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Selection for yield, protein, and oil in soybean crosses between adapted and introduced parents

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Abstract

Soybean [Glycine max (L.) Merr.] breeders can sometimes increase genetic variability in their germplasm through wide crosses with plant introduction (PI) material, and in that way lead to slow progress in developing high-yielding cultivars. A study was conducted to evaluate the potential of crosses of adapted x introduced soybean lines for improving yield and protein and oil concentrations. Five soybean cultivars adapted to South Dakota were crossed in selected combinations with four PI lines to develop F3-derived lines. The adapted and PI lines were selected for wide variation in protein and oil concentration. Thirty $F_{3.5}$ lines and parents from each of eight different crosses, including two adapted \times adapted, were evaluated in a replicated group balanced block experiment. Significant genetic variability for yield occurred among progenies of two adapted × PI crosses, and for protein and oil concentrations among progenies of two adapted × PI crosses. No significant genetic variability for any trait was found among progenies of adapted × adapted crosses. Progenies of adapted × adapted crosses generally yielded more seed and had higher oil concentrations than those from adapted × PI crosses. PI parents with high trait expression produced populations with high expression for that trait, and combined better with some adapted parents than with others. With single-trait selection, simultaneous improvement of yield and oil concentration was more successful than for yield and protein concentration, or for protein and oil. Increases in the sum of protein and oil concentrations were small, and were achieved through increased protein concentration. In addition to measuring the trait of interest before crossing with PI lines, it seems that genetic variability of populations and combining ability of adapted parents should be determined. Relationships of yield, protein, and oil should be determined for each cross, even if only one trait is of interest in the selection program.

Keywords: Plant introduction; Genetic variability; Transgressive segregation; Protein; Oil; Selection; Glycine max (L.) Merr

1. Introduction

Concern about lack of genetic variability among soybean cultivars currently grown in USA (Delannay et al., 1983; Specht and Williams, 1984) has caused soybean breeders to use PI germplasm to introduce

genetic diversity. PI germplasm is derived from accessions available in the USDA soybean germplasm collection. While PI add useful genes that are not available in adapted cultivars (Burton, 1991), they may reduce yield (Schoener and Fehr, 1979; Vello et al., 1984), and introduce other undesirable genes. Plant breeders usually cross adapted × adapted soybean germplasms because use of an unadapted parent results in fewer superior segregates in the progeny

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(Thorne and Fehr, 1970). The main concerns with crossing adapted × adapted germplasm, as breeders do now, is that it may restrict future genetic gains (Kenworthy, 1980) and increase the potential for economic loss due to genetic vulnerability.

Identifying the best PI to use in crosses is a concern for breeders. Quite often, yield is the only trait that is studied when plant breeders use unadapted germplasm to introduce new genes. Because yield decreases may result from intensified selection for protein or oil concentration, those traits should be evaluated concurrently with yield. St. Martin and Aslam (1986) found a lack of female × male interaction for various agronomic traits, including protein and oil concentrations, and concluded that performance per se may be an adequate way to choose parents. This was confirmed by Reese et al. (1988). In addressing the question of whether visual selection or actual evaluation should be used in selecting PI parents, Reese et al. (1988) reported that F2 bulks from yield-selected parents yielded more than those from visually selected parents. Shannon et al. (1972) and Burton (1985) reported negative correlations between seed yield and protein concentration where unadapted germplasm contributed the protein genes. Most of the high-protein PI available in USA collection are deemed unacceptable for commercial production because they are negatively associated with seed yield (Holbrook et al., 1989). Whether or not populations developed from adapted × PI crosses have stronger negative associations between protein concentration and seed yield than populations developed from adapted × adapted crosses has not been adequately studied. Thorne and Fehr (1970) reported transgressive segregation for yield in adapted X unadapted crosses, but three-way crosses with two adapted parents and one unadapted parent produced more high-yielding lines.

Smith (1991) suggested that soybean breeders focus on sum of protein and oil concentrations and set a target of 620 g kg⁻¹ of dry weight to develop soybean cultivars with long-term market potential. Burton (1991) reported that plant breeders should consider both yield and protein when the objective is to increase either, but this has not been routinely practiced. Selection for increased sum may result in very slow progress (Openshaw and Hadley, 1984). Using index selection for sum, Burton (1991) in-

creased protein concentration and decreased yield and oil concentration in two populations. In another population, he obtained small increases in all three traits. Most of the published work on using PI to develop cultivars have offered little, if any, discussion of protein and oil concentrations.

The objective of this study was to evaluate the phenotypic structure of soybean populations developed from adapted × adapted and adapted × PI crosses, and to evaluate the genetic potential of resulting crosses to generate lines with superior seed yield and protein and oil concentrations. Wide ranges of cultivars and PIs were used to provide a more vigorous study.

2. Materials and methods

Five adapted soybean cultivars and four PI lines from maturity group I were chosen for this study based on yield, concentrations of protein and oil, and other agronomic data from a screening trial in 1990 of 12 PI lines and 18 adapted cultivars at Brookings, South Dakota (44°N, 96°W, 501 m asl) in 1990 (Table 1). Adapted cultivars used in this study were developed and released in the North Central United States from 1944 to 1989, and are either still grown, or are used as parents in breeding programs. The cultivars are unrelated, except for Kato and Hodgson 78 which were not crossed together in this study. Hodgson 78 was developed from Hodgson by backcrossing (Hodgson (7) \times Merit). Kato (M70[Evans \times M63-217(Sib of Hodgson)] × Century) has a sib of Hodgson in it's pedigree. PI297.513 and PI437.343 originated from USSR, while PI437.666 and PI36.653 originated from China. Minimum values were set to 400 and 200 g kg⁻¹ for protein and oil concentrations, respectively. There was a wide range in protein and oil concentrations among the selected cultivars. In 1991, six different crosses of selected adapted × PI and two of adapted × adapted were made. Crosses were advanced in a winter nursery in Belize, Central America (17°N, 88°W, 5 m asl) by single-seed descent to F₃ during 1991 and 1992. A total of 200 plants were harvested randomly from each cross and threshed individually. In 1993, progeny rows of each plant were grown in the field at Brookings with parents of the crosses included as

Table 1	
Preliminary evaluation of adapted soybean cultivars and plant introductions used as parents to develop populations for testing	

Entry	Seed Yield (g m ·2)	Plant height (m)	Lodging score (1-5)	Protein (g kg ⁻¹)	Oil (g kg ⁻¹)	Sum ^a (g kg ⁻¹)
Weber	347	2.2	1.3	381	224	605
Kato	354	2.2	1.1	427	196	623
Hark	274	2.4	1.4	418	206	624
Hodgson 78	270	2.3	1.4	387	225	612
Norsoy	232	1.9	1.0	441	176	617
PI297.513	306	1.8	1.0	384	231	615
PI437.666	262	2.6	1.4	398	210	608
PI36.653	196	1.9	2.0	433	184	618
PI437.343	189	0.9	1.0	457	176	633
LSD (0.05)	85.5	0.3	1.0		18	1014
CV (%)	18.6	18.6	8.0	2.2	2.6	1.2

Sum of protein and oil concentrations.

checks. Thirty rows from each cross were selected based on lodging, maturity, and plant height and threshed them separately. Yield and protein and oil concentrations were not considered at this point. All lines selected from all crosses had a narrow range of maturity within maturity group 1.

All crosses were tested together in the same field experiment at one location in 1994, and two locations in 1995. Only one location was used in 1994 because of seed supply limitations. Tests were conducted at Brookings in 1994 and 1995 on a Brandt silty clay loam (fine-silty, mixed Udic Haploboroll, USDA taxonomy). In 1995, the study was also conducted at Watertown, South Dakota (45°N, 96°W, 560 m asl) on a Brookings silty clay loam (fine-silty, mixed, Pachic Udic Haploboroll, USDA taxonomy). Each test consisted of a group-balanced block design (Gomez and Gomez, 1984) in which each cross formed a group containing the 30 selected lines and the two parents. Therefore, within each replicate there were eight groups, each containing a different set of lines. Groups were randomized within the experiment and lines randomized within groups. The group-balanced block design allows derivation of error terms to test for differences both among and within groups. Two replicates were used at each environment.

Individual plots consisted of two-rows 3.8 m in length, spaced 0.75 m apart. Plots were seeded with 26 seeds m⁻¹ to obtain about 370,000 plants ha⁻¹ at harvest. Given a history of soybean at these sites, the seed were not inoculated. At Brookings NO₃ – N

was 22 and 21 mg kg^{-1} in 0 to 1.5 m soil depth in 1994 and 1995, respectively. At Watertown NO₃ - N was 25 mg kg⁻¹ in 0 to 1.5 m soil depth. These nutrient supply levels were judged adequate and no fertilizer was added during the growing season. Weeds were controlled by mechanical cultivation. Plots at Brookings received 630 and 721 mm of rainfall during April to October 1994 and 1995, respectively. Plots at Watertown received 533 mm of rainfall during April to October 1995. No noticeable water stress was observed and plots were not irrigated. At maturity, the plots were trimmed to 3.0 m in length and harvested with a self-propelled plot combine. Seed yield was recorded from plot weights adjusted to 13% moisture and protein and oil concentrations were measured on a moisture-free basis using near infrared reflectance spectroscopy (Model 5000, NIRSystems, Silver Spring, Maryland). Sum of oil and protein concentrations was calculated before data analyses.

The data were analyzed using the statistical analysis system (SAS) (SAS Institute, 1992) with environments combined. In the combined analyses, crosses were fixed, while lines within crosses, and environments were random. Years were ignored, and each test in a year was designated as a different environment. Analysis of variance was conducted for each environment separately and Bartlett's test for homogeneity was used to determine that the error variances were homogeneous before a combined analysis was conducted across environments. Differences among means were tested using the least significant

difference (LSD) procedure. SAS PROC VAR-COMP (SAS Institute, 1992) procedure provided estimates of variance components among and within crosses. Significance of variance components were tested using F-tests. The appropriate error terms for testing significance of variance components were determined from expected mean squares.

3. Results and discussion

3.1. Variation among parents and overall performance of crosses

The ranges in protein and oil concentrations among PI parents were wider than among adapted parents in the initial evaluations (Table 1), and the ranges in concentrations of adapted × PI crosses also were wider than adapted × adapted crosses. Significant differences were found among environments and among crosses for yield, protein, oil, and sum in the combined analysis across all crosses (Table 2). Crosses performed differently in different environments for yield and sum of protein and oil concentrations in the combined analysis, but not for protein and oil concentrations individually. This indicated that crosses intended for improvement of yield or sum of protein and oil concentrations may require more than one environment of evaluation, while for protein or oil concentration above a single environment of evaluation may be adequate to identify the best crosses. Although the lines did not differ, the genotype \times environment interaction (G \times E) was significant for all four traits in the combined analysis

Table 2 Analysis of variance for soybean crosses tested in group balanced block design across three environments

Source of variation	df		Mean Squares a			
			Yield	Protein	Oil	Sum ^b
Total	1535					
Environments (E)	2	MSI	2359423 * *	132567	30043	94688
Crosses (C)	7	MS2	94754 • •	10905 * *	3003	3252 .
E×C	14	MS3	27287 •••	3783	356	2735 • •
Replications (R) within E	3	MS4	21015	740	210	313
C × R within E	21	MS5	11205	3920	796	1230
[Genotype (G) within C] \times [R within E]	744	MS6	1157	99	32	60
G within C	248	MS7	1657	226	55	128
G within C 1	31		1306	212 :	80 .	91 *
G within C 2	31		1495	142	50	69
G within C 3	31		2764	149	43 .	74
G within C 4	31		1488	169 .	59 .	86 '
G within C 5	31		1583	315 *	45	222 · ·
G within C 6	31		1215	430	64	301 * *
G within C 7	31		1617 *	168 '	57 .	57
G within C 8	31		1790	223 · •	42	129 * *
$E \times G$ within C	496	MS8	1445	160 *	38 *	105 * *
E × G within C 1	62		1915	159	56	69
E × G within C 2	62		1032	95	23	76
$E \times G$ within C 3	62		1592	105	31	59
E × G within C 4	62		1498	115	26	84
E × G within C 5	62		1205	318 *	52	198 • •
$E \times G$ within C 6	62		1383	240	47	174 *
$E \times G$ within C 7	62		1334 *	92	25	71
E × G within C 8	62		1601 *	157 *	40	110

Significant at 0.05 and 0.01 probability levels, respectively.

^a In the combined analysis F-values were as follows: E = MS1 + MS6/MS4 + MS8; C = MS2 + MS8/MS3 + MS7; $E \times C = MS3 + MS6/MS5 + MS8$. MS6 was used to test MS4, MS5, MS8; MS8 was used to test MS7.

b Sum of protein plus oil concentrations.

(Table 2). Therefore, once the best crosses have been identified, multiple locations of testing may be needed to select superior individuals for specific traits. Within individual crosses, there were significant differences among lines for yield in three crosses, for protein concentration in six crosses, for oil concentration in four crosses, and for sum of protein and oil concentrations in five crosses. Significant $G \times E$ were found among progeny in four crosses for yield, three crosses for protein concentration, one cross for oil concentration, and five crosses for sum of protein and oil concentrations.

The two adapted × adapted crosses differed only for yield across environments. Significant genetic variation was found for yield only in two adapted X PI crosses (Table 3). Two adapted × PI crosses (involving the same PI parent) had significant genetic variation for protein and oil concentrations (Table 3). Thorne and Fehr (1970) and Khalaf et al. (1984) reported that genetic variation in (adapted \times PI) \times adapted crosses was greater than in adapted × PI crosses. Because significant genetic variability for yield and protein and oil concentrations occurred in only two adapted × PI crosses in the present study, testing PI germplasm and selecting for the best adaptability in the test environment may restrict genetic variability of the derived populations. Sweeney and St. Martin (1989) observed that geographic origin information may help to predict level of genetic variability in adapted × PI crosses. There were differences among adapted × PI crosses for all four traits (Table 4). Both adapted × adapted crosses

Table 3 Genetic variance component estimates for traits among lines within different soybean crosses

Cross	Variance component estimate						
	Yield	Protein	Oil	Sum ^a			
Kato×Hark	154	3.3	2.7	0.6			
Weber × Kato	28	37.7	2.6	26.4			
Hodgson 78 × PI437.343	77	4.2	1.8	0.2			
Norsoy × PI437.666	195 * *	4.8	1.8	0.3			
Norsoy × PI297.513	63	1.7	2.8	5.9			
Norsoy × PI36.653	47	13.0 *	4.6 • •	2.9			
Kato × PI297.513	31	10.6	0.1	2.6			
Kato × P136.653	101 * *	10.6 * *	4.5	4.4			

Significant at 0.05 and 0.01 probability levels, respectively.

Table 4
Mean performance of soybean crosses tested in three environments

Cross	Mean performance a					
	Yield (g m ⁻²)	Protein (g kg ⁻¹)	Oil (g kg ⁻¹)	Sum (g kg ¹)		
Kato × Hark	281 b	412 d	195 a	607 e		
Weber × Kato	298 a	413 cd	196 a	608 de		
Hodgson 78×PI437.343	244 d	413 cd	191 b	605 f		
Norsoy × PI437.666	256 с	427 a	186 c	613 b		
Norsoy × PI297.513	298 a	407 e	195 a	602 g		
Norsov × PI36.653	261 c	429 a	186 c	614 a		
Kato × PI297.513	262 c	415 c	195 a	609 cd		
Kato × PI36.653	241 d	419 b	192 b	611 c		

^a Means within a column followed by the same letter are not significantly different at 0.05 probability level based on least significant difference procedure.

yielded higher than all but one adapted × PI cross, and both produced higher oil concentration than all but two adapted \times PI crosses. Three adapted \times PI crosses had higher protein concentration than both adapted × adapted crosses, which also were not in the top group for sum of protein and oil concentrations. These data indicated that some PI lines in this study provided greater genetic variation for protein and oil concentrations than adapted genotypes, and that some cross combinations were better than others. Norsoy \times PI297.513 (adapted \times PI) had similar yield to Weber \times Kato (adapted \times adapted), but also was among the highest for oil concentration (Table 4). This indicated that PI germplasm may be used to improve or maintain oil concentration and still make adequate yield improvements.

3.2. Evaluation of progeny performance

Reese et al. (1988) reported that selection for yield per se was better than test crossing to identify PI parents. Also, St. Martin and Aslam (1986) reported that even if test crosses were used, choice of tester would not be important. Most cross means were above 410 g kg⁻¹ for protein concentration, but below 200 g kg⁻¹ for oil concentration, and below 620 g kg⁻¹ for sum of protein and oil concentrations (Table 4). When Norsoy was crossed with two different PI lines, both crosses were similar in yield and protein and oil concentrations. This did not

^a sum of protein and oil concentrations.

hold true for Kato, indicating that both adapted and PI parents probably should be evaluated when using PI germplasm in crosses. The same PI line (PI297.513) crossed with different adapted parents produced different yield and protein concentration, but similar oil concentration in both crosses (Table 4). This is evidence that cross evaluation may be as important as line evaluation in determining which PI to use as parents. If so, it may be worthwhile to evaluate PI lines for agronomic traits before using them in a breeding program. The best crosses should be identified early, possibly by evaluating F2 bulks by a procedure similar to that of Reese et al. (1988).

When PI36.653 was crossed with Kato, 41% of the progenies had protein concentrations exceeding 420 g kg⁻¹; and when crossed with Norsoy, 94% of the progenies exceeded 420 g kg⁻¹. When PI297.513 was crossed with Kato, 16% of the progenies exceeded 420 g kg⁻¹; and when crossed with Norsoy, only 3% of the progenies exceeded 420 g kg⁻¹. These data indicated that choice of the adapted parent probably was as important as choice of PI parent. Evaluating the parents themselves may not reveal their true potential in crosses. Also, Simpson and Wilcox (1983) found many significant associations between protein concentration and agronomic traits, such as maturity, plant height, and lodging. It may be worthwhile to evaluate such traits before PI parents are chosen to prevent unnecessary transfer of undesirable traits. In other studies dealing with choice of PI parents for use in breeding programs (St. Martin and Aslam, 1986; Reese et al., 1988; Sweeney and St. Martin, 1989), selection of the adapted parent was not discussed.

Increasing the amount of genetic variability available for selection is among the possible ways of improving the annual rate of genetic improvement (Specht and Williams, 1984). If, in addition to improving specific traits, increasing genetic variability is important, then test crossing may be justified. Selection for PI performance per se gives no indication of genetic variability of the resulting population. Neither PI437.666 nor PI297.513 would have been selected as parents for protein concentration improvement based on our initial evaluations because they had protein concentrations less than 420 g kg⁻¹ (Table 1). But in crosses of Norsoy × PI437.666, 88% of the progeny had protein concentration ex-

ceeding 420 g kg $^{-1}$. In crosses of Norsoy \times PI297.513, only 3% of the progeny had protein concentration exceeding 420 g kg $^{-1}$.

Thorne and Fehr (1970) observed transgressive segregation in adapted × PI crosses. In our study, the frequency of transgressive segregation among crosses, demonstrated by the frequency of progeny with means significantly greater than the parent with the greatest mean, was found in one cross for protein concentration (7%), four crosses for oil concentration (3.3%-10%), two crosses for sum (3.3%), and one cross for yield (10%). For protein concentration, sum of protein and oil concentrations, and yield, all crosses found with transgressive segregation were adapted × PI. For oil concentration, two of the crosses with transgressive segregation were adapted × PI, and two were adapted × adapted. Evaluation of the parents themselves does not provide information about transgressive segregation. These data indicated that, in general, progeny performance and combining ability information may be helpful in choosing PI parents. Moreover, whether or not choice of tester is important depends on the trait in question. Kenworthy (1980) suggested a testcross procedure for identifying PI parents.

3.3. Mean performance and response to selection

In Table 5 the means of the different crosses may be compared with the means of the adapted parent in each cross. Each trait had at least one, but not more than two crosses in which there were no lines with a mean above the adapted parent mean. Although some crosses were not useful for selecting desirable lines, most crosses were valuable in this regard. In previous studies two-parent crosses have not generated as much genetic variability as three-parent crosses (Thorne and Fehr, 1970; Khalaf et al., 1984), but in the present study two-parent crosses involving one PI parent appeared to be successful in generating improved lines. Sufficient genetic variation was generated to yield progenies that exceeded the values of the parents (Table 5).

A 10% selection intensity among lines within crosses yielded a positive response in most crosses for the trait of interest (Table 6). Selection for yield in two crosses produced negative yield responses, however, and in one cross selection for protein con-

Table 5

Mean performance of adapted soybean parents and proportion of lines within crosses with means larger than the adapted parent

Cross	Yield		Protein		Oil		Sum	
	Mean a (g m ⁻²)	%	Mean (g kg 1)	%	Mean (g kg ⁻¹)	%	Mean (g kg 1)	%
Kato × Hark	295	23	416	20	192	80	610	33
Weber × Kato	304	33	421	17	193	80	614	20
Hodgson 78 × PI437.343	299	0	412	67	193	20	603	63
Norsoy × PI437.666	301	0	418	97	191	0	609	83
Norsoy × P1297.513	308	17	435	0	186	100	621	0
Norsoy × PI36.653	277	27	429	53	189	17	614	47
Kato × PI36.653	256	10	425	13	189	77	614	13
Kato × PI297.513	245	80	417	40	195	57	600	40

^a In adapted × adapted crosses the mean of the highest parent was used.

Table 6 Response of yield, protein, oil, and sum of different soybean crosses to selection with a 10% selection intensity

Selected	Cross	Respons	se to selec	ction ^a	
Trait		Yield	Protein	Oil	Sum ^b
Yield	Kato × Hark	+ 3.7	- 1.0	+ 2.4	-1.0
	Weber×Kato	+6.4	-1.0	+ 1.5	-1.0
	Hodgson 78× PI437.343	1.1	-1.0	+ ().5	+0.1
	Norsoy × PI437.666	- 1.0	+1.5	- 1.0	+0.7
	Norsoy × PI297.513	+ 6.0	-1.1	+ 5.6	-1.0
	Norsoy × PI36.653	+4.0	-1.0	-1.0	-1.0
	Kato × PI297.513	+ 16.5	-1.1	+ 1.5	-1.0
	Kato × P136.653	+ 4.9	-1.0	+ 1.7	-1.0
Protein	Kato × Hark	- 1.1	+ 1.7	+ 0.1	± 1.0
	Weber × Kato	-1.0	+2.8	-1.0	+1.9
	Hodgson 78×	-1.2	+3.1	-1.0	+1.2
	PI437.343				
	Norsoy × PI437.666	-1.2	+4.0	-1.0	+1.2
	Norsoy × PI297.513	-1.0	-1.0	+4.4	-1.0
	Norsoy × PI36.653	-1.1	+ 1.8	-1.0	+ 0.9
	Kato × PI297.513	+3.9	+1.8	-1.0	+ 1.1
	$Kato \times PI36.653$	-1.0	+1.2	-1.0	+0.5
Oil	Kato × Hark	-1.1	-1.0	+ 4.8	+0.4
	Weber × Kato	-1.0	-1.0	+ 4.6	- 1.0
	Hodgson 78×	-1.2	-1.0	+1.1	+0.4
	PI437.343				
	Norsoy × PI437.666	-1.1	+ ().6	+1.0	+0.3
	Norsoy × PI297.513	+2.1	- 1.1	+6.5	··· 1.0
	Norsoy × PI36.653	-1.0	1.0	+2.4	-1.0
	Kato × PI297.513	+ 9.0	-1.0	+3.1	-1.0
	Kato × PI36.653	- 1.0	- 1.0	+4.1	- 1.0

^a Response to selection is the percent difference between mean of selected lines and mean of adapted parents using a 10% selection intensity.

centration produced a negative response for protein concentration. These may not be desirable crosses for selection to improve yield above the adapted parent. For most crosses, selection for yield resulted in negative response for protein concentration and positive response for oil concentration. Burton (1991) reported similar results when selecting based on the mean of the entire population. Hartwig and Kilen (1991) demonstrated, however, that it is possible to develop soybean lines high in protein concentration and equal in seed yield to lines having high oil concentration. Selection for protein concentration resulted in positive changes in oil concentration for two crosses (one of which was adapted × PI) and positive yield response for one cross. Table 6 reveals that Kato × PI297.513 (the highest yielding adapted cultivar crossed with the highest yielding PI) might have the best potential for yield improvement with a modest improvement in oil concentration and only a small decrease in protein concentration when yield was the trait selected. When protein concentration was the trait selected, there were increases in both yield and protein concentration and a small decrease in oil concentration. When oil concentration was the trait selected there were increases in yield and oil concentration and a small decrease in protein concentration.

Norsoy \times PI437.666 had significant genetic variance for yield (Table 3), but did not offer yield increases when yield was selected (Table 6). Kato \times PI36.653 and Norsoy \times PI36.653 however, had significant genetic variance for protein and oil concentrations, and did show increases for these traits when the trait in question was selected. Other crosses, such as Kato \times PI297.513 and Norsoy \times PI297.513, gave

^b Sum of protein plus oil concentrations.

increases when the traits were selected, even though show the progenies lacked significant genetic variation for any trait. These data indicated that whether or not a trait with significant genetic variation gave increases when selected depended on the PI used in the cross, and that increases were obtained in crosses that did not provide significant genetic variation for the traits.

No crosses were identified where all three traits gave positive responses simultaneously. It seemed difficult to achieve positive responses in more than one additional trait simultaneously by single trait selection. Brim and Burton (1979) increased yield while selecting for protein concentration using recurrent selection, but lowered oil concentration in the process. When Burton (1991) selected for yield, he obtained positive changes in oil concentration, and only small negative changes in protein concentration. Selection for oil concentration resulted in increased yield for two crosses, and a small increase in protein concentration for one cross (Table 6). When yield responses were positive, however, protein concentration responses were negative and vice versa. When Burton and Brim (1981) used recurrent selection to increase oil concentration by direct selection for that trait, they decreased protein concentration and yield.

3.4. Phenotypic correlations

Phenotypic correlations are presented in Table 7. Protein and oil concentrations were positively correlated with seed yield in all crosses, except for Norsoy \times PI36.653, Kato \times Hark, and Kato \times PI297.513. Correlations were not significant between yield and oil concentration in Norsoy × PI36.653 and Kato × PI297.513, and between yield and protein concentration in Kato × Hark. Burton (1987) reported that populations in which the traits of interest are uncorrelated are desirable populations for selection of multiple traits. The largest correlations between yield and protein concentration were found in Norsoy × PI437.666, Norsoy × PI297.513 and Norsoy × PI36.653, which involved the adapted parent with the highest protein concentration. Correlations between yield and oil were small.

Highly significant negative correlations were found between protein and oil concentrations for all crosses. In some studies where negative correlations were observed between seed yield and protein con-

Table 7
Phenotypic correlation coefficients among yield, protein and oil within different soybean crosses

Trait	Yield	Protein	Oil
Weber× F	Kato above and Ka	ato×Hark below	diagonal
Yield	-	0.29 • •	0.16 .
Protein	0.10	-	-0.63
Oil	0.26	-0.69	-
Norsoy×1	PI297.513 above a	and Norsoy × PI4	37.666 below
diagonal			
Yield	-	0.58	0.29 · ·
Protein	0.52	-	-0.38 * *
Oil	-0.10	-0.62	-
Norsoy×1	PI36.653 above ai	nd Hodgson 78×	PI437.343 below
diagonal			
Yield	-	0.45	0.17 *
Protein	0.20 • •	-	-0.52
Oil	0.30	-0.70	-
Kato×PI3	36.653 above and	Kato × PI297.513	B below diagonal
Yield	-	0.23	0.18
Protein	0.26	-	-0.80
Oil	0.05	-0.70 ··	_

 $^{^{\}circ}$, $^{\circ}$ Significantly different from zero at 0.05 and 0.01 probability levels, respectively (n = 188).

centration (Shannon et al., 1972; Burton 1985), non-adapted germplasm contributed the genes for high protein concentration. In this study, however, correlations between yield and protein concentration in adapted × PI crosses were not larger than in adapted × adapted crosses.

In summary, selection for protein concentration resulted in positive changes in sum of protein and oil concentrations in seven crosses, but only in two crosses for yield and in three crosses for oil concentration. The positive changes found in sum of protein and oil concentrations as a result of selection for oil concentration and yield also were smaller than those found for protein concentration, confirming that increases in sum of protein and oil concentrations were achieved through increases in protein concentration. Although the positive changes obtained in one trait while selecting for another were small, they indicated the possibility of at least maintaining one trait while selecting for another. These results support the conclusion of Burton (1991) that both yield and protein concentration should be considered when either trait is the target of selection, and provide additional evidence that oil concentration should also be included in these considerations.

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References

- Brim, C.A. and Burton, J.W., 1979. Recurrent selection in soybeans II. Selection for increased percent protein in seeds. Crop Sci., 19: 494-499.
- Burton, J.W., 1985. Breeding soybeans for improved protein quantity and quality. In R. Shibles (Ed.), World Soybean Res. Conf. III. Ames, Iowa, pp. 361-367.
- Burton, J.W., 1987. The development of soybeans with altered protein and oil content. In Dolores Wilkinson (Ed.), Proc. Seventeenth Soybean Seed Res. Conf. American Seed Trade Association, Washington, D.C., pp. 46-52.
- Burton, J.W., 1991. Development of high-yielding high-protein soybean germplasm. In R.F. Wilson (Ed.), Designing Value-Added Soybeans for Markets of the Future. American Oil Chemists' Society, Champaign, Ilinois, pp. 109-117.
- Burton, J.W. and Brim, C.A., 1981. Recurrent selection in soybeans. III. Selection for increased percent oil in seeds. Crop Sci., 21: 31-34.
- Delannay, X., Rogers, D.M. and Palmer, R.G., 1983. Relative genetic contributions among ancestral lines to North American soybean cultivars. Crop Sci., 23: 944–949.
- Gomez, K.A. and Gomez, A.A., 1984. Statistical Procedures for Agricultural Research. Wiley, New York, 680 pp.
- Hartwig, E.E. and Kilen, T.C., 1991. Yield and composition of soybean seed from parents with different protein, similar yield. Crop Sci., 31: 290-292.
- Holbrook, C.C., Burton, J.W. and Carter, T.E. Jr., 1989. Evaluation of recurrent restricted index selection for increasing yield while holding seed protein constant in soybean. Crop Sci., 29: 324-329.
- Kenworthy, W.J. 1980. Strategies for introgressing exotic

- germplasm in breeding programs. In F.T. Corbin (Ed.), World Soybean Res. Conf. II. Raleigh, North Carolina, pp. 217-223.
- Khalaf, A.G.M., Brossman, G.D. and Wilcox, J.R., 1984. Use of diverse populations in soybean breeding. Crop Sci., 24: 358– 360
- Openshaw, S.J. and Hadley, H.H., 1984. Selection indexes to modify protein concentration of soybean seeds. Crop Sci., 24:
- Reese, P.F. Jr., Kenworthy, W.J., Cregan, P.B. and Yocum, J.O., 1988. Comparison of selection systems for the identification of exotic soybean lines for use in germplasm development. Crop Sci., 28: 237–241.
- SAS Institute, 1992. SAS Technical Report. SAS Statistics Software: Changes and Enhancements. Release 6.07. SAS Institute, Cary, North Carolina.
- Schoener, C.S. and Fehr, W.R., 1979. Utilization of plant introductions in soybean breeding populations. Crop Sci., 19: 185-188.
- Shannon, G. Jr., Wilcox, J.R. and Probst, A.L., 1972. Estimated gains from selection for protein and yield in the F4 generation of six soybean populations. Crop Sci., 12: 824–826.
- Simpson, A.M. Jr. and Wilcox, J.R., 1983. Genetic and phenotypic associations of agronomic characteristics in four high protein soybean populations. Crop Sci., 23: 1077-1081.
- Smith, K.J., 1991. Constituent pricing: How will it impact soybean research priorities? In R.F. Wilson (Ed.), Designing Value-Added Soybeans for Markets of the Future. American Oil Chemists Society. Champaign, Ilinois, pp. 17-21.
- Specht, J.E. and J.H. Williams, 1984. Contribution of genetic technology to soybean productivity— Retrospect and prospect. In W.R. Fehr (Ed.), Genetic Contribution to Yield Gains of Five Major Crop Plants. Special Publication 7. CSSA, Madison, Wisconsin, pp. 49-74.
- St. Martin, S.K. and Aslam, M., 1986. Performance of progeny of adapted and plant introduction soybean lines. Crop Sci., 26: 753-756.
- Sweeney, P.M. and St. Martin, S.K., 1989. Testcross evaluation of exotic soybean germplasm of different origins. Crop Sci., 29: 289-293.
- Thorne, J.C. and Fehr, W.R., 1970. Exotic germplasm for yield improvement in 2-way and 3-way soybean crosses. Crop Sci., 10: 677-678.
- Vello, N.A., Fehr, W.R. and Bahrenfus, J.B., 1984. Genetic variability and agronomic performance of soybean populations developed from plant introductions. Crop Sci., 24: 511-514.