

- Gorman, M. 1976. An electrophoretic study of the genetic variation in the commercial soybean germplasm. M.S. Thesis. University of New Hampshire.
- Gorman, M. and Y. T. Kiang. 1977. Variety specific electrophoretic variants of four soybean enzymes. *Crop Sci.* 17:963-965.
- Gorman, M. and Y. T. Kiang. 1978. Models for the inheritance of several variant soybean electrophoretic zymograms. *J. Hered.* 60:255-258.
- Hildebrand, D. F., J. H. Orf and T. Hymowitz. 1980. Inheritance of an acid phosphatase and its linkage with the Kunitz trypsin inhibitor in seed protein of soybeans. *Crop Sci.* 20:83-85.
- Hildebrand, D. F. and T. Hymowitz. 1980a. Seed acid phosphatase genotypes of cultivars in the USDA soybean collection. *Soybean Genet. News1.* 7:35-41.
- Hildebrand, D. F. and T. Hymowitz. 1980b. Inheritance of β -amylase nulls in soybean seed. *Crop Sci.* 20:727-730.
- Kiang, Y. T. 1980. Genetic variation of *Glycine max*, *G. soja* and *G. javanica*. *Genetics* 94:853.
- Kiang, Y. T. 1981. Inheritance and variation of amylase in cultivated and wild soybeans and their wild relatives. *J. Hered.* (In press).
- Reiss, R. A. 1978. A study of the isozymes of amylase in germinating soybean seeds. M.S. Thesis, University of New Hampshire.

Y. T. Kiang
M. B. Gorman
Y. C. Chiang

OHIO STATE UNIVERSITY
Ohio Agricultural Research and Development Center
Department of Agronomy
Columbus, Ohio 43210

1) Epistasis and soybean breeding

Epistasis, or non-allelic interaction, may be of considerable importance in the inheritance of quantitative traits in soybeans. Hanson and Weber (1962) and Hanson et al. (1967) used a nested progeny design to partition the genetic variance among homozygous lines into additive and additive x additive (epistatic) components. In each of two populations, approximately 70% of the genetic variance for grain yield was attributable to epistasis. While others (Leffel and Hanson, 1961; Brim and Cockerham, 1961) have given evidence for the predominance of additive variance for soybean yield, the implications for breeders of a large epistatic contribution to yield are worth considering.

A. Line selection. For line selection the reference population is taken to be a collection of homozygous lines extracted at random from a population

in linkage equilibrium. The genetic value of the lines can be fitted to the model $G = \mu + A + AA$, where μ is the population mean and A and AA represent deviations associated with additive and additive x additive effects, respectively. Higher order epistatic effects are assumed to be negligible. The variance among lines can be partitioned as $\sigma_G^2 = \sigma_A^2 + \sigma_{AA}^2$. It can be shown that the expected covariance between the genetic values of a parent and its pure-line offspring is $\frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2$, and that the regression of offspring on midparent genetic value is $1 - \frac{1}{2}K$, where $K = \sigma_{AA}^2/\sigma_G^2$, the proportion of the genetic variance attributable to epistasis.

For example, take $K = 0.70$, as in the studies of Hanson and Weber (1962) and Hanson et al. (1967). Then if two lines each yielding 10% above the population mean are crossed, lines derived from the cross will, in expectation, average 6.5%, not 10%, above the population mean. The results of crossing particular pairs of parents will deviate about this expected value.

In qualitative terms, selection among homozygous lines acts on both additive and epistatic components; a superior line is likely to have both A and AA positive. Less of the AA component than the A component is passed to progeny, however, because A effects are associated with alleles while AA effects are associated with allele combinations. Such combinations are subject to breakup through independent assortment and are not necessarily transmitted intact.

In the presence of additive x additive epistasis, line performance *per se* and parental value of lines (i.e., combining ability) are imperfectly correlated. There is both specific and general combining ability, neither of which is exactly predictable from line *per se* performance. It follows that a testcross procedure, such as that proposed by Kenworthy (1980), might be useful in eliminating poor parental material. Another testcross procedure is early generation testing, which could be used to select among crosses and enable greater testing effort to be given to the more promising crosses. The test material could be F_2 -derived lines, bulk populations, or maturity-group bulks (Empig and Fehr, 1971).

B. Multi-parent crosses and intermated populations. Hanson et al. (1967) discussed the phenomenon of yield depression on intermating superior lines. The regression of offspring performance on parent mean when there are n parents is $1 - K(n-1)/n$. Thus, if $K = 0.70$, and if a ten-line synthetic is composed of lines averaging 10% above the reference population mean, lines

derived from the population are expected to average 3.7% above the reference population. The figure for a four-parent cross would be 4.75%. The number of generations of intermating has no effect on the amount of yield depression except where epistatic loci are linked.

Testcross selection could be used to identify parents that had good general combining ability and thus reduce the amount of depression that occurred with crossing or intermating.

C. Recurrent selection. Gains for recurrent selection for intrapopulation improvement derive chiefly from additive gene action. For selection among selfed families, the expected gain (ΔG) per cycle is the product of the standardized selection differential, i , and the additive portion of the genetic variance among families, divided by the phenotypic standard deviation (σ_p) of family means. Here it is assumed that dominance is absent and that the effective population size is so large that the epistatic contribution to genetic gain is negligible.

Under the model used by Hanson and Weber (1962), and Hanson et al. (1967), σ_A^2 is defined as the additive genetic variance among homozygous lines. In general, the additive genetic variance among lines is $\frac{1}{2}(1+F)\sigma_A^2$, where F is the parental inbreeding coefficient ($F = 0$ for S_1 lines, $\frac{1}{2}$ for S_2 lines, $3/4$ for S_3 lines, etc.).

The phenotypic variance among line means can be determined as

$$\sigma_P^2 = \frac{1}{2}(1+F)\sigma_A^2 + \frac{1}{4}(1+F)^2\sigma_{AA}^2 + [\frac{1}{2}(1+F)\sigma_{AL}^2 + \frac{1}{4}(1+F)^2\sigma_{AAL}^2]/L + \sigma_e^2/rL,$$

where σ_{AL}^2 , σ_{AAL}^2 and σ_e^2 represent, respectively, the variance of additive genetic x location, additive x additive genetic x location, and interplot error effects, and where L and r are, respectively, the numbers of locations and replications per location.

The expected gain per cycle in recurrent selection is, therefore, $\Delta G = \frac{1}{2}i(1+F)\sigma_A^2/\sigma_p$. Epistasis contributes to the denominator, but not to the numerator, of this expression. Therefore, if epistasis is an important factor in the inheritance of a trait, estimates of genetic gain made by assuming all genetic variance to be additive will be biased upward.

Because the coefficients of the σ_{AA}^2 and σ_{AAL}^2 terms increase with inbreeding at a faster rate than those of the σ_A^2 and σ_{AL}^2 terms, the detrimental effect of epistasis on expected gain can be minimized by testing in the early generations.

References

- Brim, C. A. and C. C. Cockerham. 1961. Inheritance of quantitative characters in soybeans. *Crop Sci.* 1:187-190.
- Empig, L. T. and W. R. Fehr. 1971. Evaluation of methods for generation advance in bulk hybrid soybean populations. *Crop Sci.* 11:51-54.
- Hanson, W. D. and C. R. Weber. 1962. Analysis of genetic variability from generations of plant-progeny lines in soybeans. *Crop Sci.* 2:63-67.
- Hanson, W. D., A. H. Probst and B. E. Caldwell. 1967. Evaluation of a population of soybean genotypes with implications for improving self-pollinated crops. *Crop Sci.* 7:99-103.
- Kenworthy, W. J. 1980. Strategies for introgressing exotic germplasm in breeding programs. In F. T. Corbin, ed., *World Soybean Research Conference II: Proceedings*. Westview Press, Boulder, Colorado.
- Leffel, R. C. and W. D. Hanson. 1961. Early generation testing of diallel crosses of soybeans. *Crop Sci.* 1:169-174.

S. K. St. Martin

2) A new recurrent selection scheme incorporating genetic male sterility.

The use of genetic male sterility to facilitate recurrent selection in soybeans has been discussed by Brim and Stuber (1973), Fehr and Ortiz (1975), Kenworthy and Brim (1979) and Brim and Burton (1979). A problem with the selection schemes that have been presented is the occurrence of male-sterile segregates in the yield-test plots and the consequent reduction of precision in measuring yield. In the proposed scheme (Table 1), male sterility is employed to recombine selected lines, but tested material consists of homozygous fertile plants.

The main feature of the scheme is the inclusion of a seed-increase generation between the harvest of S_1 plants and the yield test. During this season, a homozygous fertile line is identified and increased for testing purposes, while a segregating-sterile bulk is made up using fertile plants from segregating rows derived from the same S_0 ancestor. This bulk represents the line in the recombination block.

The expected gain per cycle from this scheme is two-thirds that from ordinary S_2 testing, i.e., $(1/2)i\sigma_A^2/\sigma_p$, as compared with $(3/4)i\sigma_A^2/\sigma_p$ (see pages 104-107 for definitions of terms). The factor 2/3 represents parental control, in that the recombination makes use of relatives of superior lines rather than the lines themselves. The phenotypic standard deviation, σ_p , is the same as in ordinary S_2 testing (unless dominance is important). Aside from

Table 1

A new recurrent selection scheme incorporating
genetic male sterility

Season	Activity
1	Grow intermating block in isolation. Harvest sterile (<i>ms ms</i>) plants.
2	Grow S_0 plants. Harvest fertile (<i>Ms ms</i>) plants.
3	Grow S_1 plants in progeny rows. Harvest 15 to 20 fertile plants (of which one-third will be <i>Ms Ms</i> , two-thirds Ms_1ms) from each row.
4	Grow S_2 plants in progeny rows. In each desirable S_0 -derived family, (a) select one homozygous fertile row and bulk seed from it for testing, and (b) bulk seed from fertile ($1/3 Ms Ms$, $2/3 Ms ms$) plants from the segregating rows. Seed from (b) provides material for the recombination should the line from (a) be selected on the basis of the yield test.
5	Conduct yield test of homozygous fertile S_2 lines (S_1 -derived lines in the S_3). For the recombination in season 6, composite segregating bulks corresponding to the best fertile lines. This will give a recombination block segregating 5 fertile: 1 sterile.

decreased parental control, the proposed scheme has the additional disadvantages of increased cycle time (five seasons vs. four for ordinary S_2 testing) and increased labor and space in the breeder's nursery.

This procedure lends itself to several modifications, one of which consists of deferring testing by one generation, so that S_3 lines (S_2 -derived lines in the S_4) are tested. In this modification, a heterozygous *Ms ms* S_1 plant is the ancestor of a homozygous fertile line to be tested and a segregating bulk to be recombined. Parental control is increased to 6/7 and expected gain becomes $(3/4)i\sigma_A^2/\sigma_p$ (where σ_p now refers to the phenotypic standard deviation among S_3 lines), compared to $(7/8)i\sigma_A^2/\sigma_p$ for ordinary S_3 testing.

References

- Brim, C. A. and J. W. Burton. 1979. Recurrent selection in soybeans. II. Selection for increased percent protein in seeds. *Crop Sci.* 19:494-498.

- Brim, C. A. and C. W. Stuber. 1973. Application of genetic male sterility to recurrent selection schemes in soybeans. *Crop Sci.* 13:528-530.
- Fehr, W. R. and L. B. Ortiz. 1975. Recurrent selection for yield in soybeans. *J. Agric. Univ. Puerto Rico* 59:222-232.
- Kenworthy, W. J. and C. A. Brim. 1979. Recurrent selection in soybeans. I. Seed yield. *Crop Sci.* 19:315-318.

S. K. St. Martin

OKLAHOMA STATE UNIVERSITY
Department of Agronomy
Stillwater, Oklahoma 74078

1) Pollination study on three varieties of soybeans using honeybees and leafcutter bees.

Soybeans are known to exhibit a high degree of flower abortion. Schaik and Probst (1958) noted that a large number of flowers open but drop off without ever forming pods. They also noted definite physical differences between shed ovules and viable ones. They stated that if flower shedding could be reduced or eliminated yield would most likely increase. Erickson et al. (1978), working with three soybean varieties obtained significantly higher yields (10-16%) in cages with honeybees (*Apis mellifera* L.) than in cages without bees for two of three varieties. We reasoned that some flowers might abort because they are never fertilized. Bees might increase the rate of fertilization by cross pollinating these flowers, thus, reduce abortion and increase yields.

We attempted to determine if honeybees and/or leafcutter bees could increase fertilization and reduce flower abortion. The experimental design used was a split-plot design with four replications. Whole plots were pollination treatments including a control with no cage and no bees, a cage with no bees, a cage with honey bees, and a cage with leafcutter bees. Sub-plot treatments included three varieties ('Crawford', 'Essex', and 'Forrest'). Planting date was June 3, 1980, and cages were erected over the designated plots on July 9, 1980 when the first plants began to flower. The cages and bees were left in the field until harvest on October 28, 1980.

Data were obtained on yield and yield components. Yield was recorded as grams/plot, and seed weight was recorded as grams/100 seeds. All plants within each plot were counted to determine plants/plot. Seeds/plant were determined indirectly.