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SELECTION FOR LATER FLOWERING IN SOYBEAN (*Glycine max* L. Merrill) F_2 POPULATIONS CULTIVATED UNDER SHORT DAY CONDITIONS*

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ABSTRACT

Several different selection strategies were used to estimate expected gain of days to flowering and other related characters in two F_2 soybean (*Glycine max* (L.) Merrill) populations. The sample originated from crosses of lines whose seeds do not contain the three lipoxygenase isozymes with the commercially cultivated IAC-12. IAC-12 is a gene carrier for an extended juvenile period. This study was conducted during the winter of 1994 in Viçosa, Minas Gerais. The plants were grown under natural photoperiod. One population was grown in a heated greenhouse, and the other in the field under natural temperature conditions. Lower temperatures early in the field planting caused a delay in flowering. Delayed flowering caused a broader amplitude in all characters evaluated, and resulted in higher selection gains for the field-grown plants than for the greenhouse-grown plants. Direct selection for number of flowering days proved to be efficient for improving this character in both populations. Gains were also obtained for other characters. Interactions of temperature and photoperiod and temperature and genotypes affected soybean flowering time and produced alterations in other correlated agronomic characters, including productivity.

INTRODUCTION

Soybean is a typical short-day plant (Kilen and Hartwig, 1971; Criswell and Hume, 1972), in which each cultivar generally shows narrow adaptation ranges for satisfactory production (Hartwig, 1970; McBlain and Bernard, 1987). There are some soybean genotypes, however, that have an above average juvenile period (Hinson, 1989; Kiihl and Garcia, 1989). These differences are very interesting for breeding research because they have a wide range of adaptation and also allow planting period flexibility.

The beany flavor and smell, which are characteristic of soybean products, result mostly from the association of short-chain carbon compounds with proteins. This is caused by the catalytic action of lipoxygenase isozymes (LOX1, LOX2 and LOX3) on polyunsaturated fatty acids like linoleic and linolenic acids in soybeans (Axelrod, 1974). Among the short-chain carbon compounds created by the effect of these enzymes, hexanal is considered the main cause of beany flavors (Oliver *et al.*, 1982). Lipoxygenase isozymes of soybean seeds are inherited in simple Mendelian form. Alleles responsible for the absence of LOX1, LOX2 and LOX3 are recessive. Mutants without these lipoxygenases have been found in world germ plasm collections (Hildebrand and Hymowitz, 1982; Kitamura *et al.*, 1983; Kitamura, 1984; Mack *et al.*, 1987). Discovery of these recessive alleles permits their elimination, producing better smelling and tasting soybean cultivars. One of the objectives of the soybean breeding program developed at the Federal University of Viçosa is to develop cultivars with an increased juvenile growth period and an improved bean quality, i.e., seeds without the three lipoxygenase isozymes.

Number of flowering days in soybean is a character that affects directly plant height, number of nodes, maturing time, lowest pod insertion, leaf area, lodging degree, and mainly grain yield, as well as other important agronomic characters of that crop (Gopani and Kabaria, 1970; Whigham and Minor, 1978). Therefore, the knowledge of an efficient selection strategy to increase gain in soybean time to flowering is of fundamental importance to obtain new cultivars adapted to a larger variation of environments.

The present study was developed to investigate various selection strategies to obtain an increase in the number of flowering days and other related characters in two soybean F_2 populations conducted under different environmental conditions.

MATERIAL AND METHODS

Two F_2 populations originated from crossbreeding lines whose seeds do not contain the three lipoxygenases isozymes (null triple), and the commercially cultivated IAC-12, which has a longer juvenile period, were used in this study. These F_2 populations were studied in Viçosa, Minas Gerais, in the winter of 1994, under natural photoperiod and different temperature conditions. One experiment was conducted in a heated and ventilated greenhouse with 15 to 18°C minimum and 28 to 32°C maximum temperatures. The field experiment, conducted under natural

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conditions, had average minimum and maximum temperatures of 10.4 and 24.5°C, respectively before and during the flowering period. Other characters evaluated included number of days from emergence until flowering (DEF), number of nodes at flowering (NNF), height of the plant at flowering (HPF), number of pods per plant (NPP), number of seeds per plant (NSP), and weight of seeds per plant (WSP).

Predictions of expected response to selection were determined for a selection pressure of 10%, using the following strategies:

Direct response to selection

The direct response to selection for each character was determined using the following equation (Eberhart, 1970):

$$GS_X = DS_X \, . \, h^2_X,$$

where
GS_X = prediction of direct gain in X;
h^2_X = heritability of character X for an individual plant;
DS_X = selection differential of character X selection, where

$$DS_X = \bar{X}_{SX} \, . \, \bar{X}_{OX},$$

where
$\bar{X}_{SX}$ = character X average of selected individuals, and
$\bar{X}_{OX}$ = original average of character X.

Correlated response

The expected response of character Y, which is called correlated response, when character X is selected, was determined by two methodologies:

a) Correlation-based method

This method, cited by Silva (1982), Pirchner (1983), Falconer (1987), Venkovsky (1987), and Cruz (1990), includes the following parameters:

$$GS_{Y(X)} = i \, . \, h_x \, . \, r_G \, . \, \sigma_{Gy},$$

where
$GS_{Y(X)}$ = selection gain in character Y, with selection for character X;
i = selection differential in units of phenotypic standard deviation, which is a percentage of the selected individuals;
h_X = square root heritability of character X;
r_G = genotypic correlation between characters X and Y; and σ_{GY} = genotypic standard deviation of character Y.

b) Heritability and selection differential-based method

Another method to predict gain of a character, based on selection in another character, was presented by Eberhart (1970) and uses the following expression:

$$GS_{Y(X)} = (\bar{X}_{SY} - \bar{X}_{OY}) \cdot h^2{}_Y = DS_{Y(X)} \cdot h^2{}_Y,$$

where
$GS_{Y(X)}$ = gain by selection in character Y, when selection is based on character X;
$\bar{X}_{SY}$ = average of character Y, from individuals selected on character X;
$\bar{X}_{OY}$ = original average of character Y;
h^2_Y = heritability of character Y, on an individual plant, and
$DS_{Y(X)}$ = indirect selection differential for character Y based on selection of character X.

Desired gain index-based selection

Pesek and Baker (1969) suggested a selection index in which the economic weights of the characters could be substituted by the gains desired by the breeder for each character selected, since these weights would be easier to determine. Formulation of the desired gain index requires knowledge of expression of the expected gains for the various characters, given in the following equation:

$$\Delta g = \frac{G \hat{b} i}{\hat{\sigma}_I},$$

where
Δg = expected gain vector;
G = dimension matrix n x n of genotype variances and covariances among the characters;
$\hat{b}$ = dimension vector n x 1 of the estimated coefficient index, and
i = selection differential, in standard deviation units ($\hat{\sigma}_I$) of index I.

In the methodology suggested by Pesek and Baker (1969), Δgd is substituted for Δg, which is the vector of the desired gains, and b is estimated by the expression:

$$\hat{b} = G^{-1} \Delta gd \frac{\hat{\sigma}_I}{i}$$

As the scalar $\frac{\hat{\sigma}_I}{i}$ does not affect the proportionality of $\hat{b}$'s, b can be estimated as $\hat{b} = G^{-1} \cdot \Delta gd$

Estimation of the index coefficients, when done in this manner, optimizes the gain in each character, according to its importance, which is defined by the breeder. Although this method does not require the establishment of economic weights for each character, economic weights can be estimated after the vector $\hat{b}$ is obtained, using the equation:

$$\hat{a} = G^{-1} \cdot P \cdot \hat{b},$$

where

$\hat{a}$ = dimension vector n x 1 of the economic weight estimates, and

P = dimension matrix n x n of phenotype variances and covariances between characters.

This study assumed that the vector of desired gains would be equivalent to the genotypic standard deviations for each character, because Crosbie *et al.* (1980) and Vieira (1988) obtained satisfactory results with this assumption.

RESULTS AND DISCUSSION

Simultaneous gains were found for all characters evaluated in the greenhouse, based on selection of only one of the characters (Tables I and II). For example, when number of days for flowering was the main character for selection, gains were achieved in other characters, including production. In this case, when number of days for flowering was selected, the expected gain in seed weight per plant was 17.1% with use of heritability and selection differential (Table I) and 15.0% based on the genetic correlation between characters (Table II).

Correlated response for some characters was greater than the direct response (Table II). This is because the selection character had lower heritability values compared with the heritability of the auxiliary character and a high positive genotypic correlation.

Estimated responses based on indirect selection by the index of Pesek and Baker (1969) for F_2 population conducted in the greenhouse (Table III) also had a smaller selection response (11%) for the number of flowering days than the direct response to selection for this character. But Cruz and Regazzi (1994) emphasized that use of a selection index allows gain optimization in all of the characters. Therefore, when choosing the best selection alternative, the possibility to achieve gains in other characters of agronomic importance should be considered, especially those with high economic value, like production. The best combination of gains in this selection strategy was number for flowering days and production for the F_2 population in a greenhouse.

Expected gain estimates by direct and indirect selection for the six agronomic characters studied in the field showed that direct selection was more efficient with use of heritability and selection differential methodology than indirect selection for all characters (Table IV). However, when the genotypic correlation between main and auxiliary characteristics was used, indirect selection for number of pods and seeds per plant had higher expected gain percentages than by direct selection for these characters (Table V). Lower heritability values of these two characters and greater genotypic correlation coefficients between characters that involved number of pods and seeds per plant were the probable causes of these results. For this reason,

Table I

Predictions of direct and indirect selection gains (%) for six characters in an F_2 soybean population obtained from the cross TN x 'IAC-12', conducted in a greenhouse in the winter of 1994, in Viçosa, Minas Gerais, using heritability and selection differentials.

Character[1]	Direct selection gain	Indirect selection gain in[2]					
		DEF	NNF	HPF	NPP	NSP	WSP
DEF	7.6	-	4.4	3.4	2.3	2.1	2.8
NNF	5.4	4.7	-	3.9	3.6	3.3	4.3
HPF	25.6	10.6	17.5	-	12.5	12.2	14.2
NPP	27.1	7.3	11.3	11.2	-	24.8	22.9
NSP	22.4	4.8	8.4	10.3	19.9	-	19.5
WSP	47.3	17.1	20.9	20.5	39.9	40.7	-

[1]DEF = Number of days from emergence to flowering, NNF = number of nodes during flowering, HPF = height of the plant during flowering, NPP = number of pods per plant, NSP = number of seeds per plant and WSP = seed weight per plant. [2]Figures out of the diagonal are showing the indirect gains for each character studied (first column) when the selection was practiced in other characters evaluated.

Table II

Predictions of direct and indirect selection gains (%) for six characters in an F_2 soybean population obtained from the cross TN x 'IAC-12', conducted in a greenhouse in the winter of 1994, in Viçosa, MG, using genotypic correlation between auxiliary and main characteristics.

Character[1]	Direct selection gain	Indirect selection gain in[2]					
		DEF	NNF	HPF	NPP	NSP	WSP
DEF	7.6	-	4.9	4.4	2.0	2.2	2.5
NNF	6.8	7.6	-	10.3	5.0	4.9	5.1
HPF	25.5	13.2	19.8	-	14.0	15.8	15.2
NPP	25.4	9.1	14.7	21.7	-	19.7	27.0
NSP	21.4	11.2	16.2	27.2	21.9	-	29.8
WSP	45.0	15.0	19.4	30.6	34.9	34.5	-

[1]See Table I for abbreviations. [2]See Table I.

Table III

Original averages ($\bar{X}_O$), averages of the selected plants ($\bar{X}_S$), heritability (h^2), and indirect gains (GS) predicted by the index of Pesek and Baker (1969), based on selection for six characters evaluated in an F_2 soybean population, obtained from the cross TN x 'IAC-12', conducted in a greenhouse in the winter of 1994, in Viçosa, MG.

Character[1/]	$\bar{X}_O$	$\bar{X}_S$	h^2	GS	GS%
DEF	38.0	40.3	0.8	1.9	4.9
NNF	7.2	8.0	0.5	0.4	5.2
HPF	38.4	42.4	0.9	3.5	9.2
NPP	26.8	37.0	0.6	5.8	21.6
NSP	56.6	79.7	0.4	9.9	17.4
WSP	11.0	16.7	0.8	4.4	40.8

[1]See Table I for abbreviations.

the gain prediction strategy that considers heritability and selection differentials should be preferred in this special case instead of genotypic correlation between main and auxiliary characteristics.

When the index of Pesek and Baker (1969) strategy was used to estimate indirect gains for the field-grown plants (Table VI), selection for number of days from emergence to flowering had the smallest gains among all applied selection methodologies (Table VII). For field experimental conditions, indirect selection based on the selection index of Pesek and Baker (1969) was not as efficient as other selection alternatives for gains in number of days for flowering. The highest gain percentages for the other characters should be considered when deciding on the best method.

The predictions of genetic gains by direct and indirect selection for the number of days for flowering, considering all selection alternatives used in this trial, are summarized in Table VII. Under both experimental conditions, direct selection had greater gain percentage, probably because of higher heritability estimates for number of days for flowering. For all applied selection strategies the expected genetic gain estimates for the F_2 population grown in the field were higher than those for the F_2 population conducted in the greenhouse. The genetic gains for number of days for flowering were affected by genotype limitations of this population and, especially, environmental influences. To achieve better gains in the first selection cycle, selection pressure could be increased, although this would reduce genetic variability that could be explored in the next generations, as observed by Cruz and Regazzi (1994).

Table IV

Predictions of direct and indirect selection gains (%) for six characters in an F_2 soybean population obtained from the cross TN x 'IAC-12', conducted in the field in the winter of 1994, in Viçosa, MG, using heritability and selection differentials.

Character[1]	Direct selection gain	Indirect selection gain in[2]					
		DEF	NNF	HPF	NPP	NSP	WSP
DEF	31.5	-	28.7	28.2	21.2	21.2	19.8
NNF	42.8	36.7	-	39.0	31.5	32.3	30.8
HPF	77.6	68.4	72.6	-	50.8	51.9	49.5
NPP	15.8	9.9	12.9	10.4	-	15.4	14.8
NSP	29.2	17.5	23.3	18.7	28.6	-	27.9
WSP	95.7	48.7	68.5	57.6	88.1	89.1	-

[1]See Table I for abbreviations. [2]See Table I.

Table V

Predictions of direct and indirect selection gains (%) for six characters in an F_2 soybean population obtained from the cross TN x 'IAC-12', conducted in the field in the winter of 1994, in Viçosa, MG, using genotypic correlation between auxiliary and main characteristics.

Character[1]	Direct selection gain	Indirect selection gain in[2]					
		DEF	NNF	HPF	NPP	NSP	WSP
DEF	29.7	-	24.5	25.7	20.9	20.5	19.2
NNF	36.7	33.5	-	36.7	28.9	29.3	28.2
HPF	66.3	59.0	62.6	-	51.8	52.2	49.6
NPP	12.8	83.0[3]	83.9[3]	88.4[3]	-	19.3[3]	50.5[3]
NSP	23.8	84.2[3]	88.1[3]	92.1[3]	19.8	-	56.3[3]
WSP	78.4	78.7	84.6	87.4	52.1	56.2	-

[1]See Table I for abbreviations. [2]See Table I. [3]Gain predictions realized with genotypic correlation estimates above 1.0.

Table VI

Original averages ($\overline{X}_O$), averages of the selected plants ($\overline{X}_S$), heritability (h^2), and indirect gains (GS) predicted by the index of Pesek and Baker (1969) based on selection for six characters evaluated in an F_2 soybean population obtained from the cross TN x 'IAC-12', conducted in the field, in the winter of 1994, in Viçosa, MG.

Character[1]	$\overline{X}_O$	$\overline{X}_S$	h^2	GS	GS%
DEF	68.0	80.9	1.0	12.9	18.9
NNF	8.5	11.2	0.9	2.4	28.3
HPF	33.2	48.5	1.0	14.6	44.0
NPP	48.1	116.2	0.1	7.3	15.3
NSP	87.8	213.2	0.2	24.3	27.7
WSP	18.6	45.3	0.6	17.1	92.0

[1]See Table I for abbreviations.

Table VII

Gain prediction (GS) and gain prediction in percent (GS%) for the number of days from emergence to flowering in two F_2 soybean populations that originated from the cross TN x 'IAC-12' conducted in a greenhouse and in the field in the winter of 1994, in Viçosa, MG.

Strategy	Greenhouse		Field	
	GS	GS(%)	GS	GS(%)
Direct selection	2.9	7.6	20.8	30.6
Indirect selection *NNF[1]	1.7	4.4	19.5	28.7
Indirect selection NNF[2]	1.9	4.9	16.7	24.5
Indirect selection HPF[1]	1.3	3.4	19.1	28.2
Indirect selection HPF[2]	1.7	4.4	17.2	25.4
Indirect selection NPP[1]	0.9	2.3	14.4	21.2
Indirect selection NPP[2]	0.74	1.96	14.2	20.9
Indirect selection NSP[1]	0.78	2.06	14.4	21.19
Indirect selection NSP[2]	0.82	2.16	13.93	20.5
Indirect selection WSP[1]	1.04	2.75	13.48	19.83
Indirect selection WSP[2]	0.95	2.52	13.04	19.2
Indirect selection IS_{PB}[3]	1.85	4.87	12.86	18.92

* See Table I for abbreviations; [1]$GS_{Y(X)} = DS_{Y(X)} \cdot h^2$; [2]$GS_{Y(X)} = i \cdot h_X \cdot r_G \cdot \sigma_{GY}$; [3]Selection index of Pesek and Baker (1969).

CONCLUSIONS

The strategy that achieved the highest gains in number of days for flowering, for both F_2 populations evaluated, was direct selection. The greater gains were because of the higher heritability for number of days for flowering.

The most effective characters to indicate later flowering plants were number of flowering nodes, evaluated in the greenhouse, and number of nodes and plant height in flowering, measured in the field.

Indirect selection based on the index of Pesek and Baker (1969) produced the highest simultaneous gains in all evaluated characters in the greenhouse. In the field, this strategy was the least efficient to indicate plants with a longer juvenile period.

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RESUMO

Diferentes estratégias de seleção foram adotadas para estimar os ganhos esperados em dias para florescimento e outros caracteres relacionados em duas populações F_2 de soja, oriundas do cruzamento entre linhagens com ausência das três isozimas lipoxigenases em suas sementes e o cultivar comercial IAC-12 portador de genes para período juvenil longo. As duas populações foram conduzidas em Viçosa, MG, no inverno de 1994, sob fotoperíodo natural e em diferentes condições de temperatura. Uma população foi conduzida em casa de vegetação, com aquecimento, e a outra, no campo, sob condições naturais de temperatura. Houve retardamento na data de florescimento das plantas conduzidas no campo, em função das baixas temperaturas observadas no início do desenvolvimento das mesmas. Este fato proporcionou aumento na amplitude de todos os caracteres mensurados, ocasionando maiores ganhos com a seleção das plantas cultivadas no campo, comparadas com as da casa de vegetação. A seleção direta em dias para o florescimento mostrou-se eficiente para ganho neste caráter nas duas populações, além de proporcionar ganhos consideráveis nos outros caracteres avaliados. Os dados demonstraram, também, que a temperatura e o fotoperíodo interagem entre si e com os genótipos, afetando a época de florescimento em soja, com conseqüentes alterações em outros caracteres agronômicos correlacionados, incluindo-se produtividade.

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