cytoplasmic effects in four traits measured in one *G. max* x *G. soja* cross. For breeders considering the transfer of useful characters from *G. soja* to *G. max*, either species may be used as female parents to obtain F_1 seed.

The type of gene action controlling individual characters in our study was compared with that reported by other workers. Variation in the

type of gene action controlling characters of *G. soja* x *G. max* crosses has been reported by Fukuda (6), Ting (12), Weber (13), and Williams (14). Additive gene action was observed for maturity date in our study and by Weber (13), and Williams (14). Dominance of the wild parent for vining was found in our study and also by Williams (14). For seed weight, partial dominance of the wild parent was observed in our study using an arithmetic scale and calculating the arithmetic mean. These observations were in agreement with the results of Ting (12) and Weber (13) but differ from the observations by Fukuda (12). The three authors used arithmetic scales, and Ting (12) also calculated the geometric mean. When Weber (13) transformed the data to a logarithmic scale, however, he observed additive gene action, which was in agreement with the results of Fukuda (6). For agronomic type, our data indicated partial dominance of the *G. soja* parent, Ting (12) reported additive gene action, and Williams (14) observed dominance of the wild parent. Of the chemical traits evaluated in our work, only protein and oil percentage were evaluated previously. For oil percentage, the results of our study and those of Weber (13), and Williams (14) indicated the presence of additive gene action. For protein percentage, additive gene action was observed in our study in one of the crosses and dominance of the *G. soja* parent for the other cross. Weber (13) reported partial dominance of the high-protein *G. soja* parent, and Williams (14) observed dominance of the high-protein *G. soja* parent. The differences observed among studies for the inheritance of some of the traits seem to be due to different plant accessions of *G. max* and *G. soja* that were used. In the case of the variation observed among studies for the inheritance of seed size, a scale effect may also be present.

RESUMEN

La herencia de caracteres agronómicos y la composición química de la semilla en cruzamientos de *Glycine max* x *Glycine soja*

Los objetivos de este estudio fueron evaluar los caracteres agronómicos de *G. max*, *G. soja* y sus híbridos F_1 en ambientes tropical y templado; determinar si en los cruzamientos recíprocos entre estas dos especies hay efectos citoplasmáticos para los caracteres agronómicos y de composición química de la semilla; y evaluar el tipo de acción génica que controla la herencia de los caracteres en estos cruzamientos. Se realizaron cruces recíprocos entre 'Century' y PI326581, y entre 'Amsoy 71' y PI424001. Treinta plantas de cada uno de los padres y 50 plantas F_1 de cada cruzamiento se sembraron en dos ambientes en Puerto Rico y uno en Iowa. Se evaluaron los siguientes caracteres: etapa R1 y R8, tamaño de la hoja, dehiscencia de las vainas, pérdida de hojas, presencia de guías, acamado, tipo agronómico, altura de la planta, peso de 100 semillas, porcentaje de aceite y proteína en la semilla, y porcentaje de los ácidos palmítico, esteárico, oleico, linoleico y linolénico en el aceite. No se observaron diferencias significativas

entre ambientes en siete de los 11 caracteres agronómicos evaluados en los dos cruzamientos. El comportamiento relativo de los genotipos para los caracteres evaluados en Iowa y Puerto Rico fue similar, lo que indica que es posible usar localidades tropicales para evaluar la progenie de cruzamientos interespecíficos. En cada uno de los dos cruces y para todos los caracteres evaluados, no se observaron diferencias significativas entre las plantas F₁ obtenidas de los cruzamientos recíprocos, lo que indica que los efectos citoplasmáticos no fueron de importancia. Los tipos de acción génica que se observaron en la herencia de los caracteres evaluados fueron aditivos, de dominancia y de dominancia parcial.

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