

ESTIMATES OF GENETIC HOMEOSTASIS IN MAIZE*

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ABSTRACT

Genetic homeostasis was estimated in maize (*Zea mays* L.) in order to determine whether selection has affected homeostasis and to determine whether homeostasis is heritable. A group of six inbred lines released before the 1960's, and another group of six, released after the 1970's, were used to develop single cross, F₂, and backcross generations. The experiments were conducted at two Iowa locations in 1985 and 1986. Individual plant measurements were taken for eight maize traits. Estimates of genetic homeostasis were obtained using a proportional measure of the environmental variance contained in the within-plot variance, the magnitude of the genotype x environment interaction, and the coefficient of variation.

Genetic homeostasis depended on the level of heterozygosity and heterogeneity of the maize genotypes and populations. The newer lines were more homeostatic than the older lines. The inbred lines were consistent for transmitting in a heritable manner the homeostatic effects, either good or bad, to their single cross, F₂, and backcross generations. In most instances, the eight traits measured followed the same tendency in all comparisons among generations within both groups. Kernel depth, however, did not have a regular pattern of transmission of the homeostatic effects across generations.

INTRODUCTION

Homeostasis is a mechanism by which living organisms achieve phenotypic stability. Homeostasis was defined as self-regulation (genetic, physiological, or mor-

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phological) of populations of plants and animals against any fluctuating and sudden change in the external environment. The concept of self-regulation was first suggested by Claude Bernard in 1865 and termed homeostasis by Cannon (1932). Lerner (1954) distinguished two types of homeostasis: genetic homeostasis was the property of a population of genotypes to resist sudden changes, whereas developmental homeostasis was the ability of individual genotypes to adapt themselves to variable conditions. Similar concepts were defined as populational homeostasis and individual homeostasis by Lewontin (1957) and populational buffering and individual buffering by Allard and Bradshaw (1964).

Genetic and developmental homeostasis have been recognized as two mechanisms of stability in improved crop cultivars. Plant breeders emphasize the development of new improved cultivars with greater yield and yield stability. To select for stability, breeders consider the implications of genotype x environment interactions. On the basis of individual contribution of cultivars, homeostasis seems to be another manifestation of genotype x environment interaction.

It has been found that heterozygous and/or heterogeneous individuals or populations were more homeostatic than homozygous and/or homogeneous individuals or populations (Adams and Shank, 1959; Reich and Atkins, 1970; Schnell and Becker, 1985). Homeostasis was inversely proportional to the variability expressed by the individuals. Therefore, most of the estimates of homeostasis were based on measurements of variability among individuals.

Shank and Adams (1960) used the coefficient of variability to measure homeostasis in maize (*Zea mays* L.). They compared homeostasis between maize inbred lines and their single crosses. This type of estimate, however, may be affected by the mean (greater or lesser) of the maize lines studied. Difficulties in estimating homeostasis probably has limited the studies reported in maize.

Our objective was to estimate genetic homeostasis in maize by using the environmental variance obtained on an individual-plant basis for two groups of maize lines. Comparisons were made between the "older" and the "newer" groups of lines to determine whether selection has affected the relative homeostasis and to determine whether relative homeostasis of the lines was heritable.

MATERIALS AND METHODS

The maize plant materials included six relatively old inbred lines (B14A, B37, L289, L317, M14, and WF9) and six relatively new inbred lines (B73, B75, B76, B77, B79, and B84). The older inbred lines were available for commercial use between 1926 and 1958, whereas the newer inbred lines were released between 1972 and 1978. Three generations were produced from each group of six inbred lines in the following

manner. Fifteen single crosses were produced for each set of six inbred lines. Each single cross was selfed to produce an F₂-generation, and each single cross was mated to its respective parents to produce a pair of backcrosses. Thus, 66 entries (six lines, 15 F₁, 15 F₂, and 30 backcrosses) were obtained from each group of inbred lines for a total of 132 entries included for evaluation. The entries represented different genetic structures. The parents, or inbred lines, were homogeneous and homozygous, whereas the single crosses were homogeneous and heterozygous. The F₂ and backcross generations were heterogeneous and heterozygous.

A randomized complete block with three replications was used as the field design. Because the different generations had different levels of vigor, a restricted randomization was used. Each generation of the relatively old and new lines was planted in one subblock. Each replication, therefore, included five subblocks or generations, one each for inbred lines, single crosses, F₂-generations, backcrosses to one parent (BC1), and backcrosses to the other parent (BC2). Border rows that included materials of similar vigor were included around each subblock. The field plots included two rows for all entries except the inbred lines, which included four rows. Each experiment was machine planted with 26 seeds in rows 5.5 m long with 76 cm between rows. The rows of each plot were thinned at the 5- to 7-leaf stage to 21 plants to provide uniform stands with well-spaced distributions within the rows. After thinning, equivalent stand densities were 50,230 plants per hectare for all entries. Recommended fertilizer and herbicide treatments for high productivity were used for each experiment.

Data for the 132 entries were collected in four experiments (two locations near Ames, Iowa) and two years (1985 and 1986). Data were collected from five competitive plants within each row of each plot. Hence, 20 individual plants were measured for the inbred lines, and 10 plants were measured for the other generations within each plot. Data were collected for eight traits. Plant and ear height and tassel branch number data were taken after all plants had completed flowering. Plant height (cm) was measured from ground level to base of tassel. Ear height (cm) was measured from ground level to nodal attachment of top ear. Number of primary tassel branches was counted for each tassel. Ear measurements and yield data were taken after the harvested ears were dried in forced-air dryers for 4 days at 46°C. Grain moisture was 6% after drying. Ear length (cm), ear diameter (cm), number of kernel rows, and kernel depth (cm) were recorded for harvested ears. Yield (gm) was determined for the shelled grain of each ear after the ear measurements were completed.

Analyses of variance were calculated for each environment and combined over the four environments for each trait. Analyses of variance were based on individual plant data. Entries sum of squares were partitioned for each generation, and each generation was further partitioned in the old and new groups of lines. A

combined analysis of variance over environments was performed for each of the 132 entries and their eight plant and ear traits. The within-plot mean square per entry provided a direct estimate of the environmental variance for the homogeneous populations, such as the inbred lines and single crosses. An unique estimate of the environmental variance was obtained by using the geometric mean of the within-plot estimates of the homogeneous populations. A separate estimate of the environmental variance was obtained for the old and for the new groups of lines. The value of the geometric mean, or estimated environmental variance, was assumed to be the same for all populations within the old and new groups of lines. For comparison purposes, a proportion of that environmental variance was calculated for each generation. That is, the proportion of the estimated environmental variance was extracted from the within-plot variance and expressed as a percentage. The calculation was

$$\% \sigma_{we}^2 = \frac{\hat{\sigma}_{we}^2}{\hat{\sigma}_w^2} \times 100$$

where $\hat{\sigma}_w^2$ is the total within-plot variance of the segregating populations (F₂, BC1, and BC2), and $\hat{\sigma}_{we}^2$ is the within-plot environmental variance of the homogeneous populations (parents and F₁'s).

In several instances, however, values greater than 100% were obtained, particularly for the inbred lines, because their within-plot variance was lower than the single crosses. Problems of scale and heterogeneity of variances probably caused estimates greater than 100% (Byrd, 1955). Nevertheless, the magnitude of the proportion ($\% \hat{\sigma}_{we}^2$) was estimated for comparisons of homeostasis.

In addition to the estimates of within-plot variance, the genotype x environment interactions and coefficients of variation ($\hat{\sigma}/\bar{x} \times 100$) were calculated to assist in the determination of homeostasis for the two groups of lines and lines within groups. Correlations were calculated to determine the extent of association between within-plot variance, coefficients of variation, and the mean for each trait within the two groups of lines.

RESULTS AND DISCUSSION

Populations and Homeostasis

Significant differences ($P \leq 0.05$ or ≤ 0.01) were detected for all sources of variation of main effects and interactions of main effects with environments for most traits (analyses not shown). The magnitudes of the mean squares for interaction

effects can be used as preliminary estimates of homeostasis among populations (Table I). The homogeneous inbred line and single-cross entries, in most instances, had greater genotype x environment interaction mean squares than did the heterogeneous F₂ and backcross populations. Comparisons of inbred lines with single crosses showed that the inbred lines had greater genotype x environment interactions than the single crosses for ear diameter, kernel rows, kernel depth, and ear and plant height, but the inbred lines had smaller interactions for yield, ear length, and tassel branches than the single crosses. The interactions of entries x environments of the entries for the new lines tended to be less than for the old lines for all traits except kernel depth (Table I). Interactions of entries x environments were not significant for number of kernel rows for both groups of lines. Among the 32 interactions included in Table I for each group of lines (four generations and eight traits), 23 were significant for old lines and 15 were significant for new lines. Significant interactions were detected for each generation of both groups of lines for grain yield except for the F₂ generation of the new lines. The relative magnitude of the interaction of the new lines with environments, however, was 27.4% less than for the old lines (Table I).

The same trends shown for the genotype by environmental interactions were exhibited by the proportion of the environmental variance and the coefficient of variation (Table II). For grain yield, the estimates of the proportion of the within-plot environmental variance ($\% \hat{\sigma}_{we}^2$) for inbred lines were 2.65 times greater than the average (60) of the single cross, F₂, and backcross generations. The F₁ hybrids showed a relatively higher proportion of environmental variance (63%), as compared with the F₂ (59%) and backcross (58%) generations for yield. Ear length, ear and plant height, and number of tassel branches exhibited the same trend as for yield. Ear diameter, kernel rows, and kernel depth for the inbred lines had smaller estimates of $\hat{\sigma}_{we}^2$ than for the single crosses, but the estimates of $\hat{\sigma}_{we}^2$ were greater than for the F₂ and backcross generations. The coefficients of variation (CV) also had higher values for inbred lines than for single crosses, but were similar to the CV's for the heterogeneous F₂ and backcross populations. The mean affected the estimates of the coefficients of variation because the mean was highly and negatively correlated with the CV's (data not shown).

With a few exceptions for some traits, inbred lines were less homeostatic than the single crosses, and the F₂ and backcross generations were the most homeostatic populations. Hence, heterogeneous and/or heterozygous maize populations were more homeostatic than homogeneous and/or homozygous populations. Similar findings have been reported for *Drosophila* (Dobzhansky and Levene, 1951), *Sorghum bicolor* Moench (Reich and Atkins, 1970), and maize (Sprague and Federer, 1951; Jones, 1958; Shank and Adams, 1960; Rowe and Andrew, 1964; Eberhart and Russell, 1969; Schnell and Becker, 1985).

Table I - Combined analyses of variance of the mean square interactions for all populations and their corresponding partitions for the old and new maize lines evaluated in four environments (env.) for eight plant and ear traits.

Source	df	Grain yield	Ear		Kernel		Height		Tassel branches
			Length	Diameter	Rows	Depth	Ear	Plant	
		q/ha	cm/10		no.	cm/10	cm		no.
Entries x env.	393	1239**	20**	4**	8**	0.8**	875**	3273**	49**
Old lines	195	1407**	25**	4**	6	0.7*	895**	3386**	59**
New lines	195	1021**	10	3	4	0.8**	741**	3025**	28**
Parents x env.	33	1336**	18**	12**	19**	2.0**	942**	3399**	53**
Old lines	15	1241**	22**	15**	10**	2.0**	874**	2963**	45**
New lines	15	1602**	12	8**	6	1.8**	1179**	4132**	38**
Single cross x env.	87	1690**	23**	3	7**	0.7**	505**	1619**	77**
Old lines	42	2104**	26**	3**	4	0.6	543**	1772**	62**
New lines	42	1226	12	2**	3	0.6	273	811	30
F2 x env.	87	1056**	20**	4**	6**	0.8**	625**	14128*	33
Old lines	42	1198**	25**	4**	7	0.7**	352	837	36
New lines	42	937	11	2**	4	0.5	540**	1498**	29
Backcrosses x env.	177	927**	17**	3	7**	0.6	588**	1647**	41**
Old lines	87	986*	23**	3	5	0.5	689**	1666**	55**
New lines	87	809**	7	3	4	0.6**	444**	1573**	22
Among generations	9	4429**	57**	4**	16**	1.3**	12267**	68767**	76**
Pooled error	1048	706	10	2	5	0.6	336	704	26
Within-plot error	15696	322	6	1	3	0.3	113	187	7

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

Heterozygote superiority, as discussed by Lerner (1954), can be a major explanation for better homeostasis in populations containing higher levels of heterozygosity over those with none or reduced levels of heterozygosity. Diverse ideas have been postulated to explain heterozygous advantage. Some attribute it to a greater biochemical versatility where pairs of enzymes cover a greater range of optimal conditions for different types of stress than single enzymes expressed from homozygous loci (Shank and Adams, 1960). An enzyme can be governed by the action of one or more genes in the heterozygous condition or from interacting alleles at different loci. A greater number of different alleles can provide more versatility in producing enzymes that can follow alternative pathways of biosynthesis functioning against changing environments.

Table II - Estimates of genetic homeostasis in different maize generations as measured by $\% \hat{\sigma}_{we}^2$ and the CV for both groups of lines and over four environments for eight traits.

Generations	Statistic ^a	Ear		Kernel		Height		Tassel branches	
		Grain yield	Length	Diameter	Row	Depth	Ear		Plant
		q./ha	cm	cm ^b	no.	cm ^b	cm	no.	
Inbred lines	$\hat{\sigma}_w^2$	136	4.1	1.1	2.7	0.33	64	102	4.4
	$\hat{\sigma}_{we}^2$, %	159	103	79	95	83	107	99	118
	CV, %	36	16	9	12	28	10	6	21
	Mean	33	13	38	14.1	6.4	82	171	10.2
Single crosses	$\hat{\sigma}_w^2$	343	4.4	0.7	2.4	0.23	74	100	6.2
	$\hat{\sigma}_{we}^2$, %	63	97	122	105	120	93	101	85
	CV, %	24	12	6	10	17	7	4	20
	Mean	79	18	45	15.7	9.1	118	226	12.2
F2's	$\hat{\sigma}_w^2$	364	6.5	1.3	3.7	0.40	161	271	9.9
	$\hat{\sigma}_{we}^2$, %	59	65	69	68	69	43	37	53
	CV, %	31	16	8	13	24	13	8	30
	Mean	61	16	43	15.2	8.2	100	199	10.4
Backcrosses	$\hat{\sigma}_w^2$	370	6.4	1.2	3.3	0.37	125	214	7.7
	$\hat{\sigma}_{we}^2$, %	58	2.1	73	76	74	55	47	68
	CV, %	31	16	8	12	24	11	7	26
	Mean	62	16	43	15.2	8.2	100	200	10.8
Geometric mean	$\hat{\sigma}_{we}^2$	216	4.2	0.9	2.5	0.28	69	101	5.2

^a $\hat{\sigma}_w^2$ is the pooled within-plot variation of each generation; $\hat{\sigma}_{we}^2$ is the geometric mean of the pooled within-plot variation of the homogeneous generations (F₁ and parents); $\% \hat{\sigma}_{we}^2$ was calculated as $\hat{\sigma}_{we}^2 / \hat{\sigma}_w^2$; and CV is the coefficient of variation calculated as $(\sigma / \bar{X}) \times 100$.

^b X 10.

Old vs. New Lines for Homeostasis

The entry \times environment mean squares were greater for the old lines for all traits except number of kernel rows (Table I). Estimates of the environmental variance obtained by the geometric mean show that estimates of environmental variance were smaller for the newer lines than the estimates for the older lines for all traits (Table III). The same pattern also was shown by the CV and the $\% \sigma_{we}^2$. These data suggest that the newer lines were more homeostatic than the older lines. Selection for improved performance of the new lines themselves and in hybrids also included homeostasis or greater stability. Geometric means of the old lines were greater than for the new lines in all instances (Table III).

Transmission of Homeostatic Effects for Yield

Estimates of genetic homeostasis for yield of each line are presented in Tables IV and V for the old and new lines, respectively. Each cell of Tables IV and V includes data in four rows, which correspond to the single cross (F₁), F₂, backcross 1 (BC1), and backcross 2 (BC2) generations. The data in the cells correspond to the combination of the two inbred lines included in the diallel set of crosses for the new and old lines. Data are the proportion of variance ($\% \sigma_{we}^2$).

WF9 had the smallest estimate of σ_{we}^2 (129%), whereas M14 had the greatest value (219%) for the old set of lines (Table IV); thus, WF9 was the more homeostatic inbred line. Intermediate homeostasis was exhibited by B14A, B37, and L317, while the least homeostatic lines were M14 and L289. By tracing the homeostatic effects of the inbred lines through their F₁, F₂, and backcross generations, WF9 averaged over generations contributed the greatest homeostasis (56%). The least homeostatic lines, M14 and L289, had average homeostatic effects of 70 and 64%, respectively. On the average, WF9 had good general homeostatic effects for single-cross (52%), F₂ (57%), BC1 (60%), and BC2 (56%) generations. The least homeostatic inbred lines, M14 and L289, conferred poorer homeostatic effects for single cross (64 and 65%), F₂ (73 and 69%), BC1 (67 and 68%), and BC2 (77 and 67%) generations. Averaged over generations, WF9 contributed 12.5% greater homeostasis than did M14 and L289. Specific homeostatic effects indicate that WF9 was superior in combinations with L317 (best with 47% for BC1 and good with 47% for F₁), B14A (F₂, 45%, good), L289 (F₁, 47%, good), and M14 (BC2, 39%, good). L289 and M14 had the poorest estimates of contributed homeostasis, and poor homeostatic effects were observed in F₂ (88%), BC1 (78%), and BC2 (92%) generations from the cross of L289 and M14.

Table III - Estimates of genetic homeostasis for both groups and for the old and new groups of maize lines for eight traits over four generations and four environments.

Population	Statistic ^a	Ear		Kernel		Height		Tassel branches	
		Grain yield	Length cm	Diameter cm ^b	Row no.	Depth cm ^b	Ear cm		Plant cm
Both groups	$\hat{\sigma}_w^2$	322	5.6	1.1	3.1	0.34	113	187	7.4
	$\hat{\sigma}_{we}^2$, %	67	76	80	82	81	61	54	71
	CV, %	30	15	8	12	23	11	7	25
	Mean	60	15.7	42.4	15.1	8.1	102	201	10.9
Old lines	$\hat{\sigma}_w^2$	345	6.8	1.3	3.2	0.39	121	198	8.6
	$\hat{\sigma}_{we}^2$, %	67	78	75	84	87	62	59	74
	CV, %	33	16	9	12	26	11	7	26
	Mean	56	16.2	41.3	14.7	7.7	101	203	11.3
New lines	$\hat{\sigma}_w^2$	299	4.4	0.9	3.0	0.30	106	175	6.2
	$\hat{\sigma}_{we}^2$, %	67	72	73	79	70	59	49	65
	CV, %	27	14	7	11	20	10	7	24
	Mean	64	15.2	43.6	15.5	8.5	102	200	10.5
Geometric mean-entries,	$\hat{\sigma}_{we}^2$	216	4.2	0.9	2.5	0.28	69	101	5.1
Geometric mean-old lines,	$\hat{\sigma}_{we}^2$	230	5.3	1.0	2.7	0.34	75	117	6.4
Geometric mean-new lines,	$\hat{\sigma}_{we}^2$	200	3.2	0.7	2.3	0.21	63	85	4.1

^a $\hat{\sigma}_w^2$ is the pooled within-plot variation of each generation, $\hat{\sigma}_{we}^2$ is the geometric mean of the pooled within-plot variation of the homogeneous generations (F_1 and parents); % $\hat{\sigma}_{we}^2$ was calculated as $\hat{\sigma}_{we}^2 / \hat{\sigma}_w^2 \times 100$; and CV is the coefficient of variation.

^b $\times 10$.

Table IV - Estimates of genetic homeostatic effects (% $\hat{\sigma}_{we}^2$ ^a) for yield in old maize inbred lines and their generations^b.

Lines (BC1)		Lines (BC2)						Average
		B14A	B37	L289	L317	M14	WF9	
B14A	F ₁	172	97	84	43	67	60	70
	F ₂		52	76	43	53	45	54
	BC1		49	81	56	55	73	63
	BC2		37	62	48	76	42	53
Average								60
B37	F ₁		151	62	52	72	49	67
	F ₂			59	47	74	68	60
	BC1			61	54	67	63	59
	BC2			74	42	83	76	63
Average								62
L289	F ₁			211	64	69	47	65
	F ₂				67	88	55	69
	BC1				68	78	53	68
	BC2				52	92	53	67
Average								67
L317	F ₁				173	55	47	52
	F ₂					89	52	60
	BC1					71	47	60
	BC2					94	72	62
Average								58
M14	F ₁					219	56	64
	F ₂						62	73
	BC1						65	67
	BC2						39	77
Average								70

Continued

Table IV - Continued

Lines (BC1)	Lines (BC2)						Average
	B14A	B37	L289	L317	M14	WF9	
WF9	F ₁					129	52
	F ₂						57
	BC1						60
	BC2						56
Average							56
P ₁	F ₁					176	62
	F ₂						62
	BC1						63
	BC2						63
Average							62
Grand mean							85

^a $\frac{\hat{\sigma}_{we}^2}{\sigma_{we}^2 / \sigma_w^2} \times 100$ is the proportion of the within-plot variability due to environmental effects calculated as

^b P = inbred lines, F₁ = single cross, F₂ = segregating generation, BC1 = backcross using the inbred line of the row as the recurrent parent, and BC2 = backcross using the inbred line of the column as the recurrent parent.

B77 (127%), B79 (134%), and B84 (135%) exhibited similar homeostatic effects for the group of new lines for yield (Table V). B77 and B79 have prolific tendencies, and this may have contributed to homeostasis for yield, particularly for different environments. B73 was intermediate (159%), and B76 (167%) and B75 (177%) were the least homeostatic for yield. The best general homeostatic effects in crosses were expressed by B77 (53%), and the best consistency for homeostasis for the other generations also was expressed by B77 (51%); B77 always had the lowest percentage of σ_{we}^2 in each generation. B77 also was involved in the best two specific homeostatic effects in crosses with B79 (45%) and B84 (46%); both of these crosses were the best in the F₂ (37 and 46%) and BC2 (41%) generations. The best specific homeostatic effect expressed in the BC2 was B77 x B73 (25%), and the poorest homeostatic inbred lines, B75 (177%) and B76 (167%), were involved in the poorest homeostatic effect, on the average, for all generations (69 and 73%). The poorest

general homeostatic effects for yield were from crosses that included B73 (81%) and B76 (80%). B75 had relatively poor general homeostatic effects in F₂ (69%), BC1 (64%), and BC2 (64%) generations, and B76 had poor homeostatic effects in all generations. For specific homeostatic effects, the poorest combinations included B73 x B76 (104%) for F₁; B77 x B76 (87%) for F₂; (B79 x B75) x B75 (102%) for BC1, and (B75 x B76) x B76 (95%) for BC2.

Table V - Estimates of genetic homeostatic effects ($\% \sigma_{we}^2$ ^a) for yield in new maize inbred lines and their generations^b.

Lines (BC1)		Lines (BC2)						Average
		B73	B75	B76	B77	B79	B84	
B73	F ₁	154	93	104	56	80	72	81
	F ₂		60	71	49	51	78	62
	BC1		44	69	54	58	80	61
	BC2		68	77	25	39	89	59
Average								66
B75	F ₁		177	84	66	79	62	77
	F ₂			87	65	65	67	69
	BC1			76	51	102	63	67
	BC2			95	52	54	51	64
Average								69
B76	F ₁			167	53	94	65	80
	F ₂				55	60	63	67
	BC1				69	90	70	75
	BC2				57	57	58	69
Average								73
B77	F ₁				127	45	46	53
	F ₂					37	46	50
	BC1					63	49	57
	BC2					41	41	43
Average								51

Continued

Table V - Continued

Lines (BC1)	Lines (BC2)						Average
	B73	B75	B76	B77	B79	B84	
B79	F ₁				134	91	78
	F ₂					74	58
	BC1					73	77
	BC2					54	49
Average							65
B84	F ₁					135	67
	F ₂						66
	BC1						67
	BC2						58
Average							65
P ₁	F ₁					149	73
	F ₂						62
	BC1						67
	BC2						57
Average							65
Grand mean							82

^a $\frac{\sigma_{we}^2}{\sigma_w^2}$ is the proportion of the within-plot variability due to environmental effects calculated as $\frac{\sigma_{we}^2}{\sigma_w^2} \times 100$.

^b P = inbred line, F₁ = single cross, F₂ = segregating generation, BC1 = backcross using the inbred line of the row as the recurrent parent, and BC2 = backcross using the inbred line of the column as the recurrent parent.

It was evident that inbred lines with better homeostasis transmitted their qualities to the other generations, and the same trend was shown for inbred lines with poorer homeostatic effects. Consistency in transmitting their homeostatic effects through their generations was also observed for the inbred lines for ear length and diameter, number of kernel rows, ear and plant height, and number of tassel branches, but not for kernel depth (data not shown). The irregular pattern in transmitting

homeostasis by the lines for kernel depth was probably because of the relatively small differences for kernel depth.

A summary of the rank of the estimates of homeostasis ($\% \hat{\sigma}_{we}^2$) exhibited by the inbred lines for each trait is presented in Table VI. Trends for the relative homeostasis of lines were evident in each group of lines. One line in each group expressed superior homeostatic effects for all traits except for ear length: WF9 for

Table VI - Rank for homeostasis of the old and new inbred lines for each trait based on $\% \hat{\sigma}_{we}^2$.

	Traits								Rank Sum
	Yield	Ear		Kernel		Height		Tassel branches	
		Length	Diameter	Rows	Depth	Ear	Plant		
		cm	cm	no.	cm	no.			
<i>Old lines</i>									
B14A	3	3	3	5	3	6	5	6	34
B37	2	4	1	2	1	3	6	5	24
L289	5	6	6	6	6	1	1	3	34
L317	4	2	4	4	5	2	4	1	26
M14	6	1	5	3	4	5	2	4	30
WF9	1	5	2	1	2	4	3	2	20
Homeostatic effects ^a	G	G	G	G	E	G	G	G	
<i>New lines</i>									
B73	4	6	2	2	2	1	6	4	27
B75	6	4	3	3	3	6	3	6	34
B76	5	2	4	5	4	5	4	5	34
B77	1	1	5	4	6	4	2	3	26
B79	2	5	1	1	1	2	1	2	15
B84	3	3	6	6	5	3	5	1	32
Homeostatic effects ^a	G	G	G	G	E	E	E	G	

^a Pattern of the transmission of the homeostatic effects was either good (G) or erratic (E).

the old group of lines and B79 for the new group of lines. WF9 and B79 exhibited less homeostasis for ear length for different reasons. WF9 produces one large ear whereas B79 produces smaller ears because B79 has a strong two-ear tendency. Greater variation for ear length occurred because environmental effects affected ear length of WF9 and B79 more than for the other lines. B14A and L289 had the poorest homeostasis (greatest rank sums) for the old group of lines. B14A had greater variation for ear and plant height and number of tassel branches, but B14A was relatively stable for ear traits. L289, however, was relatively stable for its expression of ear and plant height, but L289 had the least stability for ear traits. M14 also had a poor overall ranking, but there was no consistency among traits: M14 ranked last for stability of yield, but M14 had the best homeostatic estimate for ear length and ranked second for plant height.

B75, B76, and B84 expressed less homeostasis for the eight traits, with B73 and B77 being intermediate. B73 and B77 had good homeostasis for some traits and poor homeostasis for other traits. B73 had good homeostasis for all ear traits except ear length, and B73 tends to have a small ear similar to B79. Estimates of homeostasis for ear and plant height for B73 represented the extremes for the new group of lines; good homeostasis for ear height, but poor for plant height. Estimates of homeostasis for B77 tended to be the opposite of those for B73. B77 exhibited good homeostasis for yield, ear length, and plant height, which were poor for B73, and relatively poor homeostasis for other ear traits and ear height, which were relatively good for B73. Distinct differences occurred among the two groups of lines for their relative homeostasis for the different traits. The differences among lines also tended to occur in the different generations produced by crossing the lines (Tables IV and V).

The data examined in this study and the consistency of the data, showing the transmission of the homeostatic effects across generations, suggest that the relative stability of a line is heritable. Eberhart and Russell (1969) commented that stability could be heritable and that maize plant breeders should be able to select single-cross hybrids with greater yield stability. Scott (1967) reported that it was possible to select for stability when defined as least variation over environments. All the lines included were selected for their performance in hybrids, based on trials conducted in different environments. Superior performance was based on consistency over environments. Estimates of homeostasis, based on individual plants, were not a criterion for identifying the lines. Indirectly, however, estimates of homeostasis suggest that the new lines are more stable in different environments than the old lines, and stability also was expressed in the F₂ and backcross generations. Within both groups, some lines had better homeostasis than others. Each line, whether old or new, has a unique genotype that contributes homeostasis to its crosses for different traits. It is not obvious, however, that homeostasis at the individual plant level contributes to the

overall performance of a line in crosses. WF9 and B14A were widely used in their respective eras; WF9 exhibited relatively good homeostasis whereas B14A exhibited relatively poor homeostasis (Tables IV and VI). B73 and B79 were developed during the same era, but B79 exhibited greater homeostasis than B73 (Table VI). B73, however, was used more extensively in hybrids than B79. The relative stability of the inbred lines was transmitted to their crosses.

RESUMO

A homeostase genética em milho (*Zea mays* L.) foi estimada para determinar se ela é afetada pela seleção, ou se é hereditária. Um grupo de seis linhas endocruzadas liberadas antes dos anos 60 e um outro grupo liberado após os anos 70, foram usados para desenvolver gerações de cruzamentos simples, F₂ e retrocruzadas. Os experimentos foram conduzidos em duas localidades do Estado de Iowa em 1985 e 1986. Foram tomadas medidas individuais para oito características de milho. As estimativas da homeostase genética foram obtidas utilizando-se uma medida proporcional da variância ambiental incluída na variância dentro do bloco, a magnitude da interação genótipo x ambiente e o coeficiente de variação.

A homeostase genética depende do nível de heterozigosidade e heterogeneidade dos genótipos e populações de milho. As linhagens mais novas apresentaram-se mais homeostáticas do que as mais velhas. As linhas endocruzadas eram consistentes para a transmissão dos efeitos homeostáticos, bons ou ruins, de uma maneira hereditária para suas gerações de cruzamentos simples, F₂ e retrocruzadas. Na maioria das vezes as oito características seguiram a mesma tendência em todas as comparações entre as gerações em ambos os grupos. A altura da semente, entretanto, não teve um padrão regular de transmissão dos efeitos homeostáticos através das gerações.

REFERENCES

- Adams, M.W. and Shank, D.B. (1959). The relationship of heterozygosity to homeostasis in maize hybrids. *Genetics* 44: 777-786.
- Allard, R.W. and Bradshaw, A.D. (1964). Implications of genotype-environmental interactions in applied plant breeding. *Crop Sci.* 4: 503-508.
- Byrd, W. (1955). Genetic and environmental variances in segregating and non-segregating maize populations. Ph.D. Thesis. Iowa State University Library, Ames, Iowa.
- Cannon, W.B. (1932). *The Wisdom of the Body*. Norton, New York.
- Dobzhansky, Th. and Levene, H. (1951). Development of heterosis through natural selection in experimental population by *D. pseudoobscura*. *Am. Nat.* 85: 247-264.
- Eberhart, S.A. and Russell, W.A. (1969). Yield and stability for a 10-line diallel of single-cross and double-cross hybrids. *Crop Sci.* 9: 357-361.
- Jones, D.F. (1958). Heterosis and homeostasis in evaluation and applied genetics. *Am. Nat.* 92: 321-328.
- Lerner, I.M. (1954). *Genetic Homeostasis*. Oliver and Boyd, London.

- Lewontin, R.C. (1957). The adaptation of populations to varying environments. *Cold Spring Harbor Symp. Quant. Biol.* 22: 395-408.
- Reich, W.H. and Atkins, R.E. (1970). Yield stability of four population types of grain sorghum, *Sorghum bicolor* (L.) Moench, in different environments. *Crop Sci.* 10: 511-517.
- Rowe, P.R. and Andrew, R.H. (1964). Phenotypic stability for a systematic series of corn genotypes. *Crop Sci.* 4: 563-567.
- Schnell, F.W. and Becker, H.C. (1985). Yield and yield stability in a balanced system of widely different population structures in *Zea mays* L. *Plant Breeding (Z. Pflanzertzuchtg)* 97: 30-38.
- Scott, G.E. (1967). Selecting for stability of yield in maize. *Crop Sci.* 7: 549-551.
- Shank, D.B. and Adams, M.W. (1960). Environmental variability within inbred lines and single crosses of maize. *J. Genet.* 57: 119-126.
- Sprague, G.F. and Federer, W.T. (1951). A comparison of variance components in corn yield trials. II. Error, year x variety, location x variety components. *Agron. J.* 43: 535-541.

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