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**YIELD AND AGRONOMIC CHARACTERISTICS OF TWO SOYBEAN CROSSES  
CONTAINING GLYCINE SOJA GERMPASM**

*Iowa State University*

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Yield and agronomic characteristics of two soybean  
crosses containing Glycine soja germplasm

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## INTRODUCTION

Genetic variability must be available for plant breeders to increase yield potential and maintain pest resistance of future crop cultivars. Impressive progress has been made in soybean [Glycine max (L.) Merrill] breeding in the past 50 years, but it has been made at the expense of genetic variability (St. Martin, 1982). Reduction in variability can result from the use of a limited number of high-yielding lines or cultivars as parents of improved cultivars.

Glycine soja Sieb. & Zucc. may serve as a source of genetic variability for soybean breeders. G. soja is the wild progenitor of cultivated soybeans (Hadley and Hymowitz, 1973). This wild species has several agronomically undesirable characteristics such as vininess, hardseededness, shattering, dark seed coat color, and green stems and leaves at pod maturity. These characteristics will complicate the selection of progenies that contain G. soja germplasm. As traits are identified that may be useful in cultivated soybeans, breeders will need to know how to transfer these traits to cultivars. Backcrossing to the cultivated parent will be necessary following hybridization with a G. soja parent because the wild species is agronomically inferior to cultivated soybeans. Time and effort will be saved and there will be less chance of losing the trait being transferred if the number of backcrosses is minimized.

Two crosses between G. max and G. soja were initially made at Iowa State University in 1977, and the  $F_1$  hybrids were backcrossed to the G. max parent up to five times.  $F_2$  seed from each backcross

generation, but not from the single-cross, was used to begin selection for this study.

The objectives of my research were:

- (1) to evaluate the effect of G. soja germplasm on the yield and other agronomic traits of soybean lines derived from segregating populations,
- (2) to determine the minimum number of backcrosses that can be made without sacrificing the high yield and desirable agronomic traits of the cultivated parent, and
- (3) to determine if lines have enhanced yield potential as a result of the introgression of G. soja germplasm.



## LITERATURE REVIEW

## Genetic Vulnerability

The term "genetic vulnerability" was coined in 1970 as a result of the southern corn leaf blight epiphytotic in the United States (NPGRB, 1979). Since then, there has been an increased awareness and concern about the genetic uniformity of our major crops. The leaf blight epidemic illustrated the vulnerability of crops with a narrow genetic base.

There is a demand for crop uniformity by farmers, food producers, distributors, and consumers. Crop uniformity also arises when relatively few cultivars tend to dominate production, when only a limited number of parental lines are used in the development of new cultivars, and when only one or a few sources of pest resistance are used across large areas of production (NAS, 1972; NPGRB, 1979).

The gene pool represented by commercial soybean cultivars has not expanded substantially since it was established in the 1940s, except for specific genes for disease and insect resistance (Nelson, 1983). Johnson and Bernard (1963) reported that six Manchurian soybean cultivars, 'AK', 'Dunfield', 'Manchu', 'Mandarin', 'Mukden', and 'Richland', provided the exclusive genetic background for cultivars grown on 95% of the northern U.S. soybean acreage in the early 1960s. In the southern U.S., AK was in the background of about 60% of the cultivars. Most of the cultivars grown in the U.S. in 1972 could be traced to 11 plant introductions, (PIs), including

the six listed above plus 'Arksoy', 'Clemson', PI 54610, 'Roanoke', and 'Tokoyo'. Six cultivars, 'Amsoy', 'Bragg', 'Clark' or 'Clark 63', 'Corsoy', 'Lee', and 'Wayne', accounted for 56% of the U.S. soybean acreage in 1972, and all have Mandarin as an ancestor. Lee and Bragg were grown on 58% of the Delta acreage and both have AK and Clemson as ancestors (NAS, 1972).

Delannay et al. (1983) examined the ancestry of 158 soybean cultivars grown in the U.S. and Canada. These cultivars were traced to 50 PIs. Relatively few introductions contributed a large proportion of germplasm to cultivars grown today. For cultivars released from 1971 to 1981, four PIs contributed 50% of the germplasm, and 10 PIs contributed 80%. Mandarin, alone, contributed 30% of the germplasm. In the southern gene pool, two PIs 'CNS' and 'S-100', contributed more than 50%, and seven PIs contributed 80% of the germplasm. Those PIs contributing to the northern gene pool may be somewhat related because they all originated in Northeast China.

The number of ancestral lines has increased over the years. Most of the newly used PIs have been sources of single genes, thus contributing little new germplasm. Eight cultivars released since 1970 contain at least 25% new germplasm, although these cultivars were developed for fringe areas of production and do not greatly add to genetic diversification (Delannay et al., 1983).

Despite this narrow genetic base, there has been sufficient diversity for stability of soybean production, and the genetic

potential for yield in commercial cultivars continues to increase (NAS, 1972; Schoener and Fehr, 1979). However, it is unlikely that all the favorable alleles for yield were present in the PIs which comprise our current gene pool (Nelson, 1983). Cregan et al. (1981) tested 101 PIs from maturity groups II, III, and IV and found some which produced higher yields than Richland, Dunfield, Mukden, AK, and Manchu. This indicates that the PIs forming the genetic base of our present cultivars were not necessarily the most productive genotypes available.

St. Martin (1982) estimated values for effective population size for soybeans used in hybridization programs for yield improvement. He found that the population size for cultivar development was smaller than in populations designed for long-term recurrent selection programs in other crops.

Wych and Rasmusson (1983) reported that a narrow germplasm base also exists for malting barley. No more than 11 germplasm sources used in present day cultivars have been introduced since 1900. Despite this narrow base, sizable yield gains have been made since 1920 and substantial opportunity is believed to exist for future genetic gain. They believe that judging diversity on the basis of pedigrees is speculative, and more useful diversity may exist in narrow gene pools than is expected.

Soybean breeders have realized the advantages of increased genetic variability and have been evaluating the breeding potential of lines of diverse origins (Johnson and Bernard, 1963). Populations

with wide germplasm bases have been assembled (Schoener and Fehr, 1979; Vello et al. 1984).

#### Utilization of Exotic Germplasm

Exotic germplasm may refer either to unadapted genotypes belonging to the same species as the cultivated types or to related wild species. Use of exotic germplasm is one method for increasing genetic variability in crops. Such germplasm sources should increase diversity and may provide useful variability. Using exotic germplasm in a breeding program may have some negative effects initially, but the long term effects of increased genetic diversity may justify its use (Fehr, 1976).

Utilization of wild species as germplasm sources has been most common when desirable genes were unavailable in the cultivated species. The effort required to transfer a single gene from a wild to a cultivated species may be substantial, and the transfer of quantitative traits may be even more difficult (Stalker, 1980). Wild species and races have most frequently been used as sources of disease, insect, and nematode resistance (Harlan, 1976; Stalker, 1980). Wild species of potatoes, cacao, coffee, sugarcane, and tobacco have been used as sources of disease resistance in those crops (Harlan, 1976).

The possibility that use of exotic materials could contribute to yield seems so unlikely that it is not attempted by most plant breeders (Harlan, 1976). However, there are several examples to the contrary. Improved yields using wild germplasm have been observed

in tobacco, maize, sugarcane, strawberries, and oats (Harlan, 1976; Stalker, 1980). Reeves (1950) reported an increase in yield in the hybrid combinations of a maize inbred modified with teosinte germplasm. Malm (1968) observed heterosis for yield, protein, and other traits when inbred sorghum lines were crossed with lines developed from African PIs. He concluded that the potential values of PIs should not be overlooked.

Soybean breeders use PIs mainly for sources of pest resistance (Hartwig, 1972; Schoener and Fehr, 1979). Resistance for fungal leaf spot, soybean cyst nematode, Mexican bean beetle, and soybean looper has been identified in G. max PIs (Poehlman, 1979). PI 84.946-2 is a source of moderate resistance to brown stem rot (Tachibana et al., 1983). When PIs are used as sources of resistance, Hartwig (1972) recommends that one or more backcrosses to the adapted parent should be made to retain productivity and adaptation.

Thorne and Fehr (1970a) have experimented with soybean PIs as sources of high protein. Plant introductions may also have genes which could improve yield. Lines from the germplasm collection have not been sought for yield improvement because they lack desired agronomic qualities (Hartwig, 1972). Plant introductions crossed to commercial cultivars have not produced high-yielding cultivars. Presently, there has not been a need to use PIs for yield improvement because genetic advances for yield have been made using the existing cultivars and experimental lines (Schoener and Fehr, 1979).

Thorne and Fehr (1970b) obtained transgressive segregates for yield from populations containing 25 and 50% germplasm from PIs. Schoener and Fehr (1979) created soybean populations with 0, 25, 50, 75, and 100% PI germplasm. The population with no PI germplasm was superior in yield to all other populations. The population with 50% adapted germplasm had acceptable yield and a large amount of genetic variability. This indicates that 50% PI germplasm may be suitable for populations to be used for long-term recurrent selection.

#### Glycine soja as a Germplasm Source

The genus Glycine Willd. is presently composed of two subgenera, Glycine and Soja (Moench) F. J. Hermann (Hymowitz and Newell, 1981; Ladizinsky et al., 1979; Newell and Hymowitz, 1982). The subgenus Soja contains two species, the cultivated soybean, G. max, and a wild species, G. soja. G. max has had several different designations since first being described by Linnaeus in 1753, including G. soja Merr. The wild species was first designated as G. soja by Siebold and Zuccarini in 1846. Since then, it has been referred to as G. ussuriensis Regel and Maack and G. formosana Hoskawa (Hermann, 1962; Newell and Hymowitz, 1978). It is currently designated G. soja Sieb. & Zucc. (Verdcourt, 1970).

A third species, G. gracilis, is supposedly an intermediate form between G. max and G. soja (Fukuda, 1933; Hadley and Hymowitz, 1973; Tang and Tai, 1962). Broich (1978) indicated that G. gracilis

and all semi-wild phenotypes are evidence of natural gene flow between G. max and G. soja.

A primary gene pool, as defined by Harlan and de Wet (1971), is one in which all members are easily crossed, hybrids are generally fertile with good chromosome pairing, and gene transfer is generally good. A primary gene pool almost always includes spontaneous and cultivated races, and it corresponds with the traditional biological species concept. According to this definition, G. max, G. soja, and G. gracilis constitute the primary gene pool (Harlan and de Wet, 1971; Newell and Hymowitz, 1982). Hermann (1962) considered G. gracilis as a member of G. max. Broich and Palmer (1980b; 1981) proposed that G. gracilis be designated G. max forma gracilis.

It has been suggested that separate designations be kept for the cultivated and wild forms as a matter of practical convenience to plant breeders (Hadley and Hymowitz, 1973; Hymowitz, 1970). Broich and Palmer (1980b; 1981) indicated that G. max and G. soja should be treated as taxonomically distinct species. They base this on morphological differences determined by cluster analysis techniques and the different ecological niches occupied by these two species.

Morphologically, G. max and G. soja are quite distinct. G. max is characterized by an erect, sparsely branched, bush-type growth habit with a stout primary stem and large (12-20 g per 100 seeds) seeds (Broich, 1978). In contrast, G. soja is a procumbent or climbing vine with delicate twining stems having many branches and bearing small pods and small (1.6-3.0 g per 100 seeds) colored seeds

(Broich, 1978; Broich and Palmer, 1980b; Fukuda, 1933). G. soja shatters and has non-uniform ripening of pods and hardseededness.

The subgenus Glycine is composed of seven perennial species. Until recently, no successful hybridizations have been reported between G. max and any of the species of the Glycine subgenus. Broue et al. (1982) crossed a perennial amphiploid (G. tomentella Hayata x G. canescens F. J. Herm.) to G. max and obtained five sterile plants using embryo or ovule culture. Newell and Hymowitz (1982) successfully crossed G. tomentella and G. max using ovule culture. This is an indication that the soybean has a tertiary gene pool that is a potential source of genetic diversity.

According to Vavilov (1951), the soybean was domesticated in the Chinese center of origin which is geographically located in mountainous regions of central and western China and in the adjacent lowlands. Li (1970) thought soybeans originated in the North China Belt, which includes the Yellow River Valley and the southern part of Manchuria. This region overlaps with that in which G. soja is currently found in the wild. G. soja has been reported growing throughout the Yangtze Valley, in northern and central China, in Manchuria and adjacent Siberia, and in Taiwan, Japan, and Korea. G. soja can be found in fields, thickets, and hedgerows, and along roadsides and riverbanks in these areas (Hermann, 1962; Hymowitz, 1970; Ting, 1946).

Five of the seven species of the subgenus Glycine are found only in Australia. The other two species, which exist as both



diploids and tetraploids, are found in south China, Taiwan, the south Pacific islands, and in Australia (Hymowitz and Newell, 1981).

Because of the easy crossability, hybrid fertility, karyotype, and chromosomal behavior in meiosis, G. soja is believed to be the wild ancestor of G. max (Hadley and Hymowitz, 1973). G. max probably resulted from selections out of populations of G. soja that attracted the attention of ancient agriculturalists (Broich, 1978). It is thought that the cultivated soybean might have originated through the accumulation of qualitative and quantitative changes due to mutation, and not by any structural changes in the chromosome (Karasawa, 1936; Tang and Tai, 1962). Broich and Palmer (1980a; 1981) discussed three alleles which probably arose during the domestication of G. max, and reported that allelic differences in collections of G. soja and G. max were the result of differing selection pressures.

High chromosome homologies between cultivated and wild species enhances the probability of successful gene flow from the wild species (Stalker, 1980). Fukuda (1933) found that the chromosome number of  $F_1$  plants from crosses of G. max and G. soja were the same as both parents ( $2n=40$ ). He reported 20 bivalents at meiosis and similarity in morphology and number of chromosomes of the two species. Karasawa (1936) concluded that G. max and G. soja share the same genome because no abnormality in sporogenesis was observed in the  $F_1$ . The same conclusion was reached by Ting (1946). Weber (1950) observed a high level of fertility in  $F_1$  hybrids of G. max

and G. soja. Tang and Chen (1959) observed no meiotic irregularities in their  $F_1$  plants.

Williams (1948) was the first to report sterility in hybrids between G. max and G. soja. He observed 50% abortive pollen and ovules in some  $F_1$  plants. Broich (1978) reported between 50 and 70% sterility in  $F_1$  hybrids, which he suspected was due to a translocation. Ahmad et al. (1977) observed irregular meiosis in hybrids from G. max and G. soja. Chromatin bridges and laggards in anaphase I, metaphase II, and anaphase II suggested a paracentric inversion. They were later able to confirm at least two inversions. However, only one G. soja line, CPI44003, was used by Ahmad et al. (1977; 1979) and this line may not be representative of other G. soja lines. The chromosome structure of two other G. soja PIs may differ from that of G. max (Palmer, 1976). Delannay et al. (1982) noticed a high frequency of translocations in G. soja accessions from Russia and China. G. soja accessions from Japan and Korea had a low frequency of translocations, but did have some inversions. When G. soja lines are used which have translocations or inversions, partial sterility is expected. There are G. soja lines available without such chromosomal abnormalities which permit unrestricted gene flow between G. max and G. soja (Broich, 1978).

Several studies have been published concerning the segregation of progenies from crosses between G. max and G. soja. The  $F_1$  plants of such crosses have been reported as being intermediate to the parents for characters such as seed coat color, size and weight of

seeds, seed hardness, and number of nodes and pods (Fukuda, 1933; Karasawa, 1936; Tang and Chen, 1959). Heterosis in the  $F_1$  of G. max and G. soja crosses has been observed for height, number of branches, and number of seeds (Karawawa, 1936; Tang and Chen, 1959; Ting, 1946; Weber, 1950).

Maturity date of progenies has been reported as intermediate to their G. max and G. soja parents, and transgressive segregation in both directions also has been observed (Tang and Tai, 1962; Weber, 1950; Williams, 1948). Weber (1950) reported no dominance for genes controlling maturity. Other studies indicated that there was dominance for maturity date (Tang and Li, 1963; Tang and Tai, 1962). Heritability estimates for maturity obtained from progenies of G. max and G. soja crosses ranged from 42 to 98% (Tang and Li, 1963; Tang and Tai, 1962; Weber, 1950). Approximately seven effective factors were responsible for the expression of maturity (Tang and Li, 1963; Tang and Tai, 1962).

The inheritance of prostrate growth appears to be very complex (Ting, 1946). When G. max and G. soja are crossed, the procumbent nature of the wild parent was observed in the  $F_1$ ,  $F_2$ ,  $F_3$ , and  $BC_1$  generations, indicating dominance for this trait in G. soja (Karasawa, 1936; Weber, 1950; Williams, 1948). Tang and Chen (1959) reported that lodging, branching habit, and type of growth resembled the wild parent. The erect habit of the G. max parent was not recovered in the  $F_2$ ,  $F_3$ , or  $BC_1$  generations by Williams (1948).

Plant height measured on  $F_1$  hybrids of G. max and G. soja was closest to the wild parent, but shifted toward the G. max parent with successive selfing generations (Tang and Tai, 1962; Ting, 1946). Heritability for height estimated from progenies of crosses of G. max and G. soja ranged from 51 to 91%, and 12 effective factors controlled height (Tang and Tai, 1962). Ting (1946) considered height a quantitative trait controlled by a large number of genes.

G. soja represents a potentially useful source of genetic variability because it shares the same primary gene pool as the cultivated soybean (Broich and Palmer, 1980b). Because of the genetic difference between G. max and G. soja, it is possible that the wild species possesses variation in characters of economic value, such as pest and disease resistance, not present in cultivated soybeans (Ladizinsky et al., 1979).

High protein is a trait in G. soja which may be valuable if transferred to G. max. Seeds of commercial soybean cultivars in North America average 39.5 to 41.5% protein on a dry-weight basis (Hartwig, 1973). G. soja accessions PI 342619A and PI 342619B contain 46% protein and PI 342621A contains 51% protein. These three accessions have been used to create variability for protein in soybeans (Erickson et al., 1981; 1982). Weber (1950) reported that PI 65549 had greater than 50% protein.

Harlan (1976) reported the use of wild soybeans as a source of earliness for soybeans in Siberia.

There has been no literature reporting the yield potential in progenies obtained from crosses of soybeans with G. soja. Weber (1950) reported making two backcrosses (G. max<sup>3</sup> x G. soja) to the G. max parent. This is the highest number of backcrosses with G. max and G. soja parents that has been reported in the literature.

#### Backcrossing

Harlan and Pope (1922) first called attention to the use of the backcross method for plant breeding. It is an easy method for improvement of self-pollinated cultivars for a single trait (Briggs and Allard, 1953; Leininger and Frey, 1962).

With backcrossing, homozygosity is attained at the same rate as with selfing according to the formula:

$$\text{proportion of homozygosity} = \frac{(2^m - 1)}{2^m}$$

where  $m$  is the number of generations of selfing or backcrossing. Although the same proportion of individuals will be homozygous with selfing as with backcrossing, all individuals will have the same genotype at the completion of a backcrossing program (Allard, 1960; Briggs, 1935). The chance of recovering the parental gene combination in an  $F_2$  plant is  $1/4^n$ , but the chance is  $1/2^n$  in a  $BC_1F_1$  plant, where  $n$  is the number of heterozygous loci. Therefore, the parental type is  $2^n$  times as likely to be recovered with one backcross as it is after one generation of selfing. The chance of reassembling the parental gene combination with backcrossing compared with selfing

becomes exponentially greater as the number of gene differences between the two parents becomes greater (Anderson, 1949).

Briggs and Allard (1953) listed three requirements for successful backcrossing: a) a satisfactory recurrent parent must be used; b) maintaining worthwhile intensity of the trait being transferred must be possible; and c) the recurrent parent must be reconstituted with a reasonable number of backcrosses executed with populations of manageable size. After selection of the recurrent parent, the most important consideration is the number of backcrosses to be used because recovery of the recurrent genotype is primarily a function of the number of backcrosses (Briggs and Allard, 1953).

There is limited evidence of success in transferring quantitative traits with the backcross method (Lawrence, 1974). Backcrossing programs have been undertaken to transfer earliness into wheat and to alter seed size in lima beans (Briggs and Allard, 1953). Leininger and Frey (1962) observed the behavior of heading date, plant height, seed weight per volume, and seed yield in backcross generations  $BC_1$  through  $BC_4$  in oats (Avena sativa L.). The means for all traits regressed toward the recurrent parent with successive backcrosses, except for yield, which showed a consistent increase over both parents. Because yield maintained its high level while other traits returned to the level of the recurrent parent and there was a decrease in variance of these traits (Leininger and Frey, 1962) concluded that backcrossing may be a useful technique for increasing yield in oats.

Backcrossing has produced unexpected increases in yield in a few cases. Everson and Schaller (1955) found that linked factors of the semi-smooth gene, r, accounted for higher yields of 'Atlas' barley after this gene was transferred from 'Lion' with backcrossing. Improved yield in oats was found to be associated with two crown rust reaction genes from wild oat lines (A. sterilis L.) which were transferred by backcrossing (Frey and Browning, 1971). Frey (1972) produced 12  $BC_5F_3$  isolines in oats and found seven which deviated significantly from their recurrent parents for grain yield. Two of the isolines were lower yielding and five were higher yielding than the parents.

#### Introgressive Hybridization

Introgressive hybridization was described and defined by Anderson and Hubricht (1938) as the gradual infiltration of germplasm of one species into another as a consequence of hybridization and repeated backcrossing. Although originally described as a mechanism found in nature, introgression of exotic germplasm into adapted cultivars has been suggested as a procedure for increasing genetic diversity. Introgression is a method with which breeders can transfer useful genes identified in exotic sources into adapted genotypes without disrupting the superior gene complexes of the adapted genotypes (Lawrence and Frey, 1975).

Introgressive hybridization in nature as described by Anderson and Hubricht (1938) has been repeated artificially by plant breeders. Germplasm of wild oats was introgressed into cultivated oats by

Lawrence (1974). In eight crosses, the  $F_2$  and  $BC_1F_2$  through  $BC_5F_2$  populations were studied and compared with their parents. The lines were chosen at random from the populations regardless of their agronomic suitability. With increasing backcross generations, the generation means approached the means of the recurrent parents. Variation was large in the early generations and decreased with later ones, although there was significant genetic variation in the  $BC_5$  generation for complexly inherited traits such as yield. Transgressive segregates for yield were observed from crosses involving all A. sterilis donor parents. All transgressive segregates were more than 20% higher yielding than the recurrent parents (Lawrence, 1974).

Rogers (1982) introgressed germplasm from nine Hordeum spontaneum lines into H. vulgare cultivars. The H. spontaneum lines appeared to be sources of favorable alleles for yield because transgressive segregates for yield were identified. The increase in yield was obtained without sacrificing the agronomic characteristics of the cultivated recurrent parents.

Theoretical investigations by Bailey (1977) suggested the effect of backcrossing on a line's performance. When the recurrent parent is much superior to the donor parent, the optimum number of backcrosses to obtain a line superior to the recurrent parent is between one and four. The optimum number of backcrosses increases as the number of different alleles between the two parents increases.



Lawrence (1974) concluded from his study that there is greatest probability in obtaining transgressive segregates for yield in the  $BC_1$  through  $BC_4$  generations, with the  $BC_3$  generation being the best. He offered the following explanation. The chance of obtaining a transgressive segregate from an  $F_2$  population is small because the opportunity for recombination is low and the percentage of exotic germplasm is large. After more than three or four backcrosses, the proportion of exotic germplasm becomes small and there is less chance of detecting transgressive segregates (Lawrence, 1974).

From their introgression study with oats, Lawrence and Frey (1975) observed that all A. sterilis introductions contributed useful genes for yield, height, and heading date. They indicated that A. sterilis germplasm should be incorporated into oat breeding populations in doses of 3 to 12%.

## MATERIALS AND METHODS

Two matings were produced between two soybean cultivars and two G. soja plant introductions. 'Amsoy 71' and 'Century' were the cultivars chosen because of their adaptability to central Iowa and their good yield and agronomic characteristics. PI 424001 and PI 326581 were the wild soybeans chosen because of complete fertility in crosses with G. max. The single crosses, PI 424001 x Amsoy 71 and Century x PI 326581, were made at Ames, Iowa, in 1977. The following winter in a greenhouse, the  $BC_1F_1$  seed was obtained by backcrossing the  $F_1$  plants to their respective G. max parent.  $F_2$  seed also was obtained from the  $F_1$  plants. In 1978,  $BC_2F_1$  and  $BC_1F_2$  seed was obtained from  $BC_1F_1$  plants in the field at Ames.  $BC_3F_1$  and  $BC_2F_2$  seed was obtained from  $BC_2F_1$  plants at Ames in 1979.  $BC_4F_1$  and  $BC_3F_2$  seed was obtained from  $BC_3F_1$  plants at the Isabela Substation, University of Puerto Rico in January 1980.  $BC_5F_1$  and  $BC_4F_2$  seed was produced at Ames in 1980.  $BC_5F_2$  seed was produced in Puerto Rico in January 1981. In each backcross, at least 73  $F_1$  seeds were obtained, and the cultivars were used as the male parent.

In May 1981, 25  $F_2$  seeds from each  $BC_1F_1$  through  $BC_5F_1$  plant ( $BC_nF_2$  seed) of the Amsoy 71 (PI 424001 x Amsoy 71) and Century (Century x PI 326581) crosses were planted in single 1.5 m rows at the Burkey Farm near Ames. Each row was derived from an  $F_1$  plant and represented an  $F_1$  family (Table 1). At least 1825  $F_2$

Table 1. Number of  $F_1$  families and number of  $BC_nF_2$  plants selected

Cross	Generation	No. of $F_1$ families	No. of $BC_nF_2$ plants selected
Amsoy 71	$BC_1$	73	48
	$BC_2$	134	163
	$BC_3$	187	198
	$BC_4$	240	215
	$BC_5$	319	216
Century	$BC_1$	77	9
	$BC_2$	175	170
	$BC_3$	270	189
	$BC_4$	271	197
	$BC_5$	363	205

seeds were planted per generation from each cross. Previous observations indicated that all  $F_2$  plants from the single-cross populations were not agronomically suitable (unpublished data) and, therefore, were not included in this study. None of the seed was scarified before planting so those with the hardseeded trait of G. soja would not have germinated. In the fall of 1981,  $F_2$  plants were discarded which matured earlier than 'Corsoy' or later than 'Pella' to obtain material of maturity suitable for central Iowa. Remaining plants were discarded that had any of the following characteristics of G. soja: a) pods shattered within two weeks after maturity, b) colored seed coats, c) downward curving of the stem such

that the top of the plant was within 50 cm of the ground, and d) retention of leaves or petioles after maturity. All  $F_2$  plants remaining after selection were threshed individually. In some cases, more than one plant was harvested from a plot ( $F_1$  family) and other plots had no agronomically desirable plants. The numbers of plants harvested from each generation are listed in Table 1.

In 1982, lines derived from individual  $BC_n F_2$  plants harvested in 1981 were planted in single-row plots 60 cm long with 1 m between plots. Ranges of plots were separated by 1 m alleys. The lines were planted on 4 May at the Agronomy Research Center, near Ames, and on 7 June at the Burkey Farm. A randomized complete-block design was used with two replications at each location. The numbers of lines tested from the Amsoy 71 cross were 45 from the  $BC_1$ , and 100 from the  $BC_2$  through  $BC_5$  generations. From the Century cross, eight lines from the  $BC_1$ , and 100 from the  $BC_2$  through  $BC_5$  generations were grown. The lines of each population were subdivided into sets containing 110 entries to reduce the size of a replication. Lines from each backcross generation were divided equally and randomly among sets. Each set also contained five check cultivars and the recurrent parent. The recurrent parent was entered three or four times per set.

The traits evaluated were seed yield, maturity, lodging, and plant height. Harvested seed was dried at 38 C for 48 hours before weighing. Seed yield was expressed as grams per square meter ( $g \cdot m^{-2}$ ). Maturity was determined as the number of days after 31 August when

95% of the pods had reached their mature color. Lodging was scored on a scale from 1 (all plants erect) to 5 (all plants prostrate) at maturity. Plant height was recorded at maturity as the distance in centimeters from the soil surface to the terminal node with a pod.

Analyses of variance were performed for each trait and population using a model appropriate to the randomized complete-block design. The recurrent parent, but not the check cultivars, was included in the analyses.

The 1982 data were analyzed for the individual locations and combined across locations. Location was considered a random effect and generation was considered a fixed effect. Line was considered a fixed effect for the traits maturity, lodging, and height because the plants from which they were derived were selected for these traits. Line was considered a random effect for yield because no selection was practiced for the trait. The parent and check cultivars common to all sets of each cross were analyzed to determine if significant differences existed among sets. In each cross, the effect due to sets was not significant ( $P>0.05$ ) for yield, maturity, lodging, or height, and the sets were combined for the analyses.

For the analyses of data at individual locations, the following model was used:

$$Y_{jk} = m + R_j + L_k + e_{jk}$$

$$j = 1 \text{ to } 2$$

$$k = 1 \text{ to } 326 \text{ in the Amsoy 71 cross}$$

$$= 1 \text{ to } 327 \text{ in the Century cross}$$

where  $Y_{jk}$  = observed value of the  $k^{\text{th}}$  line in the  $j^{\text{th}}$  replication

$m$  = overall mean effect

$R_j$  = effect of the  $j^{\text{th}}$  replication

$L_k$  = effect of the  $k^{\text{th}}$  line

$e_{jk}$  = error associated with the  $jk^{\text{th}}$  observation.

For the analyses of data combined across locations in individual years, the following model was used:

$$Y_{ijk} = m + E_i + R_{ij} + L_k + (ER)_{ij} + e_{ijk}$$

$i = 1 \text{ to } 2$

$j = 1 \text{ to } 2$

$k = 1 \text{ to } 326 \text{ in the Amsoy 71 cross}$

$= 1 \text{ to } 327 \text{ in the Century cross}$

where  $Y_{ijk}$  = observed value of the  $k^{\text{th}}$  line in the  $j^{\text{th}}$  replication of the  $i^{\text{th}}$  location

$m$  = overall mean effect

$E_i$  = effect of the  $i^{\text{th}}$  location

$R_{ij}$  = effect of the  $j^{\text{th}}$  replication in the  $i^{\text{th}}$  location

$L_k$  = effect of the  $k^{\text{th}}$  line

$e_{ijk}$  = error associated with the  $ijk^{\text{th}}$  observation.

An L.S.D. was calculated for maturity, lodging and height using data combined across locations. The L.S.D. was calculated using the equation  $L.S.D. = t_{df, \alpha=0.01} \sqrt{EMS(1/n_1 + 1/n_p)}$ , where EMS = error mean square,  $n_1$  = number of values used in computing line means, and  $n_p$  = number of values used in computing recurrent parent means. Lines were discarded that differed significantly from the mean of the re-

current parent at the 1% probability level for all traits except yield. Those lines not different from the recurrent parent for maturity, lodging, and height were selected for testing in 1983. Yield was not considered in the selection of the lines.

The selected lines were grown at two locations in Iowa in 1983. Plots at the Agronomy Research Center were planted 6 May, and those at Knierim, Iowa were planted 24 May. A randomized complete-block design was used with two replications at each location. The number of lines tested from the Amsoy 71 cross were 10 from the  $BC_1$ , 51 from the  $BC_2$ , 77 from the  $BC_3$ , 85 from the  $BC_4$ , and 88 from the  $BC_5$  generation. From the Century cross, no lines from the  $BC_1$ , 51 from the  $BC_2$ , 74 from the  $BC_3$ , 92 from the  $BC_4$ , and 98 from the  $BC_5$  generation were grown. The lines from each cross were subdivided equally and randomly among sets containing 40 entries to reduce the size of a replication. Each set also contained the recurrent parent, entered once or twice, and one other check cultivar.

Plots consisted of paired rows 4.6 m long with 68 cm between rows of a plot and 1 m between plots. Ranges of plots were separated by 76 cm alleys. The plots were end-trimmed in late July to reduce the effect of the end of the row on the seed yield. The plants in the 75 cm of row at each end of the plot were removed.

The 1983 data were analyzed for the individual locations, and combined across locations. These data were analyzed as described for the 1982 data. The effect of sets of both crosses was not significant for any trait in 1983. Sets were combined for the 1983

and combined analyses. The data for lines tested in both years were combined and analyzed across locations and years. The location by year combinations were analyzed as 'environments', which were considered random. For the analyses of data combined across environments, the same model was used as for analyses across locations within years, with the term 'environment' substituted for 'location'.

In each analysis of variance, the mean squares due to lines were subdivided into two components, variation among lines within generations and variation among generations. The mean squares due to lines within generations were subdivided into six components: a) among lines within the  $BC_1$  (only with Amsoy 71 data), b) among lines within the  $BC_2$ , c) among lines within the  $BC_3$ , d) among lines within the  $BC_4$ , e) among lines within the  $BC_5$  generation and f) within the recurrent parent. The recurrent parent can be thought of as the progeny of an infinite number of backcrosses.

For the analyses of data at individual locations, the significance of lines and related components were tested against the error (Table 2). For the analyses of data combined across locations (environments), the significance of lines was tested against the location (environment) x line mean square. The line and generation components (among  $BC_1$  lines, among  $BC_2$  lines, etc ...) were tested against their respective location (environment) x line mean square, except when the interaction was not significant; then the error mean square was used to test their significance (Table 3).



Table 2. Form of the analysis of variance for data from backcross-derived lines and the recurrent parent at individual locations with fixed and random line effects

Source of variation	df <sup>a</sup>	Expected mean squares	
		Lines fixed	Lines random
Replications	(r-1)	$\sigma_e^2 + L\sigma_r^2$	$\sigma_e^2 + L\sigma_r^2$
Lines (L)	( $\ell$ -1)	$\sigma_e^2 + RL^2$	$\sigma_e^2 + R\sigma_\ell^2$
L/Generation	( $\ell$ -g)	$\sigma_{e(\ell/g)}^2 + R(L/G)^2$	$\sigma_{e(\ell/g)}^2 + R\sigma_{\ell/g}^2$
L in BC <sub>1</sub> <sup>b</sup>	( $\ell_1$ -1)	$\sigma_{e(1)}^2 + RL_1^2$	$\sigma_{e(1)}^2 + R\sigma_{\ell(1)}^2$
L in BC <sub>2</sub>	( $\ell_2$ -1)	$\sigma_{e(2)}^2 + RL_2^2$	$\sigma_{e(2)}^2 + R\sigma_{\ell(2)}^2$
L in BC <sub>3</sub>	( $\ell_3$ -1)	$\sigma_{e(3)}^2 + RL_3^2$	$\sigma_{e(3)}^2 + R\sigma_{\ell(3)}^2$
L in BC <sub>4</sub>	( $\ell_4$ -1)	$\sigma_{e(4)}^2 + RL_4^2$	$\sigma_{e(4)}^2 + R\sigma_{\ell(4)}^2$
L in BC <sub>5</sub>	( $\ell_5$ -1)	$\sigma_{e(5)}^2 + RL_5^2$	$\sigma_{e(5)}^2 + R\sigma_{\ell(5)}^2$
Parent	( $\ell_p$ -1)	$\sigma_{e(p)}^2 + RL_p^2$	$\sigma_{e(p)}^2 + R\sigma_{\ell(p)}^2$
Generation	(g-1)	$\sigma_{e(g)}^2 + RG^2$	$\sigma_{e(g)}^2 + RG^2$
Error	(r-1)( $\ell$ -1)	$\sigma_e^2$	$\sigma_e^2$

<sup>a</sup> r = replications,  $\ell$  = lines, and g = generations.

<sup>b</sup> Amsoy 71 population only.

Table 3. Form of the analysis of variance for data from backcross-derived lines and the recurrent parent combined across locations or environments

Source of variation	df <sup>a</sup>	Expected mean squares	
		Lines fixed	Lines random
Locations or Environments (E)	(e-1)	$\sigma_a^2 + R\sigma_e^2$	$\sigma_a^2 + R\sigma_e^2$
Replications/E	e(r-1)	$\sigma_a^2$	$\sigma_a^2$
Lines (L)	(l-1)	$\sigma_b^2 + R\sigma_{le}^2 + REL^2$	$\sigma_b^2 + R\sigma_{le}^2 + RE\sigma_l^2$
L/Generations (G)	(l-g)	$\sigma_{b(g/l)}^2 + R\sigma_{l/ge}^2 + RE(L/G)^2$	$\sigma_{b(g/l)}^2 + R\sigma_{l/ge}^2 + RE\sigma_{l/g}^2$
L in BC <sub>1</sub> <sup>b</sup>	(l <sub>1</sub> -1)	$\sigma_{b(1)}^2 + R\sigma_{l(1)e}^2 + REL_1^2$	$\sigma_{b(1)}^2 + R\sigma_{l(1)e}^2 + RE\sigma_{l(1)}^2$
L in BC <sub>2</sub>	(l <sub>2</sub> -1)	$\sigma_{b(2)}^2 + R\sigma_{l(2)e}^2 + REL_2^2$	$\sigma_{b(2)}^2 + R\sigma_{l(2)e}^2 + RE\sigma_{l(2)}^2$
L in BC <sub>3</sub>	(l <sub>3</sub> -1)	$\sigma_{b(3)}^2 + R\sigma_{l(3)e}^2 + REL_3^2$	$\sigma_{b(3)}^2 + R\sigma_{l(3)e}^2 + RE\sigma_{l(3)}^2$
L in BC <sub>4</sub>	(l <sub>4</sub> -1)	$\sigma_{b(4)}^2 + R\sigma_{l(4)e}^2 + REL_4^2$	$\sigma_{b(4)}^2 + R\sigma_{l(4)e}^2 + RE\sigma_{l(4)}^2$
L in BC <sub>5</sub>	(l <sub>5</sub> -1)	$\sigma_{b(5)}^2 + R\sigma_{l(5)e}^2 + REL_5^2$	$\sigma_{b(5)}^2 + R\sigma_{l(5)e}^2 + RE\sigma_{l(5)}^2$
Parent	(l <sub>p</sub> -1)	$\sigma_{b(p)}^2 + R\sigma_{l(p)e}^2 + REL_p^2$	$\sigma_{b(p)}^2 + R\sigma_{l(p)e}^2 + RE\sigma_{l(p)}^2$
Generations	(g-1)	$\sigma_{b(g)}^2 + R\sigma_{ge}^2 + REG^2$	$\sigma_{b(g)}^2 + R\sigma_{ge}^2 + REG^2$

E x L	$(e-1)(\ell-1)$	$\sigma_b^2 + R\sigma_{\ell e}^2$	$\sigma_b^2 + R\sigma_{\ell e}^2$
E x L/G	$(e-1)(\ell-g)$	$\sigma_{b(\ell/g)}^2 + R\sigma_{\ell/ge}^2$	$\sigma_{b(\ell/g)}^2 + R\sigma_{\ell/ge}^2$
E x L in BC <sub>1</sub> <sup>b</sup>	$(e-1)(\ell_1-1)$	$\sigma_{b(1)}^2 + R\sigma_{\ell(1)e}^2$	$\sigma_{b(1)}^2 + R\sigma_{\ell(1)e}^2$
E x L in BC <sub>2</sub>	$(e-1)(\ell_2-1)$	$\sigma_{b(2)}^2 + R\sigma_{\ell(2)e}^2$	$\sigma_{b(2)}^2 + R\sigma_{\ell(2)e}^2$
E x L in BC <sub>3</sub>	$(e-1)(\ell_3-1)$	$\sigma_{b(3)}^2 + R\sigma_{\ell(3)e}^2$	$\sigma_{b(3)}^2 + R\sigma_{\ell(3)e}^2$
E x L in BC <sub>4</sub>	$(e-1)(\ell_4-1)$	$\sigma_{b(4)}^2 + R\sigma_{\ell(4)e}^2$	$\sigma_{b(4)}^2 + R\sigma_{\ell(4)e}^2$
E x L in BC <sub>5</sub>	$(e-1)(\ell_5-1)$	$\sigma_{b(5)}^2 + R\sigma_{\ell(5)e}^2$	$\sigma_{b(5)}^2 + R\sigma_{\ell(5)e}^2$
E x Parent	$(e-1)(\ell_p-1)$	$\sigma_{b(p)}^2 + R\sigma_{\ell(p)e}^2$	$\sigma_{b(p)}^2 + R\sigma_{\ell(p)e}^2$
E x G	$(e-1)(g-1)$	$\sigma_{b(g)}^2 + R\sigma_{ge}^2$	$\sigma_{b(g)}^2 + R\sigma_{ge}^2$
Error	$e(r-1)(\ell-1)$	$\sigma_b^2$	$\sigma_b^2$

<sup>a</sup>e = locations or environments, r = replications,  $\ell$  = lines, and g = generations.

<sup>b</sup>Amsoy 71 population only.

## RESULTS

Analyses of variance for each location in 1982 and in 1983 indicated significant ( $P<0.05$ ) differences among lines for both the Amsoy 71 and Century crosses for all traits (Tables 4, 5, 6, and 7). Variation due to generations and lines within generations was partitioned from the variation among all lines. There were significant ( $P<0.01$ ) differences for generations in both crosses at each location for all traits in 1982 and for yield, maturity, and lodging in 1983.

In the analyses of variance combined across locations within years, there were significant ( $P<0.01$ ) differences among lines for all traits in both crosses (Tables 8, 9, 10, and 11). Yield was the only trait for which there was a significant ( $P<0.05$ ) difference among generations in both crosses in both years. Generations did not differ significantly for maturity or lodging in 1982 or for height in 1983 in either cross.

The analyses of variance combined across all environments indicated significance ( $P<0.01$ ) for lines in both crosses for all traits (Tables 12 and 13). In the Amsoy 71 cross, generations were significantly different for all traits except height. Lines within the  $BC_1$  generation were significantly ( $P<0.05$ ) different for all traits, except height. Lines within the  $BC_2$ ,  $BC_3$ ,  $BC_4$ , and  $BC_5$  generations differed significantly for all traits. Generations were significantly ( $P<0.01$ ) different for yield, maturity, and lodging, but not for height (Table 12). In the Century cross, lines

Table 4. Analyses of variance for four traits of lines from the Amsoy 71 cross at individual locations in 1982

Sources of variation	df	Mean squares							
		Ames				Burkey			
		Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
Replications	1	7668**	0.4	0.1	13	3652**	21.7**	6.6**	83
Lines (L)	325	1584**	28.3**	0.9**	76**	1316**	8.6**	0.2**	56**
L/Generation	320	1278**	26.8**	0.7**	71**	1177**	8.5**	0.2**	54**
L in BC <sub>1</sub>	9	2477**	34.0**	0.7**	120**	1877**	8.2**	0.3*	37
L in BC <sub>2</sub>	50	2155**	49.6**	1.1**	126**	1570**	12.1**	0.2**	65**
L in BC <sub>3</sub>	76	1587**	36.0**	1.0**	56**	1489**	9.8**	0.2*	56**
L in BC <sub>4</sub>	84	803**	20.7**	0.4**	62**	1071**	7.7**	0.2*	63**
L in BC <sub>5</sub>	87	983**	14.5**	0.5**	62**	781**	7.0**	0.2	42
Amsoy 71	14	378	3.7	0.1	26	719*	2.6	0.2	30
Generations	5	21202**	124.6**	13.9**	446**	10205**	13.2**	1.4**	183**
Error	325	448	3.2	0.2	35	398	2.1	0.1	35
C.V. (%)		10.3	11.9	21.5	5.7	9.8	4.7	13.1	5.6

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 5. Analyses of variance for four traits of lines from the Century cross at individual locations in 1982

Sources of variation	df	Mean squares							
		Ames				Burkey			
		Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
Replications	1	77	0	0.1	28	1141	27**	0.0	25
Lines (L)	326	1380**	19**	0.4**	44**	1186**	7**	0.2*	61**
L/Generation	322	1257**	19**	0.3**	44**	997**	7**	0.2	61**
L in BC <sub>2</sub>	50	1952**	34**	0.5**	78**	1660**	10**	0.1	62**
L in BC <sub>3</sub>	73	1527**	26**	0.3**	52**	930**	8**	0.1	65**
L in BC <sub>4</sub>	91	1211**	17**	0.2**	37**	915**	7**	0.2	65**
L in BC <sub>5</sub>	97	825**	8**	0.2**	33**	817**	6**	0.2*	56**
Century	11	504	2	0.0	7	677	3	0.1	29
Generations	4	11259**	36**	5.7**	19	16453**	9**	0.7**	89**
Error	326	532	2	0.1	18	384	2	0.1	26
C.V. (%)		9.4	8.2	16.3	4.5	8.9	5.0	13.4	5.5

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6. Analyses of variance for four traits of lines from the Amsoy 71 cross at individual locations in 1983

Sources of variation	df	Mean squares							
		Ames				Knierim			
		Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
Replications	1	81643**	0.2	0.4	2705**	90581**	940**	7.6**	6240**
Lines (L)	325	1750**	24.0**	0.4**	88**	922**	14**	0.4**	136
L/Generation	320	1592**	21.8**	0.3**	87**	817**	14**	0.3**	137
L in BC <sub>1</sub>	9	1154	54.6**	0.8**	230**	983	16**	0.4**	91
L in BC <sub>2</sub>	50	1234	43.2**	0.7**	110**	803	24**	0.5**	135
L in BC <sub>3</sub>	76	1972**	32.1**	0.4**	73**	1065**	18**	0.5**	270**
L in BC <sub>4</sub>	84	1850**	15.5**	0.2**	97**	714	11**	0.2**	100
L in BC <sub>5</sub>	87	1442**	6.5**	0.2**	71**	740	8**	0.2**	73
Amsoy 71	14	436	1.0	0.1	29	521	3	0.1	70
Generations	5	11816**	163.1**	6.3**	161**	7623**	63**	4.8**	100
Error	325	910	2.0	0.1	44	626	4	0.1	128
C.V. (%)		12.2	9.0	13.2	7.4	9.4	8.9	11.1	11.4

\*\* Significant at the 0.01 probability level.

Table 7. Analyses of variance for four traits of lines from the Century cross at individual locations in 1983

Sources of variation		Mean squares							
		Ames				Knierim			
		Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
Replications	1	263	154**	9.2**	2162**	3697**	563**	0.4**	136*
Lines (L)	326	2347	18**	0.3**	123	710**	10**	0.2**	55**
L/Generation	322	2114	18**	0.2**	123	548**	10**	0.2**	55**
L in BC <sub>2</sub>	50	2288	42**	0.4**	135	740**	15**	0.3**	72**
L in BC <sub>3</sub>	73	1984	25**	0.2**	123	596**	15**	0.2**	58**
L in BC <sub>4</sub>	91	1789	15**	0.1**	133	495*	9**	0.1**	56**
L in BC <sub>5</sub>	97	2481	5**	0.1**	116	509*	6**	0.1**	47*
Century	11	1639	2	0.1	54	151	3	0.0	15
Generations	4	21054**	36**	8.0**	111	13732**	17**	4.0**	68
Error	326	2048	1	0.1	107	352	3	0.1	33
C.V. (%)		15.6	7.1	12.8	12.9	6.8	7.5	9.3	6.8

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.



Table 8. Analysis of variance for four traits of lines from the Amsoy 71 cross combined across locations in 1982

Sources of variation	df	Mean squares			
		Yield	Maturity	Lodging	Height
Locations (E)	1	1514	85695**	111.8*	2152*
Replications(R)/E	2	5660	11	3.3	48
Lines (L)	325	2332**	29**	0.7**	89**
L/Generation (G)	320	1898**	28**	0.5**	82**
L in BC <sub>1</sub>	9	4105**	30	0.7**	46
L in BC <sub>2</sub>	50	3108**	49**	0.8	118*
L in BC <sub>3</sub>	76	2512**	37**	0.7*	85**
L in BC <sub>4</sub>	84	1323**	23**	0.2	85**
L in BC <sub>5</sub>	87	1171**	17**	0.4	68**
Parent	14	798*	4	0.1	26
Generations	5	30090**	102	11.8	530
E x L	325	568**	8**	0.4**	42*
E x L/G	320	556**	7**	0.4**	42*
E x L in BC <sub>1</sub>	9	249	12**	0.3	111**
E x L in BC <sub>2</sub>	50	618*	13**	0.6**	73**
E x L in BC <sub>3</sub>	76	564*	9**	0.4**	27
E x L in BC <sub>4</sub>	84	551	6**	0.3**	40
E x L in BC <sub>5</sub>	87	593*	4**	0.3**	36
E x Parent	14	299	2	0.1	29
E x G	650	1317**	36**	3.5**	99*
Error	1303	423	3	0.2	35
C.V. (%)		10.1	7.1	17.0	5.6

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 9. Analysis of variance for four traits of lines of the  
Amsoy 71 cross combined across locations in 1983

Sources of variation	df	Mean squares			
		Yield	Maturity	Lodging	Height
Locations (E)	1	109017	15302*	120.1*	26831
Replications(R)/E	2	86113	470	4.0	4472
Lines (L)	325	1767**	33**	0.7**	142**
L/Generation (G)	320	1505**	31**	0.5**	142**
L in BC <sub>1</sub>	9	1395	58*	1.0*	231**
L in BC <sub>2</sub>	50	1320**	62**	1.0**	179**
L in BC <sub>3</sub>	76	2166**	44**	0.7**	198
L in BC <sub>4</sub>	84	1409	23**	0.3**	135**
L in BC <sub>5</sub>	87	1287**	11**	0.3**	85
Parent	14	573	1	0.1	56
Generations	5	18569**	206*	10.9**	122
E x L	325	904*	5**	0.2**	83
E x L/G	320	905*	5**	0.2**	82
E x L in BC <sub>1</sub>	9	741	12**	0.3*	90
E x L in BC <sub>2</sub>	50	717	6**	0.3**	67
E x L in BC <sub>3</sub>	76	871	6**	0.2*	145**
E x L in BC <sub>4</sub>	84	1162**	4*	0.1	62
E x L in BC <sub>5</sub>	87	895	3	0.1	60
E x Parent	14	383	3	0.1	43
E x G	5	871	20**	0.1	139
Error	650	768	3	0.1	86
C.V. (%)		10.8	9.1	12.0	9.8

\*,\*\* Significant at the 0.05 and 0.01 probability levels,  
respectively.

Table 10. Analysis of variance for four traits of lines from the Century cross combined across locations in 1982

Sources of variation	df	Mean squares			
		Yield	Maturity	Lodging	Height
Locations (E)	1	187250**	57072**	152.8**	23
Replications (R)/E	2	559	13	0.1	27
Lines (L)	326	1794**	20**	0.3**	66**
L/Generation (G)	322	1478**	20**	0.3**	66**
L in BC <sub>2</sub>	50	2698**	36**	0.4*	100**
L in BC <sub>3</sub>	73	1789**	28**	0.3**	73*
L in BC <sub>4</sub>	91	1228	19**	0.2**	65**
L in BC <sub>5</sub>	97	928	10**	0.3	48
Parent	11	800	2	0.1	16
Generations	4	27229**	16	4.9	88**
E x L	326	772**	6**	0.2**	39**
E x L/G	322	776**	5**	0.2**	40**
E x L in BC <sub>2</sub>	50	914**	9**	0.2**	40**
E x L in BC <sub>3</sub>	73	668*	6**	0.2*	44**
E x L in BC <sub>4</sub>	91	899**	5**	0.2	37**
E x L in BC <sub>5</sub>	97	715**	3*	0.2**	41**
E x Parent	11	382	4	0.1	20
E x G	4	482	29**	1.4**	19
Error	652	458	2	0.1	22
C.V. (%)		9.2	6.2	14.7	5.0

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 11. Analysis of variance for four traits of lines from the Century cross combined across locations in 1983

Sources of variation	df	Mean squares			
		Yield	Maturity	Lodging	Height
Locations (E)	1	76391*	14097*	18.2	5528
Replications(R)/E	2	1980	358	4.8	1149
Lines (L)	326	1980**	23**	0.4**	115**
L/Generation (G)	322	1583**	24**	0.3**	114**
L in BC <sub>2</sub>	50	1793*	49**	0.6**	131*
L in BC <sub>3</sub>	73	1560	35**	0.4**	121*
L in BC <sub>4</sub>	91	1362	19**	0.2**	124**
L in BC <sub>5</sub>	97	1779**	9**	0.2**	101*
Parent	11	800	2	0.1	16
Generations	4	33975**	22	11.6**	130
E x L	326	1076	5**	0.1	64
E x L/G	322	1080	5**	0.1	64
E x L in BC <sub>2</sub>	50	1236	8**	0.1*	76
E x L in BC <sub>3</sub>	73	1020	5**	0.1	60
E x L in BC <sub>4</sub>	91	922	5**	0.1	65
E x L in BC <sub>5</sub>	97	1211	3	0.1	62
E x Parent	11	382	4	0.1	20
E x G	4	811	32**	0.4**	48
Error	652	1200	2	0.1	70
C.V. (%)		12.2	7.5	11.0	10.2

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 12. Analysis of variance for four traits of lines from the Amsoy 71 cross combined across four environments

Sources of variation	df	Mean squares			
		Yield	Maturity	Lodging	Height
Environments (E)	3	619324*	36969**	106.3**	37099*
Replications(R)/E	4	45886	241	3.7	2260
Lines (L)	325	2958**	57**	1.1**	169**
L/Generation (G)	320	2271**	54**	0.7**	167**
L in BC <sub>1</sub>	9	3834**	74**	1.1*	165
L in BC <sub>2</sub>	50	2971**	100**	1.4**	217**
L in BC <sub>3</sub>	76	3452**	76**	1.1**	205**
L in BC <sub>4</sub>	84	1569**	41**	0.4**	174**
L in BC <sub>5</sub>	87	1675**	25**	0.6**	117**
Parent	14	260	4	0.1	39
Generation	5	46950**	291**	22.6**	319
E x L	975	871**	6**	0.3**	63
E x L/G	960	864**	6**	0.3**	61
E x L in BC <sub>1</sub>	27	885	13**	0.4**	104*
E x L in BC <sub>2</sub>	150	931**	10**	0.4**	73**
E x L in BC <sub>3</sub>	228	887**	6**	0.3**	83**
E x L in BC <sub>4</sub>	252	959**	5**	0.2**	49
E x L in BC <sub>5</sub>	261	757**	4**	0.2**	44
E x Parent	42	598	2	0.1	38
E x G	15	1299**	25**	1.2**	190**
Error	1300	596	3	0.2	60
C.V. (%)		10.6	8.0	14.4	7.8

\*,\*\* Significant at the 0.05 and 0.01 probability levels, respectively.

Table 13. Analysis of variance for four traits for lines from the Century cross combined across four environments

Sources of variation	df	Mean squares			
		Yield	Maturity	Lodging	Height
Environments (E)	3	646396**	27758**	57.7**	30094**
Replications(R)/E	4	1270	185	2.4	588
Lines (L)	326	2653**	40**	0.6**	130**
L/Generation (G)	322	1929**	40**	0.5**	130**
L in BC <sub>2</sub>	50	3181**	77**	0.8**	170**
L in BC <sub>3</sub>	73	2290**	58**	0.6**	137**
L in BC <sub>4</sub>	91	1677**	35**	0.4**	151**
L in BC <sub>5</sub>	97	1387	16**	0.3**	96**
Parent	11	697	2	0.1	18
Generations	4	60931**	35	15.7**	154**
E x L	978	990**	5**	0.1**	51*
E x L/G	966	996**	5**	0.1**	51*
E x L in BC <sub>2</sub>	150	1153**	8**	0.2**	59**
E x L in BC <sub>3</sub>	219	916**	5**	0.1**	54**
E x L in BC <sub>4</sub>	273	911**	4**	0.1	47**
E x L in BC <sub>5</sub>	291	1082**	3**	0.1**	52**
E x Parent	33	758	3	0.1	29
E x G	12	522	21**	0.9**	44
Error	1304	829	2	0.1	46
C.V. (%)		11.2	6.8	13.0	6.6

\*, \*\* Significant at the 0.05 and 0.01 probability levels, respectively.

within the  $BC_2$ ,  $BC_3$ , and  $BC_4$  generations were significantly different for all traits. Lines within the  $BC_5$  generation differed significantly for maturity, lodging, and height, but not for yield. Generations differed significantly for all traits, except maturity (Table 13).

Environments were significantly ( $P < 0.05$ ) different for yield, lodging, and height, but not maturity in the Amsoy 71 cross (Table 12). In the Century cross, environments differed significantly ( $P < 0.01$ ) for all traits (Table 13). The variation due to environments contains variation due to plot type as well as that due to locations and years. The differences among environments for yield may be due, at least in part, to the plot differences. The mean yield in 1982 of all lines in the Amsoy 71 cross was  $204 \text{ g} \cdot \text{m}^{-2}$  and of the Century cross was  $232 \text{ g} \cdot \text{m}^{-2}$ . In 1983, the yield of lines in the Amsoy 71 cross was  $256 \text{ g} \cdot \text{m}^{-2}$  and of the Century cross was  $282 \text{ g} \cdot \text{m}^{-2}$ . It is not likely that maturity, lodging, or height would be affected by plot size or shape. In both crosses, there were significant ( $P < 0.05$ ) line x environment interactions for yield, maturity, and lodging.

The coefficients of variation for each trait were similar in magnitude between the Amsoy 71 and Century crosses (Tables 4 through 13). The coefficients for each trait also were similar among the individual locations, combined locations, and the combined analysis. The coefficients of variation for lodging were almost always higher than for other traits in both crosses, while those for maturity and height were generally lowest.

The rate at which the means of the backcross generations approach the recurrent parent mean is useful in deciding the optimal number of backcrosses when using G. soja as the donor parent. In the Amsoy 71 cross, mean yield increased significantly ( $P < 0.05$ ) from the  $BC_1$  to the  $BC_2$ , and from the  $BC_2$  to the  $BC_3$  generations in all environments (Tables 14 and 15). The  $BC_3$  generation was significantly lower yielding than the  $BC_4$  in 1982, but not in 1983 (Table 16). The mean yield of the  $BC_4$  generation was not significantly lower than the yield of the  $BC_5$  in 1982 or combined across years, but was in 1983 (Tables 16 and 17). The mean yield of the  $BC_4$  and  $BC_5$  generations were not significantly different from Amsoy 71 in 1983. The mean yield of the recurrent parent was significantly higher than the mean of any backcross generation in 1982 and when the means were combined across years.

In the Century cross, mean yield increased significantly ( $P < 0.05$ ) from the  $BC_2$  to the  $BC_3$ , and from the  $BC_3$  to the  $BC_4$  generations at all locations and combined across locations and across years (Tables 18, 19, 20, and 21). The mean yield of the  $BC_4$  generation was not significantly different from that of the  $BC_5$  at individual locations, or combined across locations or across years. The mean yields of the  $BC_4$  and  $BC_5$  generations were not significantly different from Century in 1983, but were lower yielding in 1982 and when combined across years.

A breeder is interested in knowing how much the yield would be increased with each backcross to the adapted, recurrent parent. In



Table 14. Mean values for the backcross generations and recurrent parent from the Amsoy 71 cross at individual locations in 1982

Generation	Trait							
	Ames				Burkey			
	Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
	(g·m <sup>-2</sup> )	(days)	(score)	(cm)	(g·m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>1</sub>	165	19	2.9 <sub>B</sub> <sup>a</sup>	96	172	32 <sub>F</sub>	3.0 <sub>B</sub>	105 <sub>BCDE</sub>
BC <sub>2</sub>	186	16 <sub>F</sub>	2.8 <sub>A</sub>	102	193	31 <sub>CDE</sub>	3.0 <sub>A</sub>	105 <sub>AC</sub>
BC <sub>3</sub>	203	15 <sub>DE</sub>	2.3	105 <sub>DEF</sub>	200	31 <sub>BDE</sub>	2.8 <sub>DEF</sub>	106 <sub>ABD</sub>
BC <sub>4</sub>	214 <sub>E</sub>	14 <sub>CE</sub>	2.0 <sub>EF</sub>	105 <sub>CEF</sub>	208 <sub>E</sub>	31 <sub>BCE</sub>	2.7 <sub>CEF</sub>	108 <sub>ACE</sub>
BC <sub>5</sub>	212 <sub>D</sub>	15 <sub>CD</sub>	2.0 <sub>DF</sub>	105 <sub>CDF</sub>	209 <sub>D</sub>	31 <sub>BCD</sub>	2.8 <sub>CDF</sub>	108 <sub>AD</sub>
Amsoy 71	227	17 <sub>B</sub>	1.9 <sub>DE</sub>	107 <sub>CDE</sub>	221	32 <sub>A</sub>	2.8 <sub>CDE</sub>	110 <sub>E</sub>

<sup>a</sup>Means with subscript A do not differ from BC<sub>1</sub>, B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Amsoy 71 at the 0.05 probability level based on pairwise comparisons.

Table 15. Mean values for the backcross generations and recurrent parent from the Amsoy 71 cross at individual locations in 1983

Generation	Trait							
	Ames				Knierim			
	Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
	(g·m <sup>-2</sup> )	(days)	(score)	(cm)	(g·m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>1</sub>	208	21	3.3	92 <sub>BDEF</sub> <sup>a</sup>	237	26	3.7 <sub>B</sub>	102 <sub>BCDEF</sub>
BC <sub>2</sub>	237	17 <sub>F</sub>	2.9	90 <sub>ACDE</sub>	255	23 <sub>DE</sub>	3.5 <sub>A</sub>	98 <sub>ACDEF</sub>
BC <sub>3</sub>	246 <sub>D</sub>	15 <sub>DE</sub>	2.6	88 <sub>BD</sub>	263 <sub>F</sub>	22 <sub>DE</sub>	3.2	100 <sub>ABDEF</sub>
BC <sub>4</sub>	247 <sub>C</sub>	15 <sub>CE</sub>	2.4 <sub>EF</sub>	90 <sub>ABC</sub>	270 <sub>EF</sub>	22 <sub>BCE</sub>	3.0 <sub>EF</sub>	98 <sub>ABCEF</sub>
BC <sub>5</sub>	256 <sub>F</sub>	15 <sub>CD</sub>	2.4 <sub>DF</sub>	90 <sub>ABD</sub>	271 <sub>DF</sub>	22 <sub>BCD</sub>	3.1 <sub>DF</sub>	99 <sub>ABCDF</sub>
Amsoy 71	259 <sub>E</sub>	16 <sub>B</sub>	2.4 <sub>DE</sub>	94 <sub>A</sub>	271 <sub>CDE</sub>	24	3.1 <sub>DE</sub>	99 <sub>ABCDE</sub>

<sup>a</sup>Means with subscript A do not differ from BC<sub>1</sub>, B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Amsoy 71 at the 0.05 probability level based on pairwise comparisons.

Table 16. Mean values for the backcross generations and recurrent parent from the Amsoy 71 cross across locations for individual years

Generation	Trait							
	1982				1983			
	Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
	(g·m <sup>-2</sup> )	(days)	(score)	(cm)	(g·m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>1</sub>	169	26 <sub>BF<sup>a</sup></sub>	3.0 <sub>BCDEF</sub>	101 <sub>B</sub>	223	24	3.5	97 <sub>CEF</sub>
BC <sub>2</sub>	189	24 <sub>ACDEF</sub>	2.9 <sub>ACF</sub>	104 <sub>ACD</sub>	246	20 <sub>CDF</sub>	3.2	94 <sub>CDEF</sub>
BC <sub>3</sub>	201	23 <sub>BDEF</sub>	2.5 <sub>ABDEF</sub>	105 <sub>BDEF</sub>	255 <sub>D</sub>	19 <sub>BDEF</sub>	2.9	94 <sub>ABDEF</sub>
BC <sub>4</sub>	211 <sub>E</sub>	23 <sub>BCEF</sub>	2.4 <sub>ACEF</sub>	106 <sub>BCEF</sub>	259 <sub>CF</sub>	19 <sub>BCEF</sub>	2.7 <sub>EF</sub>	94 <sub>BCEF</sub>
BC <sub>5</sub>	211 <sub>D</sub>	23 <sub>BCDF</sub>	2.4 <sub>ACDF</sub>	106 <sub>CDF</sub>	263 <sub>F</sub>	19 <sub>CDF</sub>	2.7 <sub>DF</sub>	94 <sub>ABCDF</sub>
Amsoy 71	224	25 <sub>ABCDE</sub>	2.3 <sub>ABCDE</sub>	109 <sub>CDE</sub>	265 <sub>F</sub>	20 <sub>BCDE</sub>	2.7 <sub>DE</sub>	96 <sub>ABCDE</sub>

<sup>a</sup>Means with subscript A do not differ from BC<sub>1</sub>, B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Amsoy 71 at the 0.05 probability level based on pairwise comparisons.

Table 17. Mean values for the backcross generations and recurrent parent from the Amsoy 71 cross across four environments

Generation	% <u>G. max</u> germplasm	Trait			
		Yield	Maturity	Lodging	Height
		(g·m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>1</sub>	75	196 (80) <sup>b</sup>	25	3.2 <sub>Ba</sub>	99 <sub>BCDEF</sub>
BC <sub>2</sub>	87	218 (89)	22 <sub>F</sub>	3.1 <sub>A</sub>	99 <sub>ACDE</sub>
BC <sub>3</sub>	94	228 (93)	21 <sub>DE</sub>	2.7 <sub>F</sub>	100 <sub>ABDEF</sub>
BC <sub>4</sub>	97	235 <sub>E</sub> (96)	21 <sub>CE</sub>	2.6 <sub>EF</sub>	100 <sub>ABCEF</sub>
BC <sub>5</sub>	99	237 <sub>D</sub> (97)	21 <sub>CD</sub>	2.6 <sub>DF</sub>	100 <sub>ABCDF</sub>
Amsoy 71	100	245	22	2.5 <sub>CDE</sub>	102 <sub>ACDE</sub>

<sup>a</sup>Means with subscript A do not differ from BC<sub>1</sub>, B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Amsoy 71 at the 0.05 probability level based on pairwise comparisons.

<sup>b</sup>Numbers in parentheses are yield expressed as a percentage of the mean yield of Amsoy 71.

Table 18. Mean values for the backcross generations and recurrent parent from the Century cross at individual locations in 1982

Generation	Trait							
	Ames				Burkey			
	Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
	(g·m <sup>-2</sup> )	(days)	(score)	(cm)	(g·m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>2</sub>	228	19	2.4	93 <sub>CDEF</sub> <sup>a</sup>	200	31 <sub>C</sub>	2.9 <sub>C</sub>	94 <sub>CDEF</sub>
BC <sub>3</sub>	240	18 <sub>EF</sub>	2.2	94 <sub>BDEF</sub>	215	31 <sub>BDE</sub>	2.8 <sub>BEF</sub>	94 <sub>BDF</sub>
BC <sub>4</sub>	249 <sub>E</sub>	18 <sub>F</sub>	2.0 <sub>E</sub>	94 <sub>BCEF</sub>	225 <sub>EF</sub>	31 <sub>CE</sub>	2.7 <sub>EF</sub>	94 <sub>BCF</sub>
BC <sub>5</sub>	250 <sub>D</sub>	18 <sub>CF</sub>	1.9 <sub>D</sub>	93 <sub>BCDF</sub>	228 <sub>DF</sub>	31 <sub>CD</sub>	2.7 <sub>CDF</sub>	92 <sub>B</sub>
Century	261	18 <sub>CDE</sub>	1.8	95 <sub>BCDE</sub>	232 <sub>DE</sub>	32	2.6 <sub>CDE</sub>	95 <sub>BCD</sub>

<sup>a</sup> Means with subscript B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Century at the 0.05 probability level based on pairwise comparisons.

Table 19. Mean values for the backcross generations and recurrent parent from the Century cross at individual locations in 1983

Generation	Trait							
	Ames				Knierim			
	Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
	(g·m <sup>-2</sup> )	(days)	(score)	(cm)	(g·m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>2</sub>	268	18	2.7	82 <sub>CDEF</sub> <sup>a</sup>	256	23 <sub>CEF</sub>	2.8	84 <sub>CDEF</sub>
BC <sub>3</sub>	285 <sub>F</sub>	17 <sub>EF</sub>	2.3	80 <sub>BDEF</sub>	273	23 <sub>BF</sub>	2.5	85 <sub>BDEF</sub>
BC <sub>4</sub>	297 <sub>EF</sub>	17 <sub>F</sub>	2.2	80 <sub>BCEF</sub>	279 <sub>E</sub>	24 <sub>EF</sub>	2.4	85 <sub>BCF</sub>
BC <sub>5</sub>	299 <sub>DF</sub>	17 <sub>CF</sub>	2.0	79 <sub>BCDF</sub>	281 <sub>D</sub>	24 <sub>BDF</sub>	2.3	84 <sub>BCF</sub>
Century	300 <sub>CDE</sub>	17 <sub>CDE</sub>	1.9	79 <sub>BCDE</sub>	291	24 <sub>BCDE</sub>	2.2	83 <sub>BCDE</sub>

<sup>a</sup> Means with subscript B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Century at the 0.05 probability level based on pairwise comparisons.

Table 20. Mean values for the backcross generations and recurrent parent from the Century cross across locations for individual years

Generation	Trait							
	1982				1983			
	Yield	Maturity	Lodging	Height	Yield	Maturity	Lodging	Height
	(g·m <sup>-2</sup> )	(days)	(score)	(cm)	(g·m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>2</sub>	214	25 <sub>CDEF<sup>a</sup></sub>	2.6 <sub>CF</sub>	93 <sub>CDEF</sub>	262	21 <sub>CDEF</sub>	2.7	83 <sub>CDF</sub>
BC <sub>3</sub>	228	24 <sub>BDEF</sub>	2.5 <sub>BDEF</sub>	94 <sub>BDF</sub>	279	20 <sub>BDEF</sub>	2.4	83 <sub>BDEF</sub>
BC <sub>4</sub>	237 <sub>E</sub>	25 <sub>BCEF</sub>	2.3 <sub>CEF</sub>	94 <sub>BCF</sub>	288 <sub>EF</sub>	20 <sub>BCEF</sub>	2.3 <sub>EF</sub>	83 <sub>BCEF</sub>
BC <sub>5</sub>	239 <sub>D</sub>	24 <sub>BCDF</sub>	2.3 <sub>CDF</sub>	93 <sub>B</sub>	290 <sub>DF</sub>	20 <sub>BCDF</sub>	2.2 <sub>DF</sub>	81 <sub>BDF</sub>
Century	246	25 <sub>BCDE</sub>	2.2 <sub>BCDE</sub>	95 <sub>BCD</sub>	296 <sub>DE</sub>	20 <sub>BCDE</sub>	2.1 <sub>DE</sub>	81 <sub>BCDE</sub>

<sup>a</sup>Means with subscript B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Century at the 0.05 probability level based on pairwise comparisons.

Table 21. Mean values for the backcross generations and recurrent parent from the Century cross across four environments

Generation	% G. max germplasm	Trait			
		Yield	Maturity	Lodging	Height
		(g•m <sup>-2</sup> )	(days)	(score)	(cm)
BC <sub>2</sub>	88	238 (88) <sup>b</sup>	23 <sub>DEF</sub> <sup>a</sup>	2.7	88 <sub>CDF</sub>
BC <sub>3</sub>	94	253 (93)	22 <sub>DEF</sub>	2.5	88 <sub>BDF</sub>
BC <sub>4</sub>	97	262 <sub>E</sub> (97)	23 <sub>BCEF</sub>	2.3 <sub>EF</sub>	88 <sub>BCF</sub>
BC <sub>5</sub>	99	265 <sub>D</sub> (98)	23 <sub>BCDF</sub>	2.3 <sub>DF</sub>	87 <sub>F</sub>
Century	100	271	23 <sub>BCDE</sub>	2.1 <sub>DE</sub>	88 <sub>BCDE</sub>

<sup>a</sup>Means with subscript B do not differ from BC<sub>2</sub>, C do not differ from BC<sub>3</sub>, D do not differ from BC<sub>4</sub>, E do not differ from BC<sub>5</sub>, and F do not differ from Century at the 0.05 probability level based on pairwise comparisons.

<sup>b</sup>Numbers in parentheses are yield expressed as a percentage of the mean yield of Century.



both crosses, the increase in yield obtained with each additional backcross became progressively smaller (Figure 1). This is expected if additive effects are controlling yield because the percentage of adapted germplasm recovered with each additional backcross is only half as large as the percentage recovered with the previous backcross. Although the Century cross has a higher level of yield, both crosses had similar curves. The quadratic regression of yield on number of backcrosses was significant ( $P < 0.01$ ) for both populations.

It is also appropriate to compare yield of each generation with the percentage of adapted germplasm in these generations (Figure 2). Mean yield of each generation was calculated as a percentage of the yield of the recurrent parent. Yield regressed on percentage of adapted germplasm showed a significant linear but not quadratic response for both crosses. A slope of 0.75 was obtained for the Amsoy 71 cross and a slope of 0.93 for the Century cross (Figure 3).

A plant breeder is as concerned with extreme types as with means in a selection program. The usefulness of generation means is limited because they tell nothing about the range of values present among lines of each generation. With each additional backcross, plants lose half of their donor germplasm. As a result, there should be less variation among lines in the  $BC_5$  generation than among lines in earlier generations. This variation can be estimated by calculating genetic variance component estimates for the lines in each generation.

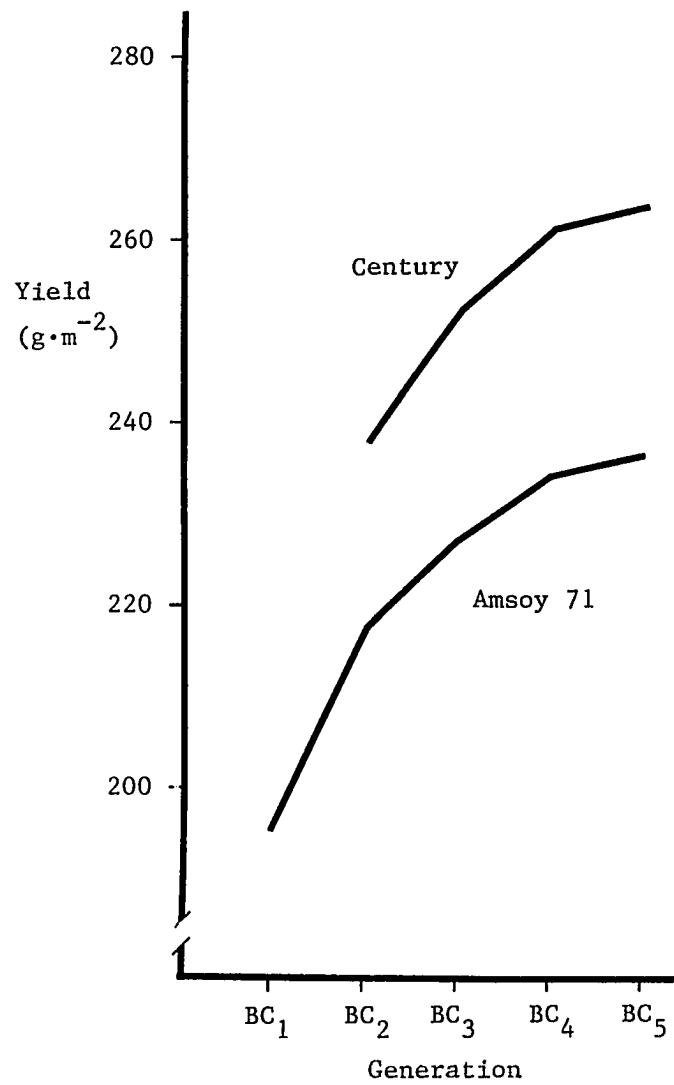


Figure 1. Mean yield of each backcross generation versus the number of backcross generations

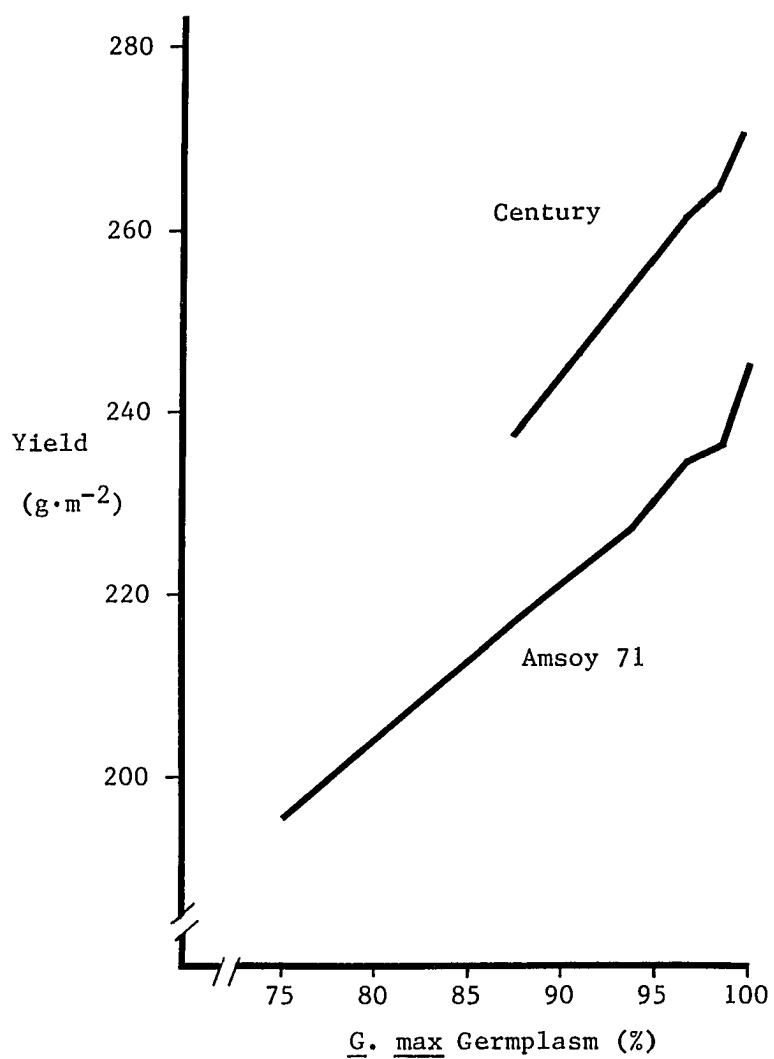


Figure 2. Mean yield of backcross generations and recurrent parents versus their percentage G. max germplasm

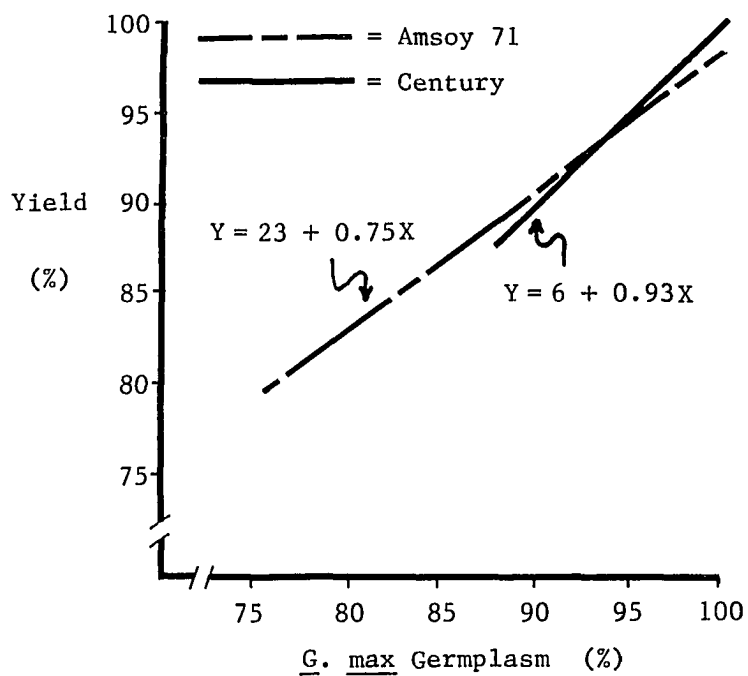


Figure 3. Yield of backcross generations, expressed as a percentage of the yield of the recurrent parent, regressed on the percentage of G. max germplasm in the backcross generations

The genetic variance of lines for yield in each generation decreased with successive backcrosses (Figure 4). The  $BC_3$  generation in the Amsoy 71 cross had greater variance than did the  $BC_2$  generation. This can be observed in the frequency distribution of lines in these two generations (Figure 5). Except for the  $BC_1$  generation in the Amsoy 71 cross, the distribution of lines in each generation in both crosses resembled a normal distribution, indicating randomness of lines with respect to yield (Figures 5 and 6). The  $BC_1$  generation of the Amsoy 71 cross was represented by only 10 lines, which explained why it did not have a normal distribution. The other generations were represented by a minimum of 51 lines, which is a large enough sample to obtain a continuous distribution. The distribution of the  $BC_4$  generation is almost identical to that of the  $BC_5$  generation in both crosses. The distribution of lines from the  $BC_4$  generation was similar to that of the lines from the  $BC_5$  generation in both crosses. Although lines in the  $BC_5$  generation contain only 1.6% G. soja germplasm, their distribution was much broader in both crosses than the distribution of the recurrent parent (Figures 5 and 6).

Nine out of the 10 lines in the  $BC_1$  generation of the Amsoy 71 population had a yield significantly ( $P < 0.05$ ) less than Amsoy 71 (Figure 5). One line was identified which yielded as well as Amsoy 71. Almost half of the lines in the  $BC_2$  generation of both populations had yields that were not significantly different from the recurrent parent (Figures 5 and 6). By the third backcross, a majority of the

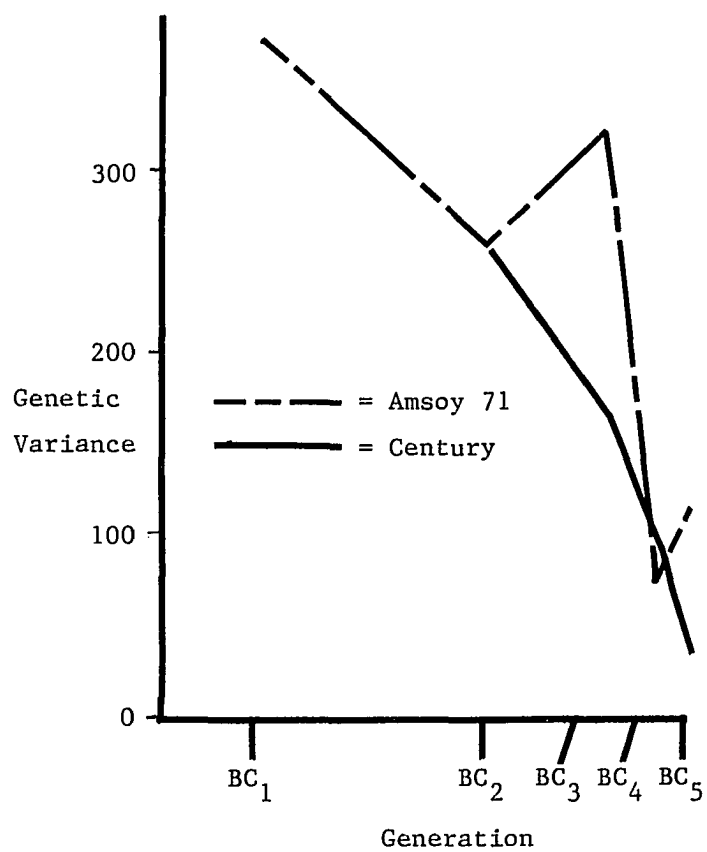


Figure 4. Genetic variance of yield versus the number of backcross generations

Figure 5. Frequency distributions of yields of the lines from each backcross generation and of the recurrent parent from the Amsoy 71 cross. Shaded areas denote segregates significantly ( $P < 0.05$ ) different from Amsoy 71 ( $\bar{x}$  = mean of the generation; s.d. = standard deviation)

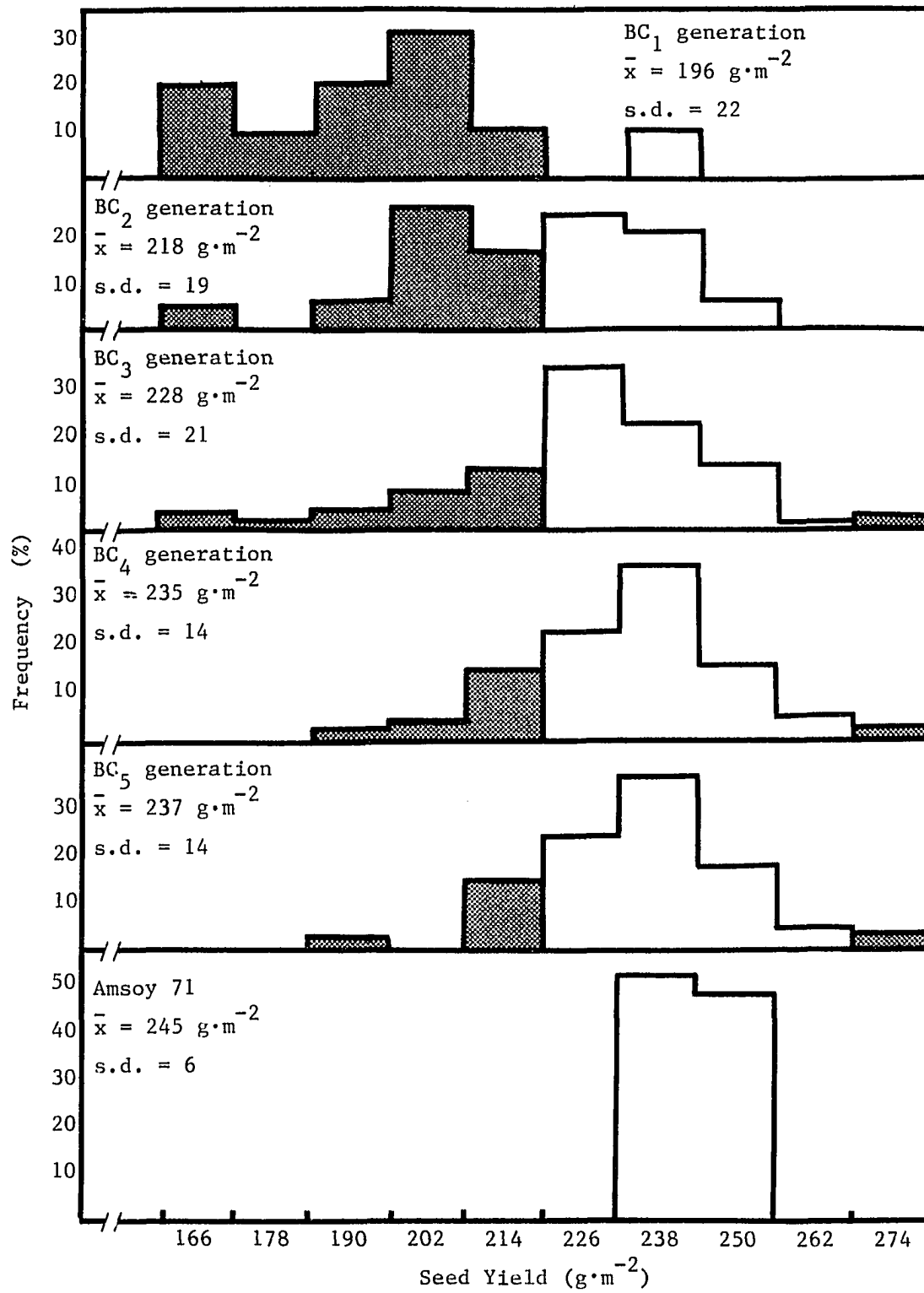
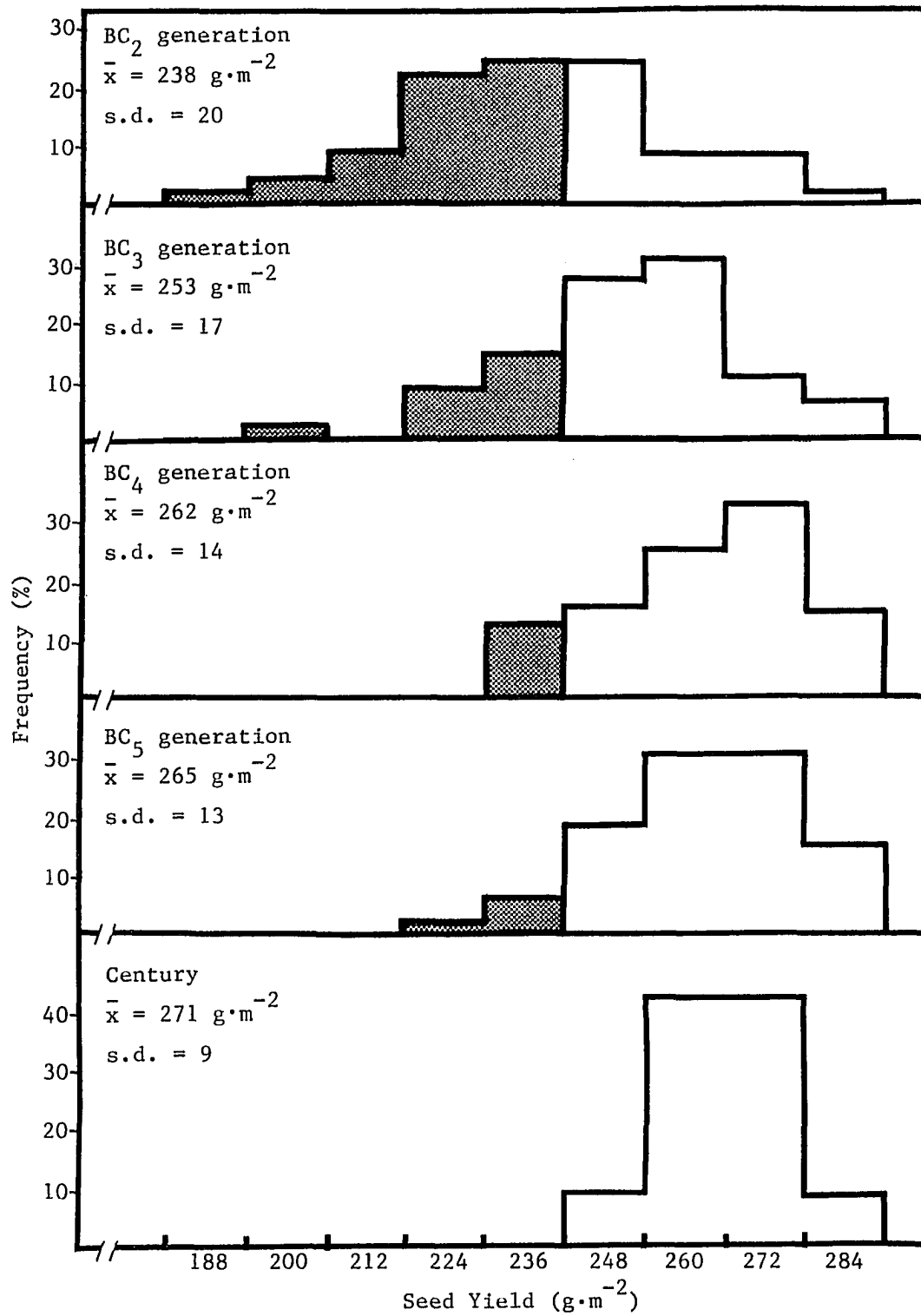




Figure 6. Frequency distributions of yields of the lines from each backcross generation and of the recurrent parent from the Century cross. Shaded areas denote segregates significantly ( $P < 0.05$ ) different from Century ( $\bar{x}$  = mean of the generation; s.d. = standard deviation)



lines were similar in yield to the recurrent parent. There were two lines in the  $BC_3$ , one line in the  $BC_4$ , and two lines in the  $BC_5$  generation in the Amsoy 71 cross that were significantly higher yielding than the recurrent parent. These lines averaged 11% higher in yield than Amsoy 71. The highest yielding line was 15% higher in yield than the recurrent parent. There were no lines in the Century cross in any generation that yielded more than Century.

The 10 highest yielding lines of the  $BC_2$  through  $BC_5$  generations were identified to determine the number of  $BC_1F_1$  plants from which these lines were derived. All the lines in the Amsoy 71 cross were derived from 46  $BC_1F_1$  plants and those in the Century cross were derived from 50  $BC_1F_1$  plants. The 40 highest yielding lines (10 from each of four generations) from the Amsoy 71 cross traced to 26 different  $BC_1F_1$  plants. No  $BC_1F_1$  plant was in the pedigree of more than three lines. The 40 highest yielding lines from the Century cross traced to 28 different  $BC_1F_1$  plants. One plant was in the pedigree of four high-yielding lines and two other plants were in the pedigree of three lines. This indicated that a wide array of  $BC_1F_1$  plants contributed to the highest yielding lines. No single  $BC_1F_1$  plant dominated the pedigree of these lines.

Selection for maturity was practiced on single  $BC_nF_2$  plants and on lines derived from these plants. The maturity dates of the two G. soja parents have been determined in a separate study (unpublished data). The maturity of PI 424001 averaged 30 days earlier than Amsoy 71, and the maturity of PI 326581 averaged 15 days earlier than

Century. Although PI 424001 matured much earlier than Amsoy 71, the lines from the early backcross generations of the Amsoy 71 cross matured later than Amsoy 71 (Figure 7). The mean maturity of the BC<sub>1</sub> generation was significantly ( $P < 0.05$ ) later than Amsoy 71 at one location in 1982 (Table 14), at both locations in 1983 (Table 15), and combined across years (Table 17). By the second backcross, the mean maturity was within one day of Amsoy 71. The delayed maturity of the BC<sub>1</sub> lines may indicate transgressive segregates for maturity or may be caused by the limited number of lines (10) representing this generation.

There were no differences among the maturity dates of the backcross generations and the maturity of the recurrent parent in the Century cross (Table 21; Figure 7). At each location, the mean maturity date was never more than one day different from that of Century (Tables 18 and 19). At individual locations, generation means were significantly different from the mean of Century; however, when data were combined across locations, no differences existed (Table 20). The lack of significant differences between maturity dates of the lines containing less than 25% G. soja germplasm and the G. max parents indicated that selection was successful for this trait. Many of the lines discarded in 1982 had maturities earlier or later than their recurrent parent.

Selection was also practiced for lodging resistance, but was not as effective as for maturity. Mean lodging scores of the backcross generations decreased with decreasing percentages of G. soja germplasm (Figure 8). This trend toward decreasing lodging was

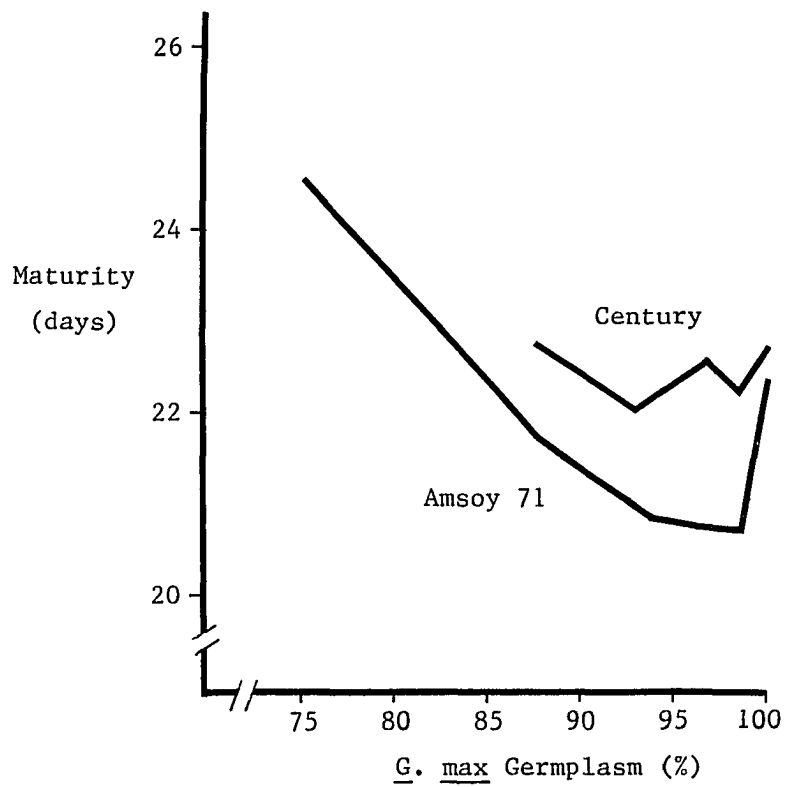


Figure 7. Mean maturity date of backcross generations and recurrent parents versus their percentage of G. max germplasm

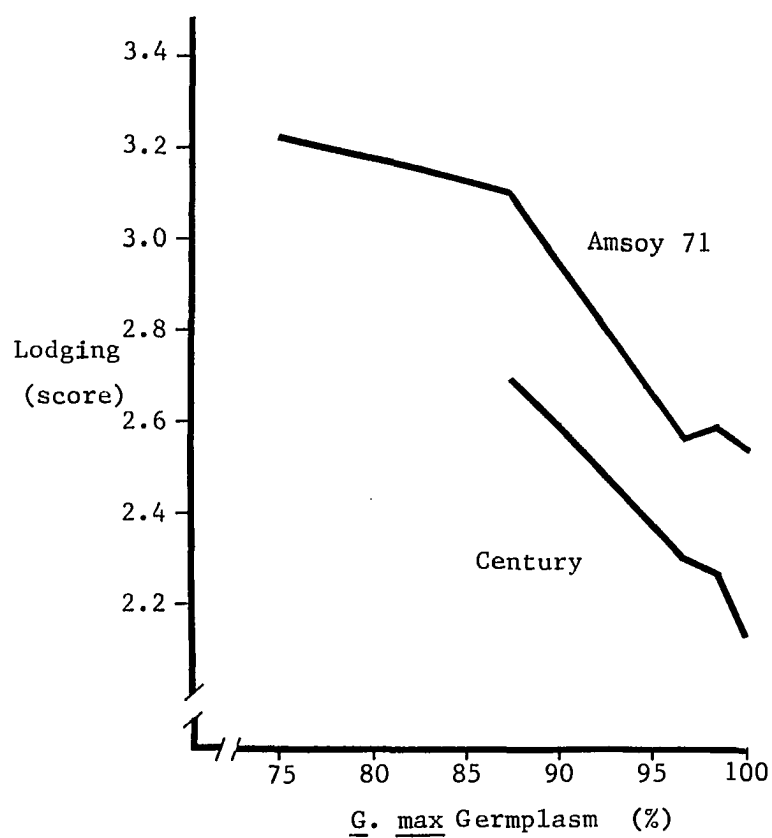


Figure 8. Mean lodging score of backcross generations and recurrent parents versus their percentage of G. max germplasm

observed at each location for both crosses (Tables 14, 15, 18, and 19). Amsoy 71 had less lodging resistance than Century and each backcross generation in the Amsoy 71 cross had a higher score than the same generations in the Century cross. In the Amsoy 71 cross, the lodging scores of the  $BC_3$  through  $BC_5$  generations were not significantly ( $P < 0.05$ ) different from the score of Amsoy 71 (Table 17). However, the scores were 0.1 or 0.2 higher than for Amsoy 71. The  $BC_2$  and  $BC_3$  generations had significantly more lodging than the recurrent parent in the Century cross (Table 21). By the fourth backcross, the mean lodging scores were only 0.2 greater than for Century.

G. soja has a prostrate growth habit; therefore, it has a lodging score of 5.0. Transgressive segregates for lodging resistance were rare in the Amsoy 71 cross (Figure 9) and did not exist in the Century cross (Figure 10). Some lines were obtained in the  $BC_1$  generation of the Amsoy 71 cross and in the  $BC_2$  generation of the Century cross that had lodging scores similar to the recurrent parent. By the  $BC_3$  generation in the Amsoy 71 cross and by the  $BC_4$  generation in the Century cross, a majority of the lines were similar to the recurrent parent for lodging.

Selection for height among the lines was effective because the generation means were similar to the height of the recurrent parent (Figure 11). The length of the longest branches of PI 424001 averaged 20 cm less than the height of Amsoy 71 (unpublished data). Without selection, lines having G. soja parentage would be expected to be

Figure 9. Frequency distributions of lodging of the lines from each backcross generation and of the recurrent parent from the Amsoy 71 cross. Shaded areas denote segregates significantly ( $P < 0.05$ ) different from Amsoy 71 ( $\bar{x}$  = mean of the generation; s.d. = standard deviation)



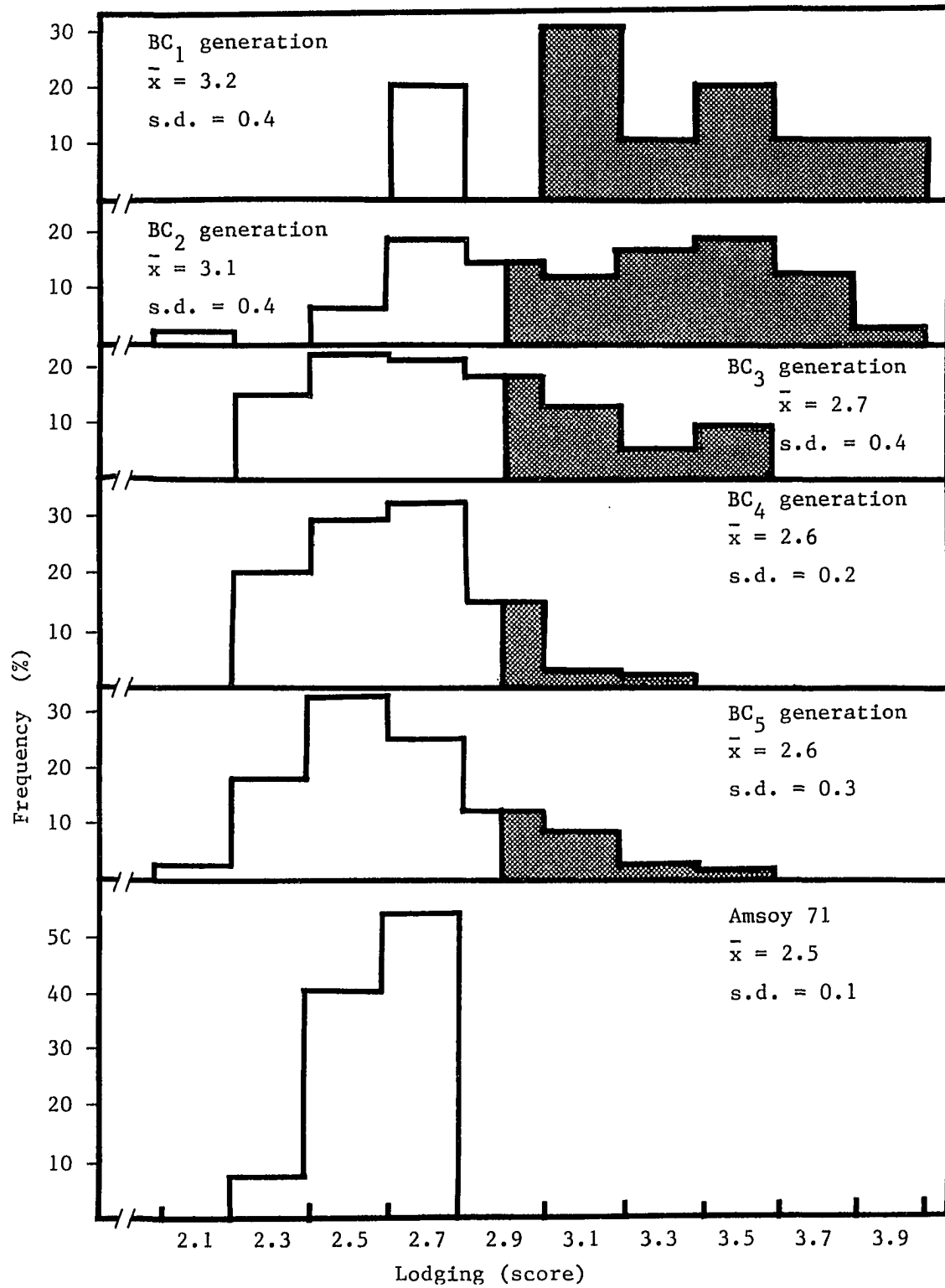
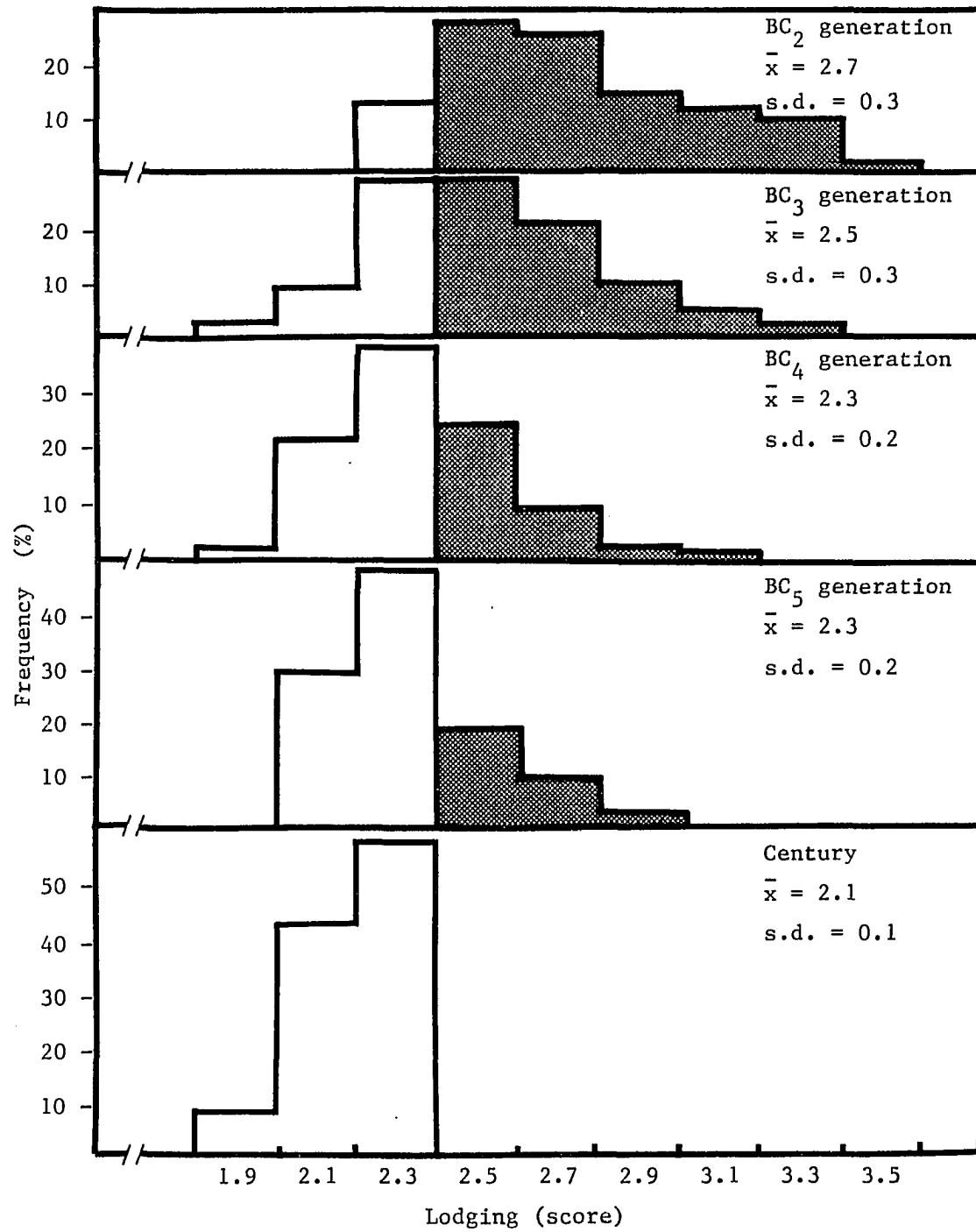


Figure 10. Frequency distributions of lodging of the lines from each backcross generation and of the recurrent parent from the Century cross. Shaded areas denote segregates significantly ( $P < 0.05$ ) different from Century ( $\bar{x}$  = mean of the generation; s.d. = standard deviation)



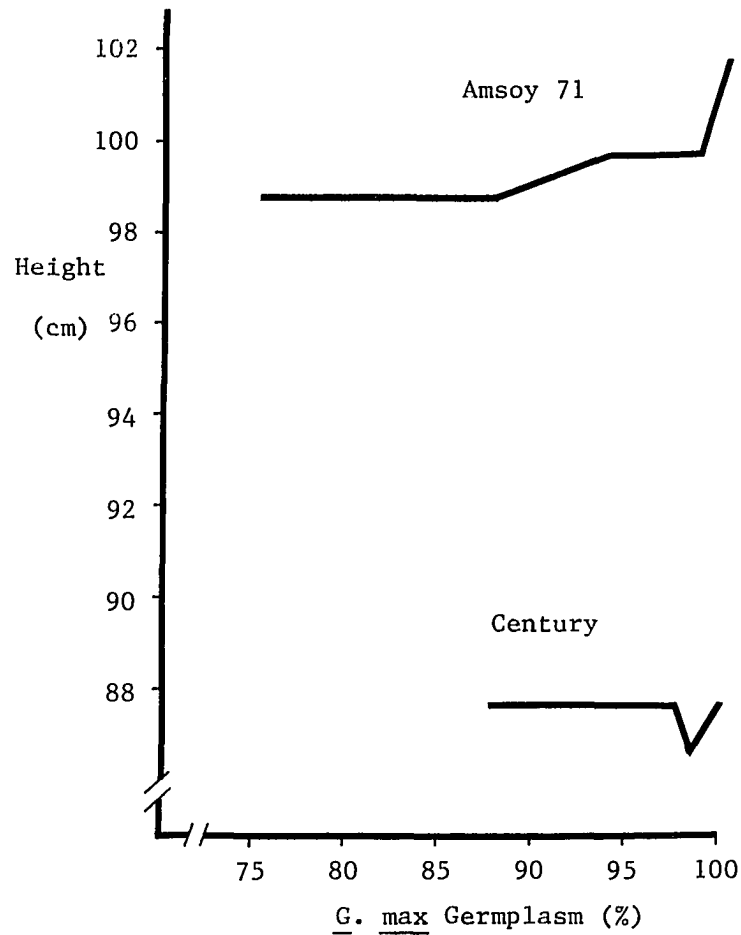


Figure 11. Mean height of backcross generations and recurrent parent versus percentage of their G. max germplasm

shorter than Amsoy 71, assuming additive gene action. Data from individual locations in 1982 indicated that the height of lines containing PI 424001 germplasm generally were shorter than Amsoy 71 (Table 14). In 1983, all generation means for height were not significantly different from the height of Amsoy 71 (Table 15). In data combined across all environments, the mean height of the BC<sub>1</sub> generation was similar to that of the recurrent parent (Table 17). Some lines in each generation from the BC<sub>2</sub> through the BC<sub>5</sub> generation were taller than Amsoy 71, which indicated transgressive segregation for height.

The longest branches of PI 326581 averaged 18 cm longer than the height of Century. There was no evidence that lines containing PI 326581 germplasm were taller than Century. In 1982, the mean heights of the backcross generations were one or two cm shorter than Century, but that difference was not significant (Table 20). In 1983, the BC<sub>2</sub> through the BC<sub>3</sub> generation means were two centimeters taller than Century (Table 20). These differences were not significant. Shorter and taller segregates had been discarded in 1982. Despite this selection, transgressive segregates significantly shorter than Century were observed in each backcross generation.

The number of lines in each backcross generation that did not differ significantly ( $P < 0.05$ ) from the recurrent parent for all traits was determined. In the Amsoy 71 cross, no lines in the BC<sub>1</sub> and only four lines in the BC<sub>2</sub> generation were similar to Amsoy 71 for all traits. Twenty-five lines in the BC<sub>3</sub>, 47 lines in the BC<sub>4</sub>,

and 51 lines in the BC<sub>5</sub> generation were similar to Amsoy 71. In the Century cross, no lines in the BC<sub>1</sub>, seven lines in the BC<sub>2</sub>, 27 lines in the BC<sub>3</sub>, 49 lines in the BC<sub>4</sub>, and 69 lines in the BC<sub>5</sub> generation were similar to Century for all traits. Except for the BC<sub>1</sub> generation, 100 lines in each generation were initially tested in both cross.

Phenotypic correlation coefficients were calculated between the data obtained for yield, maturity, lodging, and height in 1982 and in 1983. In both crosses, significant ( $P < 0.01$ ) correlations existed between the four traits measured in both years. The coefficients ranged from 0.41 to 0.83. These significant correlations indicated that the information obtained in 1982 from single-row short plots was in good agreement with the information obtained from the longer paired-row plots in 1983.

## DISCUSSION

A linear relationship was observed between yield, expressed as a percentage of the yield of the recurrent parent, and percentage G. max germplasm. This suggested that yield was controlled primarily by genes with additive effects in these crosses. For each percentage of G. soja present in a G. max background, the expected yield reduction should be between 0.75 and 1.0 percent. It is not appropriate to estimate the expected yield of lines with more than 25% G. soja germplasm for the Amsoy 71 cross or more than 12.5% for the Century cross. Lines containing higher percentages of G. soja germplasm were not agronomically suitable. Lines with a greater percentage of G. soja germplasm would preclude mechanical harvest because of the vining and shattering of this material. Therefore, at least one backcross is necessary to obtain lines which can produce a harvestable yield.

A general decrease in variance among lines was observed from the BC<sub>2</sub> to the BC<sub>5</sub> generation for yield. Significant variation among lines in the BC<sub>5</sub> generation for all traits in the Amsoy 71 cross and for maturity, lodging, and height in the Century cross indicated that a small amount of G. soja germplasm can create considerable variability. This variability suggested that backcrossing was successful in recombination between the G. max and G. soja genomes. Lawrence (1974) also observed significant variation in the BC<sub>5</sub> generation following introgression of A. sterilis into cultivated oats.

The material in this study was handled in a manner similar to those used by applied soybean breeders. Selection was practiced on  $BC_n F_2$  plants from which lines were derived, and on the lines themselves. Therefore, the percentages of agronomically acceptable lines obtained in this study can be assumed to be realistic. No line in the  $BC_1$  generation was similar to the recurrent parent for yield, maturity, lodging, and height in either cross. A few lines in the  $BC_1$  generation of the Amsoy 71 cross were similar to Amsoy 71 for one, two, or three of these traits but not for all four. In a backcrossing program, the backcross-derived lines must be similar to the recurrent parent for all traits. A line not similar to the recurrent parent for maturity, lodging, height, and especially yield, would not be considered acceptable.

In the  $BC_2$  generation, 7% of the lines in the Amsoy 71 cross and 4% of the lines in the Century cross were similar to their recurrent parent for all four traits. These percentages increased to about 25% by the  $BC_3$  generation. Therefore, the presence of more than 6.3% G. soja germplasm will make it difficult for the breeder to select lines similar to the adapted parent. It is possible to obtain such lines with as much as 12.5% wild germplasm if a large number of lines (e.g. 100) were evaluated in several environments.

G. soja does not appear to be a source of improved yield potential for soybeans. In the Amsoy 71 cross, a total of 311 lines from all generations were tested in four environments. Five of these were identified as transgressive segregates for yield. This number



represents less than 2% of the lines in this population. These were identified as transgressive segregates because they were significantly higher yielding than Amsoy 71 at the 5% probability level. However, with this level of probability, 2.5% of the lines are expected to yield more than the recurrent parent by chance. It is possible that these five transgressive segregates are chance events which are not actually higher yielding than Amsoy 71. More extensive testing of these lines should verify whether they actually have enhanced yields due to the introgression of PI 424001 germplasm. The results from the Century cross indicated that no yield improvement could be obtained by crossing G. max with PI 326581, because no transgressive segregates for yield were identified.

Introgression of wild germplasm can be expected to disrupt coadapted gene complexes of the cultivated species. Lawrence and Frey (1975) obtained transgressive segregates from eight crosses involving A. sativa and A. sterilis. Polyploid species are more likely to accept genes from other species than are diploids because polyploids have more genetic buffering capacity (Stalker, 1980). Transgressive segregates in oats may be possible to produce because of their polyploid genome structure masking unfavorable alleles but allowing the expression of favorable ones (Rogers, 1982). The presence of transgressive segregates for yield in oats but not in soybeans could be, at least in part, due to the differences in the ploidy levels of these species. Oats are hexaploid and soybeans are diploid. However, Rogers (1982) obtained transgressive segregates

for yield in barley, which is diploid, following the introgression of H. spontaneum germplasm.

Lawrence and Frey (1975) obtained transgressive segregates from all eight crosses involving A. sativa and A. sterilis and these segregates were at least 20% higher yielding than the A. sativa parent. Rogers (1982) obtained transgressive segregates from nine H. spontaneum lines introgressed into barley cultivars. The lack of transgressive segregates in my study was not due to lack of genetic variability because significant amounts of variability for yield were created in almost all backcross generations in both crosses. It should be noted that only two different crosses were used in this study. Possibly other G. max x G. soja crosses may produce transgressive segregates for yield, as was the case in oats and barley.

The process of backcrossing and performing extensive yield trials requires a large amount of time and resources. It is unlikely that a breeder would be willing to spend that much time and effort in search of a high-yielding segregate when the chance of obtaining one is 2% or less. An equal amount of effort with two adapted parents is more likely to produce high-yielding segregates. As long as breeders continue to successfully improve yielding ability using only adapted material, there will be no incentive to use unadapted sources. Vello et al. (1984) concluded that populations containing G. max plant introduction germplasm are not as useful for short-term improvement of yield as are populations developed from domestic cultivars. Murphy and Frey (1984) compared intraspecific oat

populations with populations containing 12.5% A. sterilis. They found segregates which exceeded the yield of the highest yielding parents in all populations, but more segregates came from the intraspecific population, indicating the superiority of adapted parents in short-term yield improvement.

It is more likely that G. soja will be used as a source of traits not presently available in soybeans rather than for yield improvement. G. max introductions have proven useful as sources of specific genes for pest resistance such as for the soybean cyst nematode (Heterodera glycines) (Poehlman, 1979). These traits are easily transferred using the backcross procedure. My study has demonstrated that when G. soja is used as a donor parent, the yield and agronomic traits of the cultivated soybean can be recovered with as few as three backcrosses. Therefore, should a gene be identified in G. soja which would prove valuable in the cultivated species, transfer can be accomplished with backcrossing. The resulting line would have all the desirable agronomic traits of the recurrent parent as well as the full intensity of the trait being transferred from G. soja, assuming no linkages.

Transferring a quantitative trait, such as high protein content, from G. soja to G. max would require testing after each backcross. This procedure is the same as when a quantitative trait is backcrossed from one G. max line to another. However, transferring a quantitative trait from G. soja to G. max has the additional disadvantage of requiring large population sizes from which to select

agronomically desirable lines. Enough lines must remain to be able to select for the trait being transferred. According to Weber (1950), a breeding program designed to transfer high protein from G. soja to G. max would encounter considerable difficulty. He stated that it appears possible to obtain the same gene action for high protein using only cultivated soybeans, although the allelic differences may not be as large as between G. soja and G. max.

A backcrossing program using G. soja as the donor parent would differ in several ways from one using a G. max donor parent. It may be advantageous to backcross onto more plants than usual to allow for some visual selection for agronomic types. For example, at the time of crossing, the shattering nature of the plants is not known. When crossing onto  $BC_1F_1$  plants to produce  $BC_2F_1$  seed, extra seed may be produced so that at harvest,  $BC_2F_1$  seed can be harvested from only nonshattering  $BC_1F_1$  plants.

After the final backcross has been made, the population from which lines are derived should be larger than populations composed of entirely G. max germplasm. This will allow for selection of the plants with the best agronomic characteristics. It would be desirable to observe the backcross-derived lines before they are yield tested. Yield testing is expensive and if unacceptable lines could first be discarded in progeny rows, resources would not be wasted by testing lines which do not have the necessary agronomic qualities. As an alternative procedure, all the lines could be grown in small plots such as short rows or hill plots in the first season, as was done

in this study. Notes could be taken on the agronomic suitability of these lines throughout the season. But instead of harvesting all the lines, harvest could be limited to those showing desirable agronomic characteristics. This avoids using an extra season for visual selection.

It is obviously more difficult to transfer traits from G. soja into G. max than from another G. max line or cultivar. If a desired trait is not present in any soybean cultivar or line, G. max plant introductions would be the next source to screen. Only when the trait is known to exist solely in a G. soja accession should inter-specific transfer be considered because of the difficulties caused by the undesirable characteristics of the wild species.

Anderson and Hubricht (1938) stated that the final result of introgressive hybridization in nature depends on the balance between the deleterious effects of the foreign germplasm and its advantageous effects. Likewise, the success of introgression of G. soja into the cultivated soybean depends on the ability of G. max to tolerate the small amounts of wild germplasm that accompanies a desired gene being transferred in a backcross. This study has demonstrated that the yield and agronomic qualities of cultivated genotypes can be maintained in genotypes containing up to 12.5% wild germplasm. The use of G. soja as a source of diversity for cultivated soybeans ultimately will depend on the presence of traits in G. soja which are absent in the G. max gene pool.

## SUMMARY AND CONCLUSIONS

The effect of G. soja germplasm on the yield and agronomic traits of soybean cultivars was evaluated. Two G. soja accessions were crossed to two soybean cultivars and the hybrids were backcrossed five times to the cultivated parent. Agronomically acceptable lines were selected from each of the five backcross generations but not from the single-cross population from both crosses. These lines were evaluated for yield, maturity, lodging, and height at four environments during 1982 and 1983.

Significant variation was present for all traits among lines from most backcross generations as a result of introgression with G. soja. A linear relationship was observed between the percentage yield of the lines relative to the recurrent parent and their percentage of G. max germplasm. Selection for maturity and height was effective because lines from the backcross generations were similar to the recurrent parent for these traits. Although the lines also were selected for lodging resistance, lines containing greater percentages of G. soja germplasm had less lodging resistance.

A minimum of two backcrosses to the adapted parent was necessary to recover lines similar to that parent for yield, maturity, lodging, and height. However, because very few acceptable lines from the  $BC_2$  generation were recovered, a third backcross is recommended to insure the recovery of a reasonable number of lines.

The introgression of germplasm from the G. soja accessions into the soybean cultivars did not improve the yield potential of the lines. Adapted x adapted crosses are more likely to produce transgressive segregates for yield.

The increased difficulty in selection of agronomically acceptable progenies when G. soja is used as a parent will restrict the use of it in soybean improvement programs. G. soja should be used only when it possesses desired traits not present in the G. max gene pool.

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