

1995

Inheritance and Number of Genes Affecting Quantitative Traits Within F2 Maize Populations

D. H. Schmidt


Iowa State University

A. R. Hallauer

Iowa State University, hallauer@iastate.edu

Copyright © Copyright 1995 by the Iowa Academy of Science, Inc.

Follow this and additional works at: <https://scholarworks.uni.edu/jias>

 Part of the [Anthropology Commons](#), [Life Sciences Commons](#), [Physical Sciences and Mathematics Commons](#), and the [Science and Mathematics Education Commons](#)

Recommended Citation

Schmidt, D. H. and Hallauer, A. R. (1995) "Inheritance and Number of Genes Affecting Quantitative Traits Within F2 Maize Populations," *Journal of the Iowa Academy of Science: JIAS*, 102(3-4), 32-40.

Available at: <https://scholarworks.uni.edu/jias/vol102/iss3/4>

This Research is brought to you for free and open access by UNI ScholarWorks. It has been accepted for inclusion in Journal of the Iowa Academy of Science: JIAS by an authorized editor of UNI ScholarWorks. For more information, please contact scholarworks@uni.edu.

Inheritance and Number of Genes Affecting Quantitative Traits Within F₂ Maize Populations¹

D. H. SCHMIDT² AND A. R. HALLAUER

Department of Agronomy, Iowa State University, Ames, Iowa 50011 USA

Populations derived from crosses of elite genotypes are commonly used in plant breeding programs. Knowledge of the genetic variation among individuals and their progenies within F₂ populations is essential for effective selection of important traits. The genetic variation and number of effective factors affecting the expression of quantitative traits within 30 F₂ maize (*Zea mays* L.) populations were determined by different methods suggested for study of F₂ populations. Estimates of heritability and number of effective factors varied among F₂ populations for each trait, primarily because of the differences in trait expression between parents of crosses and the environmental effects upon individual plants. Average estimates of heritabilities for grain yield ranged from -0.03 to 0.63 among methods of estimation and ranged from 0.02 to 0.75 among methods of estimation for the same F₂ population. The range of estimates of heritability and gene number among crosses and methods of estimation suggests that estimates are unique for a specific F₂ population and for a specific method of estimation. If the newer techniques of marker-assisted selection are applied to F₂ populations, the effectiveness of marker-assisted selection may vary among F₂ populations.

INDEX DESCRIPTORS: *Zea mays* L., Corn, Genetic variability, Selection

Most traits of economic importance in plants are quantitatively inherited. The heritable portion of quantitative traits depends on an unknown number of genes with small effects with respect to the total variation. Falconer (1981) stated that quantitative genetics emphasizes the inheritance of those differences among individuals that are of degree rather than kind, quantitative rather than qualitative. The number of genes that affect quantitative traits and the role of the environment on those genes' expression of these traits are an indication of the inheritance of quantitative traits. Heritability indicates the level of resemblance between relatives. Estimates of heritability indicate the ability of measured phenotypic values to predict breeding values. Heritability is an important parameter for making decisions in plant breeding methods, from the choice of breeding methods to predicting genetic gain in selection.

Marker-assisted selection (MAS) has been suggested to enhance selection for quantitative traits (Lande, 1992; Lande and Thompson, 1990). Use of MAS requires estimates of heritability on an individual-plant basis. Variances of different generations of related populations are useful to estimate the heritability of quantitative traits and the minimum number of genes (genetic factors) affecting the traits within a population. Different methods of estimating heritabilities and the number of genes affecting a trait have been suggested.

The objectives of this research were to compare heritability estimates obtained by different methods, to compare methods of estimating the number of genes affecting traits, and to compare estimates of heritability and number of genes for two sets of maize (*Zea mays* L.) lines. Each set included six inbred lines, representing inbred lines from pre-1960 and post-1970 eras of maize breeding.

MATERIALS AND METHODS

Two groups of six inbred lines, designated as older (pre-1960) and newer (post-1970), were included. The group of older inbred lines included L289, L317, M14, WF9, B14A, and B37, and the group of newer inbred lines included B73, B75, B76, B77, B79, and B84 (Gerdes et al., 1993). The six inbred lines within each of the two groups were crossed in a diallel manner (reciprocals were bulked) to produce 15 single crosses within each group. The 15 single crosses

within each group were selfed to produce the F₂ generations and backcrossed to both parents to produce the two backcross (BC1 and BC2) generations. Each group, therefore, included 15 F₁, 15 F₂, 15 BC1 (parent 1), and 15 BC2 (parent 2) entries derived from the six-parent diallel within each group.

Data were obtained at two locations near Ames, IA for 2 years. Experimental design was a restricted randomized complete block design with three replications at each of the four environments. The five generations (inbred lines, F₁, F₂, BC1, and BC2), each with different inherent levels of vigor, were grouped into subblocks within each replication. Location of subblocks within replications and entries to plots within subblocks was by randomization. Each subblock was bordered with materials of similar vigor. Plots included two rows for the F₁, F₂, BC1, and BC2 entries and four rows for the inbred lines. Plots were overplanted and thinned at the 5- to 7-leaf stage to an equivalent stand of 50,000 plants ha⁻¹. Recommended production practices for high-yield maize production were used at each location.

Data were collected on individual plants within each row of each plot for eight plant and ear traits. Plant and ear height and tassel branch number were measured on the first five competitive plants in each row, or 10 plants plot⁻¹. Plant height (cm) was the distance from the ground to the tip of the main axis of the tassel, and ear height (cm) was the distance from the ground to the node of the top ear. Tassel branch number was a count of the branches on the tassel, excluding the main axis of the tassel. Data were collected on 9,360 plants for the three preharvest traits.

Ear trait data were recorded for the first five (inbred lines) and 10 (F₁, F₂, BC1, and BC2) competitive plants of each plot row, or 20 plants plot⁻¹. Ears were harvested by hand, dried to 60 g kg⁻¹ grain moisture, measured for ear length (cm) and ear diameter (cm), number of kernel rows counted, and shelled to determine kernel depth (cm) and yield (g). Kernel depth was the difference between ear and cob diameter measurements.

Analyses of variance were completed for each environment and combined across the four environments. Analyses of variance were on individual-plant data with entries considered fixed effects and with environments, replications, and plants within entries considered as random effects. The primary objective of the study was to examine the variation among plants within entries. Inbred lines were considered homozygous and homogeneous. Variation among plants within

¹Journal Paper J-16388 of the Iowa Agric. and Home Econ. Exp. Stn., Ames, IA 50011. Project 3082.

²Present address: Research Manager, Pioneer Hi-Bred International, Inc., 7301 N.W. 62nd Ave., P.O. Box 85, Johnston, IA 50131-0085.

Table 1. Means and within-plot variation expected in the inbred lines (P₁ and P₂) and the F₁, F₂, and backcross (BC1 and BC2) generations of a cross of P₁ and P₂.

Generation	Mean with respect to generations present	Within-plot variation
P ₁ , P ₂	P ₁ , P ₂ ^a	σ_{we}^2 ^b
F ₁	(1/2) (P ₁ + P ₂)	σ_{we}^2
F ₂	(1/4) (P ₁ + P ₂ + 2F ₁) and (1/2) (BC1 + BC2)	σ_{wg}^2 ^c + σ_{we}^2
BC1	(1/2) (P ₁ + F ₁)	σ_{wg}^2 ^d + σ_{we}^2
BC2	(1/2) (P ₂ + F ₁)	σ_{wg}^2 ^d + σ_{we}^2

^aP₁ and P₂ indicate inbred lines 1 and 2, respectively, and BC1 and BC2 indicate backcrosses to P1 and P2, respectively.

^b σ_{we}^2 = nonheritable variance among plants within a plot.

^c σ_{wg}^2 = $\sigma_A^2 + \sigma_D^2$, where σ_A^2 is the additive genetic variance and σ_D^2 is variance due to dominant deviations, assuming no epistasis.

^d σ_{wg}^2 = (1/2) $\sigma_A^2 + \sigma_D^2 - \sigma_{AD}$ for BC1 and (1/2) $\sigma_A^2 + \sigma_D^2 + \sigma_{AD}$ for BC2 where σ_{AD} is the covariance of additive and dominant effects.

the inbred lines and F₁ plots would be due to within-plot environmental effects (σ_{we}^2). The F₂ and backcross (BC1 and BC2) populations were heterogeneous; i.e., 50% heterozygous and 50% homozygous. Variation (σ_w^2) within F₂, BC1, and BC2 populations, therefore, would include environmental (σ_{we}^2) and genetic variation (σ_{wg}^2) among individuals within plots, or $\sigma_w^2 = \sigma_{we}^2 + \sigma_{wg}^2$ (Table 1). Single-plant data were pooled across replications and environments to calculate heritabilities and minimum number of effective factors for eight traits for 30 crosses (15 crosses between six older inbred lines and 15 crosses between six newer inbred lines). To estimate heritabilities and minimum number of effective factors, it is necessary to separate the genetic variance (σ_{wg}^2) from the total within-plot variance (σ_w^2). This was accomplished by subtracting the within-plot

Table 2. Relations used to obtain estimates of additive genetic variance (σ_A^2) and total genetic variance (σ_G^2) to estimate narrow-sense (h_A^2) and broad-sense (h_G^2) heritabilities on an individual-plant basis.

Estimate of σ_A^2 :
1) $2\sigma_{F2}^2 - (\sigma_{BC1}^2 + \sigma_{BC2}^2)$
2) $2(2\sigma_{F2}^2 - \sigma_{we}^2 P_{1, P2, 2F1}) - [(\sigma_{BC1}^2 - \sigma_{we}^2 P_{1F1}) + (\sigma_{BC2}^2 - \sigma_{we}^2 P_{2, F1})]$
Estimate of h_A^2 :
1) Warner (1952) – $h_A^2 = [2\sigma_{F2}^2 - (\sigma_{BC1}^2 + \sigma_{BC2}^2)]/\sigma_{F2}^2$
2) Modified Warner – $h_A^2 = \{[2\sigma_{F2}^2 - (\sigma_{P1}^2, \sigma_{P2}^2, 2\sigma_{F1}^2)^{1/4}] - [\sigma_{BC1}^2 - (\sigma_{P1}^2\sigma_{F2}^2)^{1/2}] - [\sigma_{BC2}^2 - (\sigma_{P2}^2\sigma_{F1}^2)^{1/2}]\}/\sigma_{F2}^2$
Estimate of σ_G^2 :
$\sigma_{F2}^2 - \sigma_{we}^2$, where σ_{we}^2 estimated from σ_{P1}^2 , σ_{P2}^2 , and σ_{F1}^2 .
Estimate of h_G^2 :
1) Burton (1951) – $h_G^2 = (\sigma_{F2}^2 - \sigma_{F1}^2)/\sigma_{F2}^2$
2) Mahmud and Kramer (1951) – $h_G^2 = [\sigma_{F2}^2 - (\sigma_{P1}^2, \sigma_{P2}^2)^{1/2}]/\sigma_{F2}^2$
3) Weber and Moorthy (1952) – $h_G^2 = [\sigma_{F2}^2 - (\sigma_{P1}^2, \sigma_{P2}^2, \sigma_{F1}^2)^{1/3}]/\sigma_{F2}^2$
4) Modified Weber and Moorthy – $h_G^2 = [\sigma_{F2}^2 - (\sigma_{P1}^2, \sigma_{P2}^2, 2\sigma_{F1}^2)^{1/4}]/\sigma_{F2}^2$

environmental variance (σ_{we}^2) from the total within-plot variance ($\sigma_w^2 + \sigma_{we}^2$) in the F₂ and BC1 and BC2 populations. Estimates of the within-plot environmental variance (σ_{we}^2) were obtained from the homogeneous inbred lines and F₁ generations. Estimates of σ_{we}^2 and

Table 3. Mean values for eight traits for two sets (older and newer) of maize inbred lines evaluated in four environments.

Inbred	Traits								
	Grain yield	Kernel row	Ear		Kernel depth	Tassel branches	Height		
			Diameter	Length			Plant	Ear	
	q ha ⁻¹	no.	-----	cm	-----	mm	no.	-----	cm
Older lines									
L289	32	12.1	3.5	14.0	5.4	16.7	184	93	
L317	19	13.3	3.4	14.7	4.8	12.6	195	113	
M14	32	14.9	3.7	12.9	6.2	6.6	138	58	
Wf9	41	15.5	4.1	12.1	8.4	13.7	158	69	
B14A	23	13.4	3.6	14.2	5.4	8.4	176	77	
B37	22	12.7	3.5	13.0	5.3	6.0	179	82	
\bar{X}	28	13.6	3.6	13.5	5.9	10.7	172	82	
Newer lines									
B73	39	16.9	4.2	12.0	7.1	6.7	193	93	
B75	34	13.3	3.8	11.7	7.6	2.0	163	73	
B76	39	13.2	4.1	13.3	7.1	7.4	165	79	
B77	35	13.2	3.5	13.9	6.1	11.1	185	81	
B79	33	16.6	4.0	11.2	6.3	15.6	156	79	
B84	46	14.7	4.1	13.9	7.7	15.0	167	87	
\bar{X}	38	14.6	4.0	12.7	7.0	9.6	172	82	

separation of σ_{wg}^2 (for broad-sense heritability estimates) and σ_A^2 (for narrow-sense heritability estimates) were obtained in various ways (Table 2). Standard errors of heritability estimates were calculated by the method proposed by Dickerson (1969).

Estimates of the minimum number of genes contributing to the variation of the traits within the 30 F_2 populations were computed by the method presented by Wright (1952) and expanded by Lande (1981):

$$n = (\mu_{p2} - \mu_{p1})^2 / 8\sigma_g^2,$$

where n is minimum effective number of genetic factors; μ_{p1} and μ_{p2} are mean values of inbred parents P_1 and P_2 , respectively, in terms of standard phenotypic deviations; and σ_g^2 is the estimate of genetic variance, either σ_A^2 or σ_G^2 . The standard error (SE) of n was computed by Lande's formula:

$$SE(n) = (\sigma_n^2)^{1/2}, \text{ where } \sigma_n^2 = 4\{(\sigma_{p1}^2 + \sigma_{p2}^2)/n\} / (\mu_{p1} + \mu_{p2}) + \sigma^2(\sigma_g^2) / \sigma_g^2.$$

RESULTS AND DISCUSSION

The mean values for eight traits for the two sets of inbred lines

evaluated in four environments are listed in Table 3. The greatest variation among the older group of lines was for grain yield (19 to 41 q/ha), tassel branch number (6.0 to 16.7), and plant and ear height (138 to 195 and 58 to 113 cm, respectively). There was less variation among newer lines for grain yield (33 to 46 q/ha) compared with older lines, but substantial variation existed among the newer lines for tassel branch number (2.0 to 15.6) and plant and ear height (156 to 193 and 73 to 93 cm, respectively). The average grain yield for the newer lines was 9.5 q/ha greater than for the older lines, indicating an overall trend for increased yield for the newer lines. Parental line data were used to estimate within-plot environmental effects and to estimate σ_A^2 , h_n^2 (Warner, 1952), σ_{wg}^2 , and h_g^2 (Mahmud and Kramer, 1951; Weber and Moorthy, 1952).

Differences among methods for estimates of heritability and for estimates of gene number (n) were detectable more often for grain yield and tassel branch number, traits for which the parental differences were greatest. Estimates of heritability and n will be presented for each cross for grain yield and tassel branch number to illustrate the variation among crosses for the same trait with various methods of estimation. Estimates were determined significantly different

Table 4. Estimates of narrow- (h_n^2) and broad-sense (h_g^2) heritabilities and their standard errors (SE) for grain yield for each of 15 F_2 populations from a diallel cross of six older lines and six newer lines evaluated in four environments.

Cross	Method of Estimation (Table 2)											
	Burton		Mahmud & Kramer		Weber & Moorthy		Modified Weber & Moorthy		Warner		Modified Warner	
	h_g^2	SE	h_g^2	SE	h_g^2	SE	h_g^2	SE	h_n^2	SE	h_n^2	SE
Older lines												
L289 x L317	-0.11	0.19	0.63	0.15	0.47	0.15	0.36	0.15	-0.41	0.42	-0.40	0.35
L289 x M14	-0.27	0.21	0.59	0.15	0.40	0.15	0.28	0.15	-0.08	0.37	-0.08	0.36
L289 x Wf9	-0.17	0.20	0.66	0.16	0.49	0.15	0.37	0.15	-0.08	0.37	-0.07	0.35
L289 x B14A	0.09	0.18	0.60	0.15	0.47	0.15	0.40	0.14	-0.17	0.38	-0.16	0.36
L289 x B37	0.05	0.18	0.67	0.16	0.53	0.15	0.44	0.15	0.22	0.38	0.22	0.39
L317 x M14	-0.61	0.26	0.54	0.15	0.31	0.15	0.34	0.15	-0.19	0.39	-0.19	0.34
L317 x Wf9	-0.12	0.20	0.65	0.15	0.49	0.15	0.37	0.15	0.17	0.35	0.17	0.35
L317 x B14A	0.02	0.18	0.75	0.16	0.61	0.16	0.51	0.15	0.36	0.34	0.36	0.33
L317 x B37	0.09	0.18	0.71	0.16	0.58	0.15	0.49	0.15	0.00	0.37	0.01	0.35
M14 x Wf9	-0.11	0.19	0.63	0.15	0.47	0.15	0.36	0.15	-0.54	0.44	-0.53	0.35
M14 x B14A	0.20	0.17	0.73	0.16	0.61	0.15	0.53	0.15	0.32	0.34	0.33	0.31
M14 x B37	-0.03	0.19	0.59	0.15	0.45	0.15	0.36	0.15	0.00	0.37	0.10	0.33
Wf9 x B14A	0.24	0.16	0.69	0.16	0.59	0.15	0.52	0.15	0.29	0.35	0.29	0.34
Wf9 x B37	-0.37	0.22	0.51	0.15	0.31	0.15	0.33	0.15	0.33	0.36	0.32	0.34
B14A x B37	0.46	0.16	0.68	0.16	0.62	0.15	0.58	0.15	-0.46	0.42	-0.46	0.35
Newer lines												
B73 x B75	0.35	0.16	0.64	0.15	0.56	0.15	0.52	0.15	-0.24	0.40	-0.24	0.37
B73 x B76	0.32	0.16	0.56	0.15	0.49	0.15	0.45	0.15	0.04	0.36	0.04	0.33
B73 x B77	0.14	0.17	0.65	0.15	0.53	0.15	0.45	0.15	-0.85	0.50	-0.85	0.37
B73 x B79	0.36	0.16	0.65	0.15	0.57	0.15	0.53	0.15	-0.20	0.39	-0.20	0.32
B73 x B84	-0.08	0.19	0.46	0.14	0.32	0.14	0.24	0.14	0.15	0.35	0.16	0.34
B75 x B76	-0.04	0.19	0.49	0.15	0.36	0.14	0.28	0.14	-0.07	0.37	-0.06	0.35
B75 x B77	0.02	0.18	0.57	0.15	0.43	0.15	0.35	0.14	-0.50	0.43	-0.49	0.39
B75 x B79	0.53	0.16	0.58	0.15	0.47	0.15	0.41	0.14	0.14	0.36	0.15	0.29
B75 x B84	-0.09	0.19	0.57	0.15	0.41	0.15	0.31	0.14	-0.37	0.41	-0.37	0.35
B76 x B77	-0.04	0.19	0.63	0.15	0.47	0.15	0.38	0.15	0.25	0.35	0.26	0.32
B76 x B79	0.37	0.16	0.60	0.15	0.53	0.15	0.50	0.15	0.28	0.35	0.28	0.30
B76 x B84	0.03	0.18	0.58	0.15	0.45	0.15	0.36	0.14	0.00	0.37	0.01	0.33
B77 x B79	0.16	0.17	0.72	0.16	0.59	0.15	0.51	0.15	0.49	0.34	0.49	0.31
B77 x B84	-0.01	0.18	0.65	0.15	0.50	0.15	0.40	0.15	-0.09	0.38	-0.09	0.33
B79 x B84	0.18	0.17	0.45	0.14	0.37	0.14	0.33	0.14	-0.40	0.42	-0.40	0.36

from each other if the estimates were not included in the estimated 95% confidence interval of each other (confidence intervals not included). Fifteen pair-wise comparisons were made for each of the 30 crosses for the traits available for estimates of heritability and of n. Abbreviations for methods of estimation are: Burton (B), Mahmud and Kramer (M&K), Weber and Moorthy (W&M), Modified Weber and Moorthy (MW&M), Warner (W), and Modified Warner (MW).

Estimates of heritability for grain yield ranged from -0.61 (h^2_B , B, L317 x M14) to 0.75 ($h^2_{M&K}$, M&K, L317 x B14A) for older line crosses and from -0.85 (h^2_W , W, B73 x B77) to 0.72 ($h^2_{M&K}$, M&K, B77 x B79) for newer line crosses (Table 4). The subtraction of the environmental component of variation from the variance estimate for the F₂ and the backcross to each parent (BC1 and BC2) did very little to change the heritability estimate determined by W vs. MW. Similar to estimates of heritability, estimates of n differed among crosses and among methods for grain yield (Table 5). Estimates of n for older line crosses ranged from n = -100.9 (B, Wf9 x B37) to n = 207.4 (M&K, L317 x B37) and, for newer line crosses, from n = -111.7 (W, B79 x B84) to n = 206.5 (M&K, B77 x B84). Standard errors (SE) were

large for estimates of heritability and for estimates of n for the methods evaluated.

Estimates of heritability for tassel branch number ranged from -0.35 (h^2_W , W, Wf9 x B37) to 0.81 (h^2_{MW} , MW, L289 x B14A) for older line crosses and from -0.10 (h^2_W , W, B76 x B84) to 1.25 (h^2_{MW} , MW, B75 x B79) for newer line crosses (Table 6). Estimates of n for older line crosses ranged from n = -0.7 (W, Wf9 x B37) to n = 4.3 (both M&K and MW, L289 x B37) (Table 7). Estimates of n for newer line crosses ranged from n = -0.1 (W, B76 x B84) to n = 6.0 (MW, B75 x B79). Similar to yield, SE for estimates were often as large as the estimates themselves. The greatest values of n were detected in the crosses that had the greatest difference in parental values for tassel branch number for older (L289 and B37) and newer line crosses (B75 and B79).

An arithmetic pooling of estimates over crosses and years provided a mean value for heritability estimates and for estimates of n for the methods evaluated for pre-1960 and post-1970 eras of maize breeding (Tables 8 and 9). A decrease in trend for heritability was detected for grain yield by all methods except B when comparing

Table 5. Estimates of minimum number of genes (n) and standard errors (SE) for grain yield for each of 15 F₂ populations from a diallel cross of six older lines and six newer lines evaluated in four environments.

Cross	Method of Estimation (Table 2)											
	Burton		Mahmud & Kramer		Weber & Moorthy		Modified Weber & Moorthy		Warner		Modified Warner	
	n	SE	n	SE	n	SE	n	SE	n	SE	n	SE
Older lines												
L289 x L317	-0.1	1.0	0.3	5.5	0.3	4.1	0.2	3.1	-0.2	3.6	-0.2	3.5
L289 x M14	-9.5	18.8	20.8	38.2	14.2	26.4	9.8	18.6	-2.8	10.6	-2.8	10.3
L289 x Wf9	-1.9	9.1	7.3	34.9	5.4	25.9	4.1	19.7	-0.9	5.3	-0.8	4.7
L289 x B14A	3.6	10.0	24.3	47.5	19.2	37.7	16.1	31.8	-6.7	17.0	-6.6	15.9
L289 x B37	9.8	38.4	138.9	142.5	109.9	114.2	91.2	96.6	45.6	68.6	46.7	63.6
L317 x M14	-26.3	46.7	23.4	40.8	13.1	23.5	6.1	12.3	-8.1	18.3	-7.9	18.6
L317 x Wf9	-0.8	5.3	4.3	28.3	3.2	21.1	2.5	16.3	1.1	7.7	1.1	7.4
L317 x B14A	1.7	16.5	67.5	124.3	54.6	100.9	45.5	84.4	32.3	62.8	32.4	62.0
L317 x B37	26.9	57.6	207.4	210.1	167.9	171.9	142.2	147.9	1.3	75.7	1.8	63.9
M14 x Wf9	-11.5	26.0	64.9	95.3	48.1	71.4	36.9	55.7	-56.2	87.5	-55.1	85.2
M14 x B14A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
M14 x B37	-1.1	8.0	24.8	49.6	18.5	37.4	14.7	30.1	0.0	0.0	0.4	9.5
Wf9 x B14A	34.1	56.9	98.2	151.0	82.8	127.8	73.3	113.8	41.1	71.6	41.4	68.7
Wf9 x B37	-100.9	110.9	138.6	133.4	84.1	86.8	88.9	91.4	7.2	69.9	7.3	60.5
B14A x B37	27.5	58.6	40.1	84.9	36.6	77.6	34.6	73.4	-27.4	60.2	-27.4	59.4
Newer lines												
B73 x B75	18.0	33.8	32.6	59.6	28.6	52.5	26.3	48.4	-12.1	26.2	-12.1	24.8
B73 x B76	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
B73 x B77	5.5	15.2	26.3	65.3	21.3	53.0	18.2	45.4	-34.4	86.0	-34.5	86.0
B73 x B79	31.5	52.8	55.9	91.4	49.3	80.8	45.6	75.0	-17.6	37.2	-17.4	34.1
B73 x B84	-6.0	16.9	35.7	50.7	24.9	36.2	18.6	28.2	11.7	25.2	12.0	23.9
B75 x B76	-1.2	6.9	17.3	31.1	12.5	22.8	9.6	17.9	-2.3	10.1	-2.1	9.1
B75 x B77	0.0	0.5	1.1	10.3	0.8	7.9	0.7	6.4	-0.9	9.0	-0.9	8.8
B75 x B79	1.0	9.3	1.1	10.2	0.9	8.3	0.8	7.2	0.3	2.6	0.3	2.6
B75 x B84	-22.9	53.4	149.8	122.8	108.4	92.5	82.8	75.6	-97.8	107.4	-96.9	102.6
B76 x B77	-1.4	7.5	22.5	54.9	17.0	41.6	13.6	33.4	8.9	23.3	9.2	23.6
B76 x B79	27.1	44.6	44.3	71.1	39.4	63.5	36.6	59.2	20.9	37.8	20.7	35.6
B76 x B84	2.4	17.4	55.2	76.4	42.3	59.2	34.2	48.7	0.3	24.6	0.6	21.3
B77 x B79	2.1	11.1	9.4	47.8	7.8	39.6	6.7	34.2	6.5	33.1	6.5	33.1
B77 x B84	-1.5	58.4	206.5	196.1	159.9	154.5	128.8	128.2	-27.4	88.1	-27.4	78.3
B79 x B84	50.7	60.9	125.1	103.5	103.4	88.3	92.0	82.0	-111.7	117.8	-111.7	110.7

older with newer line crosses. An increase in heritability for tassel branch number from older to newer line crosses was detected for all methods. Evaluating trends based on arithmetic pooling of mean squares, the ratio of additive genetic variance to phenotypic variance (h_n^2) has decreased for yield, kernel-row number, ear diameter, ear length, kernel depth, and ear height. These changes, however, were not significant at 95% confidence level (as determined by confidence interval overlap, data not shown) and indicate neither a gain nor loss in genetic variance for the traits evaluated due to selection over time.

No change in n was detected from older to newer line crosses for any traits except kernel depth. Selection has seemingly decreased the number of factors affecting kernel depth in the newer lines. Warner's method determined a change in n from 6.6 factors for older line crosses to 0 factors for newer line crosses (Table 9). Estimates of n were detected as 0.0 for some traits because of a lack of difference between parental values, whereas negative estimates were because environmental variances were greater than the total variance. The range of the confidence intervals for negative estimates of n include a positive value. Estimates of n for yield decreased from older to

newer line crosses for all methods except B (-0.9 to 0.8) and W (-0.6 to -0.3). Estimates of n for tassel branch number tended to increase from older line to newer line crosses.

Most of the statistically significant comparisons detected among broad-sense heritability methods occurred for comparisons of B with M&K, W&M, and MW&M. Burton's method does not utilize σ_{we}^2 as determined by the within-plot variation of the parents, whereas the remaining three methods of h_n^2 (M&K, W&M, and MW&M) include the parental within plot component of variation for estimation of σ_{we}^2 . Estimates determined by the M&K, W&M, and MW&M methods did not differ greatly because the formulas are similar. Choice of method for estimating h_n^2 on a single-plant basis is determined by the generations available and researcher preference. The choice of methods, if the F_1 , F_2 , and parental single-plant data are available, could be among any one of these four methods. Estimates may differ because of method used, trait(s) of interest, and cross evaluated. Warner (1952) argued that the use of parental lines as an estimate of the environment would overestimate the variance because weaker plants tend to be more susceptible to environmental extremes.

Table 6. Estimates of narrow- (h_n^2) and broad-sense (h_b^2) heritabilities and their standard errors (SE) for number of tassel branches for each of 15 F_2 populations from a diallel cross of six older lines and six newer lines developed in four environments.

Cross	Method of Estimation (Table 2)											
	Burton		Mahmud & Kramer		Weber & Moorthy		Modified Weber & Moorthy		Warner		Modified Warner	
	h_b^2	SE	h_b^2	SE	h_b^2	SE	h_b^2	SE	h_n^2	SE	h_n^2	SE
Older lines												
L289 x L317	0.21	0.17	0.40	0.14	0.35	0.14	0.31	0.14	0.61	0.34	0.66	0.31
L289 x M14	0.56	0.16	0.51	0.15	0.53	0.15	0.54	0.15	0.34	0.34	0.35	0.33
L289 x Wf9	0.41	0.16	0.34	0.14	0.36	0.14	0.37	0.14	0.63	0.33	0.63	0.32
L289 x B14A	0.36	0.16	0.56	0.15	0.50	0.15	0.47	0.16	0.76	0.33	0.81	0.32
L289 x B37	0.50	0.16	0.63	0.15	0.59	0.15	0.57	0.15	0.61	0.33	0.63	0.31
L317 x M14	0.39	0.16	0.56	0.15	0.51	0.15	0.48	0.15	0.51	0.34	0.54	0.33
L317 x Wf9	0.39	0.16	0.62	0.15	0.55	0.15	0.52	0.15	0.75	0.33	0.75	0.33
L317 x B14A	0.18	0.17	0.59	0.15	0.48	0.15	0.42	0.15	0.14	0.37	0.19	0.37
L317 x B37	0.42	0.16	0.61	0.15	0.56	0.15	0.53	0.15	0.25	0.35	0.28	0.33
M14 x Wf9	0.22	0.17	0.46	0.14	0.39	0.14	0.35	0.14	0.08	0.35	0.11	0.32
M14 x B14A	0.28	0.16	0.46	0.14	0.41	0.14	0.38	0.14	0.00	0.37	0.00	0.33
M14 x B37	0.21	0.17	0.35	0.14	0.31	0.14	0.28	0.14	-0.11	0.38	-0.12	0.34
Wf9 x B14A	0.48	0.16	0.50	0.15	0.49	0.15	0.49	0.15	0.35	0.35	0.39	0.35
Wf9 x B37	0.20	0.17	0.35	0.14	0.30	0.14	0.28	0.14	-0.35	0.41	-0.31	0.38
B14A x B37	0.64	0.16	0.59	0.15	0.60	0.15	0.61	0.15	0.07	0.37	0.07	0.29
Newer lines												
B73 x B75	0.38	0.16	0.77	0.16	0.64	0.16	0.62	0.15	0.28	0.35	0.34	0.34
B73 x B76	0.58	0.16	0.72	0.16	0.52	0.15	0.66	0.16	0.71	0.33	0.71	0.32
B73 x B77	0.40	0.16	0.78	0.16	0.42	0.14	0.64	0.15	0.03	0.34	1.03	0.33
B73 x B79	0.40	0.16	0.79	0.16	0.71	0.16	0.65	0.16	0.97	0.34	0.99	0.33
B73 x B84	0.18	0.17	0.52	0.15	0.43	0.15	0.37	0.14	0.53	0.33	0.59	0.31
B75 x B76	0.32	0.16	0.72	0.16	0.62	0.16	0.57	0.15	0.39	0.34	0.45	0.30
B75 x B77	0.47	0.16	0.87	0.17	0.79	0.17	0.73	0.16	0.30	0.35	0.59	0.30
B75 x B79	0.49	0.16	0.84	0.17	0.77	0.16	0.71	0.16	0.93	0.34	1.25	0.35
B75 x B84	0.41	0.16	0.78	0.17	0.70	0.16	0.64	0.16	0.52	0.35	0.94	0.32
B76 x B77	0.39	0.16	0.61	0.15	0.55	0.15	0.65	0.16	0.23	0.36	0.51	0.30
B76 x B79	0.23	0.17	0.61	0.15	0.51	0.15	0.46	0.15	-0.03	0.37	0.00	0.34
B76 x B84	0.30	0.16	0.42	0.14	0.38	0.14	0.36	0.14	-0.10	0.38	-0.03	0.35
B77 x B79	0.47	0.16	0.73	0.16	0.66	0.16	0.62	0.15	0.65	0.33	0.65	0.31
B77 x B84	0.41	0.16	0.58	0.15	0.53	0.15	0.50	0.15	0.36	0.34	0.37	0.30
B79 x B84	0.35	0.16	0.56	0.15	0.50	0.15	0.47	0.14	0.31	0.34	0.31	0.32

Assumptions, such as exclusive additive genetic variance, are strict and errors large. Standard errors calculated for the study were large and may be grossly underestimated (Zeng et al., 1990).

The variation in estimates of heritability was as great among methods of estimation as among crosses. One consistent concern in the estimation of heritability has been the separation of σ_{we}^2 and σ_{wg}^2 for the variability among individual phenotypes. Different combinations of generations for the estimation of σ_{we}^2 have been suggested (Table 1). The type of crop species (autogamous vs. allogamous) studied could affect the estimates of σ_{we}^2 . The differences in relative vigor between P_1 and P_2 and F_1 would be expected to be less for autogamous crop species as compared with allogamous crop species. Estimates of σ_{we}^2 derived from P_1 , P_2 , and F_1 of autogamous species may be more similar than for allogamous crop species. For maize, there was concern that the estimates of σ_{we}^2 may be overestimated among P_1 and P_2 individuals and underestimated among F_1 individuals because of vigor differences relative to the variation among

the heterogeneous F_2 , BC1, and BC2 individuals. Different combinations for pooling the variability among P_1 , P_2 , and F_1 generations have been suggested to alleviate concerns about the σ_{we}^2 estimates derived from homogeneous vs. heterogeneous populations (Table 1). Warner (1952) suggested a method that did not include the homogeneous P_1 , P_2 , and F_1 generations to separate σ_{we}^2 and σ_w^2 for estimation of heritability. Warner's method included only the heterogeneous F_2 and BC1 and BC2 generations, which would eliminate the concerns for either the underestimation (F_1) or overestimation (P_1 and P_2) of σ_{we}^2 . Warner's method, however, provides an estimate of the additive genetic variance (σ_A^2), whereas the other methods estimate the total genetic variance (σ_G^2).

Comparisons among methods of estimation for grain yield show that the Burton (1951) and Warner (1952) estimates were relatively smaller and similar among crosses compared with relatively greater estimates among crosses for the Mahmud and Kramer (1951) and Weber and Moorthy (1952) methods. Burton (1951) used the F_1

Table 8. Broad- (h_b^2) and narrow- (h_n^2) sense heritability estimates and standard errors (SE) for eight agronomic traits averaged over crosses for two sets of lines (Older and Newer) and all crosses (All), determined by an arithmetic pooling of mean squares.

Trait	Method of Estimation											
	Burton		Mahmud & Kramer		Weber & Moorthy		Modified Weber & Moorthy		Warner		Modified Warner	
	h_b^2	SE	h_b^2	SE	h_b^2	SE	h_b^2	SE	h_n^2	SE	h_n^2	SE
Yield												
Older	-0.01	0.18	0.66	0.15	0.51	0.15	0.41	0.15	-0.00	0.37	-0.00	0.34
Newer	0.13	0.17	0.60	0.15	0.48	0.15	0.41	0.14	-0.06	0.37	-0.06	0.32
All	0.06	0.18	0.63	0.15	0.50	0.15	0.41	0.14	-0.03	0.37	-0.03	0.33
Kernel-row number												
Older	0.38	0.16	0.26	0.14	0.31	0.14	0.33	0.14	0.32	0.34	0.34	0.32
Newer	0.37	0.16	0.36	0.14	0.38	0.14	0.35	0.14	0.14	0.35	0.15	0.32
All	0.37	0.16	0.32	0.14	0.35	0.14	0.35	0.14	0.24	0.35	0.25	0.32
Ear diameter												
Older	0.50	0.16	0.38	0.14	0.44	0.14	0.50	0.15	0.31	0.34	0.38	0.32
Newer	0.40	0.16	0.42	0.14	0.43	0.14	0.43	0.14	-0.20	0.39	-0.16	0.34
All	0.46	0.15	0.31	0.14	0.43	0.14	0.47	0.15	0.08	0.36	0.12	0.33
Ear length												
Older	0.28	0.16	0.36	0.14	0.33	0.14	0.32	0.14	-0.01	0.37	0.00	0.34
Newer	0.37	0.16	0.39	0.14	0.39	0.14	0.38	0.14	-0.04	0.37	0.00	0.32
All	0.30	0.16	0.37	0.14	0.36	0.14	0.34	0.14	-0.03	0.37	-0.00	0.33
Kernel depth												
Older	0.35	0.16	0.14	0.14	0.28	0.14	0.26	0.14	0.37	0.34	0.39	0.32
Newer	0.44	0.16	0.30	0.14	0.35	0.14	0.38	0.14	-0.06	0.37	-0.03	0.33
All	0.38	0.16	0.20	0.14	0.30	0.14	0.30	0.14	0.18	0.35	0.18	0.32
Tassel-branch number												
Older	0.37	0.16	0.52	0.15	0.47	0.15	0.45	0.14	0.39	0.33	0.41	0.32
Newer	0.39	0.16	0.69	0.16	0.58	0.15	0.58	0.15	0.53	0.33	0.62	0.31
All	0.37	0.16	0.60	0.15	0.52	0.15	0.51	0.15	0.44	0.33	0.50	0.32
Plant height												
Older	0.57	0.16	0.59	0.15	0.59	0.15	0.59	0.15	0.36	0.34	0.34	0.31
Newer	0.70	0.16	0.70	0.16	0.68	0.16	0.70	0.16	0.44	0.34	0.48	0.31
All	0.63	0.16	0.64	0.15	0.64	0.15	0.64	0.15	0.41	0.34	0.41	0.31
Ear height												
Older	0.51	0.16	0.65	0.15	0.61	0.15	0.59	0.15	0.54	0.33	0.53	0.32
Newer	0.58	0.16	0.57	0.15	0.58	0.15	0.58	0.15	0.37	0.34	0.36	0.31
All	0.54	0.16	0.61	0.15	0.59	0.15	0.58	0.15	0.46	0.33	0.46	0.31

generation to estimate σ_{we}^2 and broad-sense heritabilities, whereas Warner (1952) obtained a direct estimate of σ_A^2 to estimate narrow-sense heritabilities. But the Burton (1951) and Warner (1952) methods had, on the average, similar heritability estimates (Table 8). Mahmud and Kramer (1951) and Weber and Moorthy (1952) estimated σ_{we}^2 as geometric mean of variability among P₁ and P₂ individuals and among P₁, P₂, and F₁ individuals, respectively. Estimates of broad-sense heritabilities for grain yield among crosses (Table 4) and average of crosses (Table 8) were similar for the methods of Mahmud and Kramer (1951) and Weber and Moorthy (1952). For these 30 F₂ populations, there was a large disparity among methods of estimation for grain yield. Measurements for the same generations and individuals were used for all methods; hence, the differences in heritabilities among methods estimation were because of the methods used to separate σ_{we}^2 and σ_{wg}^2 .

The differences among methods in estimates of heritability for number of tassel branches were not as great as for grain yield. The

trends among methods of estimation for number of tassel branches were similar to those for grain yield, but the estimates of heritability were greater for number of tassel branches (Table 8). The estimates of heritability for number of tassel branches, however, were not as consistent for both groups of lines as were the estimates for grain yield.

Estimates of broad-sense heritability were consistent among the methods of Burton (1951), Mahmud and Kramer (1951), and Weber and Moorthy (1952) for all traits except grain yield (Table 8). Warner's (1952) method provides an estimate of σ_A^2 , and the narrow-sense heritability estimates were smaller, as expected, than the other methods for all traits and both groups of lines. It seems that the inclusion of the parents (P₁ and P₂) to estimate σ_{we}^2 for grain yield provided more consistent estimates of heritability among crosses than use of only the F₁ generation to estimate σ_{we}^2 or of Warner's method, which did not include the P₁, P₂, and F₁ generations (Table 4). Fifteen of the 30 crosses had negative narrow-sense heri-

Table 9. Estimates of the minimum number of genes (n) and standard errors (SE) for eight traits averaged over crosses for two sets of lines (Older and Newer) and all crosses (All) determined by an arithmetic pooling of mean squares.

Trait	Method of Estimation											
	Burton		Mahmud & Kramer		Weber & Moorthy		Modified Weber & Moorthy		Warner		Modified Warner	
	n	SE	n	SE	n	SE	n	SE	n	SE	n	SE
Yield												
Older	-0.9	21.4	76.2	104.6	59.1	81.8	48.0	67.4	-0.6	30.1	-0.3	26.3
Newer	0.8	4.5	3.6	20.2	2.9	16.3	2.5	13.9	-0.3	2.5	-0.4	2.5
All	2.5	9.6	28.3	60.4	22.3	47.8	18.5	39.8	-1.5	12.1	-1.5	10.5
Kernel-row number												
Older	0.1	0.1	0.1	0.0	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.1
Newer	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
All	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ear diameter												
Older	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Newer	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
All	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ear length												
Older	0.1	0.1	0.2	0.1	0.2	0.1	0.2	0.1	0.0	0.1	0.0	0.1
Newer	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
All	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kernel depth												
Older	6.2	2.8	2.3	2.4	5.1	2.4	4.7	2.6	6.6	4.2	7.0	3.2
Newer	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
All	1.5	0.6	0.8	0.5	1.2	0.5	1.2	0.6	0.7	1.0	0.7	0.8
Tassel-branch number												
Older	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.1
Newer	0.3	0.2	0.6	0.2	0.5	0.2	0.5	0.2	0.4	0.3	0.5	0.2
All	0.2	0.1	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Plant height												
Older	10.8	28.6	11.1	29.5	11.2	29.7	11.1	29.5	6.9	18.8	6.5	17.4
Newer	6.1	20.3	6.0	20.1	5.9	19.7	6.1	20.3	3.8	13.0	4.2	14.0
All	8.4	24.7	8.5	25.0	8.4	24.7	8.5	25.0	5.4	16.1	5.5	16.2
Ear height												
Older	30.3	28.1	39.3	35.5	36.9	33.4	35.5	32.5	32.4	31.6	31.7	29.4
Newer	0.1	1.8	0.1	1.8	0.1	1.8	0.1	1.8	0.1	1.2	0.1	1.2
All	7.4	13.2	8.4	15.0	8.2	14.5	8.0	14.5	6.4	11.7	6.3	11.3

tability estimates for grain yield with Warner's method. It seems that $\sigma_{w_e}^2$ was not consistent for the F_2 , BC1, and BC2 generations. By pooling the BC1 and BC2 generations, the expected frequency of genotypes in BC1 and BC2 generations is similar to that of the F_2 generation. But the frequencies of genotypes within the BC1 and BC2 generations are different from that for the F_2 generation. It seems that the estimates of $\sigma_{w_e}^2$ in the BC1 and BC2 generations were greater than in the F_2 generation for some crosses. The Warner (1952) method was developed to remove the problems associated with the estimation of $\sigma_{w_e}^2$ and the method intuitively seems preferable to the other methods. Either the estimates of $\sigma_{w_e}^2$ were overestimated by the Warner (1952) method or the additive genetic variance (σ_A^2) was small compared with the total genetic variance for some F_2 populations.

Populations (F_2 , BC1, and BC2) produced from crosses of specific pairs of inbred lines are unique. The total genetic variance ($\sigma_{w_g}^2$), the additive genetic variance (σ_A^2), and the environmental variance among plants ($\sigma_{w_e}^2$) will vary among populations because of differences in parental genotypes and the effects of the environment on specific genotypes. The greater the differences in number of alleles between the two parents (P_1 and P_2), the greater is the expected genetic variability within F_2 , BC1, and BC2 populations. The extent of the genetic variability will affect selection directly for different traits within the same cross and the same trait in different crosses. All these factors will have to be considered if MAS is used within F_2 , BC1, and BC2 generations. The effectiveness of MAS will be affected in the same manner as the methods of selection used in classical pedigree selection methods, given the same number and coverage of molecular markers throughout the genome for each F_2 population. The greater the number of distinct alleles between the two parents, the greater is the likelihood that MAS will enhance selection. The relative success of MAS will be similar to that expected in the classical pedigree selection methods, based primarily on the phenotypes. It is envisioned, however, that MAS will enhance the effectiveness of selection based on phenotypes, but adequate markers and linkage of markers with loci affecting the traits considered in selection will be necessary. MAS will be more effective for some traits (e.g., plant height) than for other traits (e.g., grain yield) because of the trait's

relative complexity. But Lande (1992) has suggested that MAS will be more efficient than phenotypic selection for traits having lower heritabilities than for traits having higher heritabilities. The effectiveness of MAS also will vary among F_2 populations because of differences in heritabilities and minimum numbers of effective factors for the same trait.

REFERENCES

- BURTON, G.W. 1951. Quantitative inheritance in pearl millet (*Pennisetum glaucum*). *Agron. J.* 43:409-417.
- DICKERSON, G.E. 1969. Techniques for research in quantitative animal genetics. p. 36-79. In *Techniques and procedures in animal science research*. American Society Animal Science, Albany, NY.
- FALCONER, D.S. 1981. *Introduction to quantitative genetics*. 2nd ed. Longman, Inc., New York.
- GERDES, J.T., C.F. BEHR, J.G. COORS, and W.E. TRACY. 1993. *Compilation of North American Maize Breeding Germplasm*. Crop Science Society America, Madison, WI.
- LANDE, R. 1981. The minimum number of genes contributing to quantitative variation between and within populations. *Genetics* 99:541-553.
- LANDE, R. 1992. Marker assisted selection in relation to traditional methods of plant breeding. p. 437-451. In H.T. Stalker and J.P. Murphy (ed.) *Plant Breeding in the 1990s*. CAB International, Melksham, UK.
- LANDE, R., and R. THOMPSON. 1990. Efficiency of marker-assisted selection in the improvement of quantitative traits. *Genetics* 124:743-756.
- MAHMUD, I., and H.H. KRAMER. 1951. Segregation for yield, height, and maturity following a soybean cross. *Agron. J.* 43:605-609.
- WARNER, J.N. 1952. A method for estimating heritability. *Agron. J.* 44:427-430.
- WEBER, C.R., and B.R. MOORTHY. 1952. Heritable and nonheritable relationships and variability of oil content and agronomic characters in the F_2 generation of soybean crosses. *Agron. J.* 44:204-209.
- WRIGHT, S. 1952. The genetics of quantitative variability. p. 5-41. In E.C.R. REEVE and C.H. WADDINGTON (ed.) *Quantitative Inheritance*. H. M. Stationery Office, London.
- ZENG, Z.B., D. HOULE, and C.C. COCKERHAM. 1990. How informative is Wright's estimator of the number of genes affecting a quantitative character? *Genetics* 126:235-237.