MUTATIONS AFFECTING QUANTITATIVE TRAITS IN THE SELFED PROGENY OF DOUBLED MONOPLOID MAIZE STOCKS[1]

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MONOPLOIDS occur normally in maize with low frequency and may be identified in the seedling stage by means of an appropriate system of genetic markers (CHASE 1949). A small percentage of such monoploid plants may exhibit sectorial diploidization. When sectors include all or parts of the ear and tassel, some seeds are produced upon self-fertilization. Each plant arising from such a seed is presumed to be completely homozygous since it represents, in a double state, the chromosomal complement of a single gamete. Since the frequency of detectable mutations is, to a great degree, a function of the genetic uniformity of the experimental material and of the techniques used, it was felt that doubled monoploid stocks would provide excellent material for a study of mutations affecting quantitative traits in maize.

Some of the changes observed in the present study were qualitative and, on the basis of limited data, appear to result from changes at a single locus. These were of limited interest, and no detailed data on them will be presented. The changes of primary interest were those whose effects led to significant changes in one or more of the several quantitative attributes studied. Since there are definite limitations in the types of analyses that may be used in a study of quantitative changes, the term "mutation" will be used in a broad sense, with no implication as to the exact nature of the change involved.

MATERIAL AND METHODS

Monoploids were isolated from stocks representing diverse genetic origins ranging from long-time inbred lines to synthetics. Seeds resulting from the self-fertilization of the monoploid plants were used as source material for this study. Such seeds were planted the following season and the resulting plants self-pollinated. The following year a progeny row was grown, representing each self-pollinated ear. Self-pollination was continued, and at harvest time two siblings were saved from each progeny row. This procedure was continued through successive generations. No conscious selection was practiced in any generation, ex-

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cept for the one necessary restriction that each selfed ear saved have a minimum of 150 kernels. If a monoploid plant is designated as S_0, the diploid progeny resulting from self-pollination of such a plant as S_1, etc., this study covered generations from S_3 through S_6. Seeds produced in each generation were dried, shelled, and placed in cold storage until needed.

Qualitative changes in phenotype are directly observable. Quantitative changes are less readily recognized. All direct comparisons were made in replicated plantings to ensure that observed variation had some genetic basis. The material available for study was assigned to experiments on the basis of S_2 origin. Each experiment, with two minor exceptions, consisted of progenies from the parental S_2, the two S_3, the four S_4, and the eight S_5 ears tracing to a single S_2 plant. Using the remnant seed of these parental ears, each item was planted in replicated ten-plant progeny rows. The field design was a randomized block with ten replications. Eleven such progeny sets were grown, each as a separate experiment. Individual plant records were obtained for eight attributes in each experiment. In addition, individual plant records for date of silking were taken in three of the 11 experiments.

Stands were good, but not entirely uniform. A mean was calculated for each plot to minimize unequal frequencies, and an analysis of variance was performed on the plot means. An analysis of means would be expected to indicate significant differences if a mutant form had become fixed in the homozygous condition. It also might be possible to obtain a significant difference in means from comparisons between normal and segregating progenies if the mutant form represented a relatively large change. Significant differences were ignored unless they were consistent with the hierarchal structure of the experiment. With this restriction, only changes resulting in significant differences between parent and progeny or between siblings within a given generation were considered as representing genetic changes.

Significant differences arising through chance would be expected to be distributed at random among the 105 comparisons possible among the 15 entries comprising a single experiment. Of such comparisons only 21 are consistent with the parent-progeny or between-sibling relationships imposed by the hierarchal structure. Therefore, the great majority of significant differences arising from chance should be inconsistent with the hierarchal structure. Actually the majority of the significant differences observed were consistent with genetic expectations indicating that chance differences could play no more than a minor role in the present study.

Changes for which segregation was still occurring would be expected to increase the "within plot" variances. Variances were calculated for each plot, and an analysis of variance of these variances was made. Environmental variability was so great, however, that few of the analyses indicated significant differences. This approach was not pursued further, and thus, the only valid estimate of genetic change presented was that provided by the analysis of plot means.

For purposes of calculating mutation frequency, it was assumed that the only mutations that could be detected were those that had advanced to the equivalent

of an F_3 generation and that had become homozygous for the phenotypic change. In the majority of the experiments, this limited mutation frequency estimates to the gametes involved in the production of the parental S_1, S_2, two S_3 and four S_4 plants—or a total of 16 gametes. If the possibility of detecting a segregating progeny were accepted, the number of gametes tested per experiment would be increased to 32. An illustration of the form of the analysis of variance used is illustrated in Table 1. The variability associated with "entries" may be partitioned in a number of ways. Since the item of primary interest was the variation among progenies, the partition illustrated was chosen. The t test was used for estimating the significance of differences between the means using replication × entries as an estimate of σ_e^2.

EXPERIMENTAL RESULTS

It appears unnecessary to present detailed records of entry means for each attribute in each experiment. Typical results are presented in Table 2. Significant differences inconsistent with the hierarchal structure were ignored. In the data on ear length presented in Table 2, entry 120 had a mean ear length of 114.5 mm. This value differs significantly from entries 100 and 110. However, the sibling progenies of this ear grown as entries 121 and 122 were not significantly different from entries 000 or 100. Significant differences of this pattern might be attributed to the vagaries of sampling and were not counted as mutations. If it is assumed that a significant difference was conditioned either by several genes or by the effect of a heterozygote, then reversals of the type suggested by contrasts of entry 120 with its parent and progeny could have a logical explanation. Entry 222 differed significantly from its parent 220 and was considered as representing one mutational change. This procedure introduces a possible bias, since performance records were not available for S_7 progenies. It would appear, however, that this bias would not materially exceed five percent.

TABLE 1

An illustration of the form of analysis of variance used for each attribute in the several experiments. (Ear length mm, experiment 80)

Source of variation	d.f.	m.s.
Replications	9	128.19
Entries	14	166.10
Parents *vs.* progeny		
S_3 *vs.* S_4 mean	1	58.12
S_4 *vs.* mean of S_5's within S_4's	2	172.34
S_5's *vs.* mean of S_6's within S_5's	4	221.21
Between progeny		
Between S_4's	1	38.09
Between S_5's within same S_4	2	185.26
Between S_6's within same S_5	4	160.46
Replication × entries	126	60.50
Total	149	

TABLE 2

Representative data indicating the type of parent-progeny differences that were interpreted as mutational changes

Coded pedigree	Generation	Experiment 81 Ear length (mms)	Experiment 81 Leaf width (cms)	Experiment 81 Date of silking after July 1	Experiment 83 Weight of shelled grain (gms)	Experiment 89 Plant height (cms)
000	S_3	122.8	11.9	24.5	53.2	123.2
100	S_4	127.2	11.9	24.7	41.8	122.8*
200	S_4	124.5	12.1	24.8	43.7	121.2†
110	S_5	122.6	11.7*	24.6*	43.3*	96.2*
120	S_5	114.5	11.7	25.1	44.8	120.7
210	S_5	125.8	12.0	24.4	57.4†	123.3
220	S_5	122.9*	12.0	24.5	47.2	115.0†
111	S_6	120.1	11.4*	25.6*	30.6*	102.3
112	S_6	129.3	11.7	25.7*	40.9	102.8
121	S_6	124.8	11.8	25.4	29.3	119.6
122	S_6	119.4	12.1	24.6	34.8	122.2
211	S_6	125.1	11.9	24.8	70.3†	118.4
212	S_6	124.8	11.9	25.3	57.9	122.2
221	S_6	127.0	12.2	24.9	35.4	115.0
222	S_6	130.9*	12.1	24.9	36.8	117.2
C.V.		6.03	2.91	3.48	29.71	6.44
L.S.D. (.05)		7.10	0.30	0.77	11.70	6.70
No. of mutations		1	1	1	2	2

* † Items marked by a common superscript represent significant parent-progeny differences each of which was interpreted as a single mutation.

TABLE 3

Total number of mutations per attribute for each of the 11 families (experiments)

Expt. no.	Plant height	Leaf width	No. of tassel branches	No. of kernel rows	Ear length	Ear diameter	Wt. per 100 kernels	Wt. of shelled grain per plant	Date of silking	Total of experiments
80	1	1	1	0	1	1	0	2		7
81	2	1	1	2	2	1	2	1	1	13
82	1	1	2	0	1	0	0	1	2	8
83	2	2	0	0	1	1	1	2	.	9
85	1	1	2	0	1	0	1	0	.	6
86	1	0	0	1	2	0	0	0	.	4
87	1	2	1	0	0	0	0	1	.	5
88	0	1	0	0	2	0	0	0	.	3
89	2	2	3	3	2	2	4	2	2	22
90	1	0	1	1	0	1	0	0	.	4
91	2	2	2	1	2	0	0	0	.	9
Total	14	13	13	8	14	6	8	9	5	90

Using the criteria just described, the total number of significant changes (mutations) for each attribute in each experiment was calculated. The data are presented in Table 3. The most striking characteristic of these data is the large number of mutations. As mentioned previously, the procedure used estimates mutations in only eight plants or 16 gametes per experiment (16 plants or 32

gametes if segregating progenies are assumed to produce a recognizable effect). Experiments 85 and 89 were exceptions to this rule. Experiment 85 involved five and experiment 89 involved 11 tested plants. An average for all experiments indicates a mutation rate of approximately six mutations detected per attribute per 100 gametes tested.

With quantitative traits, it is conceivable that one mutation might affect more than a single attribute. This possibility was explored by comparing the time of detection and the subsequent distribution pattern of all possible pairs of presumed mutations. When this was done, the number of independent mutations was reduced by approximately 25 percent. The correspondence of distribution does not constitute proof of pleiotropism, but it appears desirable to accept the more conservative figure of 4.5 mutations per attribute per 100 gametes tested.

If a mutation rate, u, is assumed, then the probability that a haploid having sectors of diploid tissue in the male and female inflorescence or a homozygous diploid will give rise to heterozygous progeny through mutation at a single locus is equal to $2u$. Since all progenies were perpetuated by self-fertilization, any heterozygosity arising by mutation would be halved in each succeeding generation. Since new mutations could arise in each generation, the total heterozygosity at any generation could be expressed as $2u\ (1 + \frac{1}{2} + \frac{1}{4} + \frac{1}{8} + - - -) = 4u$, as shown by HALDANE (1936). The frequency of heterozygous plants could not be determined accurately in these experiments; thus, this method could not be used for estimating the mutation rate. The only estimates of mutation rates that could be obtained were those based upon the number of significant changes presented in Table 3.

The estimated value, 4.5 per attribute per 100 gametes, cannot be interpreted in terms of mutations per locus without a considerable number of simplifying assumptions. The necessary assumptions appear to be so unrealistic that calculated values have little significance. They do, however, suggest either that the mutation rate is substantially greater than the commonly accepted figure, 10^{-5}, or that the number of loci is substantially greater than previous estimates of 5000 (CROW 1948).

Additional evidence supporting mutation as the mechanism causing increased genetic variability can be obtained from the analysis of variance, particularly the three "within generation" estimates. If the significant differences among siblings or between parent and progeny were solely the result of some form of structural hybridity arising in the haploid parent, the between-progeny variances with self-fertilization would be expected to decrease in subsequent generations according to the series $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$ $- - -$. Data bearing on this point are presented in Table 4. The values presented are estimates of genetic variance averaged over the 11 experiments. The variance estimates for the individual experiments were obtained from the relationship $\sigma_g^2 = \sigma_p^2 - \sigma_e^2$, where σ_g^2 is the genetic variance, σ_p^2 is the mean square variance for the appropriate "between-progeny" component, and σ_e^2 is the error variance. Contrasts between the magnitude of between S_4's *vs.* S_6's within S_5 are available from 83 analyses. In 11 of the comparisons the estimates were equal. In 53 of the remaining 72 cases the S_6's within the S_5 estimates were greater. This would appear to rule out structural hybridity as an

TABLE 4

Average estimates of genetic variance for the three "between progeny" partitions for each attribute studied

Attribute	Between progeny variances		
	S_4 within S_3	S_5 within S_4	S_6 within S_5
Plant height	10.69	51.31	69.79
Leaf width	—1.83	4.75	—0.64
Number of tassel branches	0.51	98.71	4.44
Number of kernel rows	0.86	4.29	0.45
Ear length	25.97	48.65	12.53
Ear diameter	0.10	0.58	0.62
Weight per 100 kernels	1.44	3.29	3.53
Weight of shelled grain	—17.79	79.26	47.98
Date of silking	—0.04	13.00	0.57

important factor and suggests that the process inducing variation must be a continuing one.

The very considerable variation among the estimates for the "between-progeny" components is a result of the small number of degrees of freedom. Thus, the mean square for each of the subdivisions is poorly estimated and would have a large associated standard error. Disregarding the algebraic magnitude, the frequency with which the difference between a particular "between" mean square was less than the error estimate suggests a definite trend. The percentages of negative estimates for between S_4, S_5's within S_4, and S_6's within S_5 were 59.0, 37.4, and 23.1, respectively. A more detailed statistical treatment of the available data appears unwarranted. The analysis used indicates that genetic variability increases with continued self-fertilization. More precise estimates of genetic variability must come from a different experimental approach. Seed preparation for such studies is currently underway.

Evidence for genetic change also is provided by crosses of S_5 lines within a family to their S_3 parent and by crosses of S_3 and S_5 lines to unrelated tester inbreds. The pertinent data for one such series of comparisons involving the attribute, number of tassel branches, are presented in Table 5. The F_2 distributions from crosses involving the S_5 lines HD 601-2-1-2 or HD 601-2-3-1 with their S_3 parent, HD 601-2, were significantly different, indicating that the two distributions could not be considered as random samples drawn from a single homogeneous population. When each of these three lines was crossed to either W92 or W17RB as a common tester parent, χ^2 was highly significant for each set of F_2 distributions.

In the W92 series the significance among the set of three results from the dissimilar performance of HD 601-2 and HD 601-2-1-2. The differences between HD 601-2 and HD 601-2-3-1 were not sufficiently large to be considered significant. However, when W17RB was used as a common tester, all differences were judged significant. Thus, in each of three comparisons HD 601-2-1-2 and

TABLE 5

F_2 distributions for a number of tassel branches in test crosses comparing related S_3 and S_5 lines from a single family

Test crosses	No. of tassel branches midclass values 2.5	6.5	10.5	14.5	18.5	22.5	26.5	30.5	Total no.	Mean
HD601-2 × HD601-2-1-2	..	2	31	43	58	56	21	12	223	18.95
HD601-2 × HD601-2-3-1	..	..	2	11	50	81	31	6	181	21.78
W92 × HD601-2	..	..	10	17	53	46	27	23	176	21.51
W92 × HD601-2-1-2	..	8	24	80	89	41	4	..	246	16.94
W92 × HD601-2-3-1	..	2	11	27	56	49	23	18	186	20.69
W17RB × HD601-2	4	18	39	62	41	24	..	..	188	14.65
W17RB × HD601-2-1-2	125	128	15	2	..	..	..	..	270	4.97
W17RB × HD601-2-3-1	83	127	42	13	6	3	..	..	274	6.73

HD 601-2-3-1 were shown to be genetically unlike. In one of two comparisons, HD 601-2-3-1 was indicated as genetically distinct from HD 601-2. The differences between 2-1-2 and 2-3-1 and between these and the parent form HD 601-2 must have been of recent origin. Some type of mutation appears to provide the best explanation for these observed differences. Dissimilar genotypes and modifier backgrounds may account for the differences observed between the two sets of crosses involving unrelated tester material.

Combining ability: The original S_3 line and one or more of its divergent S_5 generation derivatives were crossed to two long-time inbred lines, WF9 and B14, and the test crosses evaluated in replicated yield trials. The material comprising each family was grown as a separate experiment with each entry replicated ten times. Standard field plot techniques were used. The data are presented in Table 6.

A significant difference between S_3 parent and S_5 progeny was observed in two of the 38 contrasts. In these instances, the lower yield was associated with earlier maturity. The proportion of significant differences observed was no greater than might be expected on the basis of sampling. If more than a single genetic change would be required to modify yield performance at the hybrid level, the time period involved was too short to expect significant differences even though a high mutation rate might be involved. Furthermore, the only mutations that could be expressed in the test crosses would be those having some degree of dominance.

DISCUSSION

Attempts to obtain an estimate of mutation rate for loci conditioning quantitative traits involve a number of unwieldly problems. First, the methodology is cumbersome, and the testing of even a small population involves a very considerable expenditure of time and effort. Second, when changes are detected, a precise genetic analysis is not feasible. In spite of these and other limitations, the number

TABLE 6

Yield in bushels per acre for test crosses comparing original S_3 lines and one or more of their S_5 generation derivatives

Pedigree	Yield in bushels per acre when combined with WF9	B14	Average
HD698–1	89.2	89.5	89.4
HD698–1–2–1	85.1	89.3	87.2
HD698–1–3–2	85.0	87.7	86.4
HD601–2	77.2	85.1	81.2
HD601–2–1–4	83.1	82.9	83.0
HD601–2–1–6	77.1	75.6*	76.4*
HD601–2–3–6	80.0	89.4	84.7
HD601–6	70.5	81.2	75.8
HD601–6–1–2	76.7	83.6	80.2
HD513–3	92.5	81.8	87.2
HD513–3–1–1	97.3	84.1	90.7
HD513–5	88.1	86.5	87.3
HD513–5–3–3	85.3	87.5	86.9
HD510–1	82.0	85.2	83.6
HD510–1–1–1	84.6	87.5	86.0
HD510–5	75.9	82.3	79.1
HD510–5–1–2	80.1	80.3	80.2
HD510–9	79.0	84.0	81.5
HD510–9–2–2	81.2	82.1	81.6
HD502–2	80.3	67.9	74.1
HD502–2–1–1	89.7	68.5	79.1
HD502–2–1–2	85.1	68.5	76.8
HD502–2–2–1	86.8	69.3	78.0
HD502–2–2–2	86.7	69.5	78.1
HD502–8	89.0	68.9	79.0
HD502–8–2–1	88.6	70.2	79.4
HD502–8–2–2	85.9	68.6	77.2
HD73–1†	85.6	83.5	84.6
HD73–1–1–1	80.2	89.9	85.0
HD73–1–3–1	84.7	85.2	85.0
W22	82.8	87.0	84.9

* Yield difference significant at the 5 percent level.
† HD73 was derived from the inbred line W22.

of the significant genetic changes obtained in the present study is sufficiently great to warrant some speculation as to a possible cause.

Structural hybridity and mutable systems are known to have a marked influence on increasing the frequency of certain types of mutations. Meiosis in monoploids has been studied by FORD (1952), MCCLINTOCK (1953), and RANDOLPH

(1932). Pachytene preparations of monoploid plants exhibit varying degrees of apparent chromosome doubleness. This doubleness may arise from foldback areas within chromosomes or non-homologous association between chromosomes. If such non-homologous pairing gives rise to genetic crossing over, then the resulting gametes might possess structural dissimilarities. Zygotes derived from such gametes might be heterozygous for various types of chromosomal aberrations which could give rise to duplication-deficiency phenomenon in any progeny resulting.

However, the seeds used to initiate the present study had their origin in diploid sectors on the ear. Also functional pollen is shed from only diploid sectors of the tassel. Since diploid maternal tissue is involved in both cases, it is presumed that meiosis would be normal and that non-homologous pairing would be of little or no importance. While the material used in this study was not subjected to cytological analysis, there are additional reasons to feel that chromosomal aberrations could have played only a minor role in the observed changes. Reciprocal translocations would lead to semisterility, which was not observed. Duplications would lead to severe gametic competition and would rapidly be eliminated. All of the chromosomal deficiencies known in maize are lethal in the homozygous condition and most are haplo-lethal in the male gametophyte. Inversions, depending upon the size of the inverted segment, would lead to some reduction in fertility. Again, such types were not observed, but they could have been overlooked. The selection of seed ears that possessed a minimum of 150 kernels, as mentioned earlier, would impose some restriction against plants carrying a major chromosome aberration. Furthermore, the evidence presented in Table 4 indicates that the process involved is continuing and not limited to the monoploid phase. The testcross data in Table 6 provided no evidence for sterility and would appear to rule out any possibility of involvement of either homozygous inversions or translocations.

Several mutable gene systems have been reported for maize. For the most part these appear to be rather specific in their effects and to affect only a limited number of attributes. If a mutable gene system were postulated to account for the present results, it would have to have an effect on a number of different quantitative attributes; and each of the monoploids involved in this study must have carried such a system. This appears quite unlikely unless one further assumes that, in some manner, the monoploid condition is either directly or indirectly responsible for the origin or is the result of the mutable system. Any resulting instability would need to have its origin in something other than major chromatin rearrangements for the reasons just outlined. Furthermore, if such an explanation were valid, one would have to assume either that a large number of such changes was involved in each monoploid parent or that any of a large number of loci could have an important influence on each of the attributes studied.

The possibility that monoploidy may play some role in the origin of mutable systems is conceivable. The possibility that genetic instability may be widespread throughout the maize genome has been established by McCLINTOCK (1950, 1951, 1953), BRINK and NILAN (1952), and others. However, the mutable systems reported thus far have dealt with qualitative effects. One could argue

that if mutable systems are involved in the present study, they must represent a special class, since the increase in frequency appears to have been restricted to quantitative traits leaving qualitative effects not markedly in excess of normal expectation. This argument has definite limitations, since the parental material used in the production of monoploids carried relatively few genes that would have been satisfactory as markers. Furthermore, nothing is known as to the number of loci where mutational changes could produce an effect on a quantitative trait such as plant height. If a sufficiently large number of loci were assumed, then the apparent discrepancy between frequencies of changes affecting quantitative and qualitative traits might disappear.

The possible role of monoploidy as a causal factor in the origin of mutable systems can be evaluated only when comparable studies have been conducted with long-time inbred material. Seed preparation for such a study has been finished, but the field comparisons remain to be completed.

The estimates of frequency of genetic change provided by this study are subject to several types of bias. The restriction that any ear saved to propagate a line must have a minimum of 150 kernels would ensure the elimination of all lethals and sublethals. It would also reduce the estimates of frequency of occurrence for changes having a markedly depressing effect on yield level. The procedures used in the identification of genetic changes would preclude the detection of anything except major changes. For example, the data provide a strong suggestion of small stepwise changes that were not significant in any direct parent-progeny comparison but that were highly significant when S_3 *vs.* S_6 comparisons were made. Changes of this sort were ignored in the mutation frequency tabulations. Presumably, also, other changes that failed to achieve significance in the present study may represent real alterations and would have been judged significant had a larger number of replications been used.

In several instances, significant differences were observed between parent and progeny that were not retained in subsequent generations. These could be considered as chance deviations, segregation, or some form of reverse mutation. If the mutation rate is as high as the present data suggest, the possibility of reverse mutations or additional changes whose effects simulate reverse mutations cannot be ignored. However, in the present case significant differences of this sort were excluded from the tabulation. Other mutations may have gone undetected because of failure to become established in a homozygous condition.

Significant differences between parent and progeny, subject to the restrictions just outlined, were interpreted as representing a changed condition at a single locus. This would appear to be the simplest interpretation possible. However, there remains a possibility that the observed changes represent the culmination of a series of changes each having a smaller and nonsignificant effect. If this were true, each significant change might result from the multigenic alteration rather than a single locus effect. Each of these possibilities would lead to an underestimation of the true mutation frequency.

Since the individual changes were not tested for possible allelism, a possibility remains that a given mutation might be counted more than once. For example,

in one line of descent a difference in plant height might be apparent in one of two S_4 progenies. The other S_4 progeny could be heterozygous for the same mutation, and this change might be established as a distinct type in either the S_5 or S_6 generation. This may have been a factor in the present study. An attempt has been made, however, to minimize this possible bias by disregarding changes in different lines of descent which led to similar mean values. Thus two or more significant parent-progeny differences in S_5 or S_6 characterized by similar means were recorded as representing only a single mutation. Any duplications remaining would, of course, lead to an overestimation of the mutation frequency. It is the opinion of the authors that any net bias is in the direction of underestimation rather than overestimation.

If the mutation rate of normal inbred lines of corn is as high as these studies suggest, one might question how stability of appearance and performance could be maintained. It is a well-established fact that changes in phenotype do occur, since long-time inbred lines, when exchanged and maintained by different workers over a period of time and under different environments, become noticeably distinct. The degree of stability achieved is probably a direct result of the continuing selection practiced. In propagation of an inbred line, recognizable deviants would be avoided at pollination time unless they appeared to be of superior type. A second selection for typical plants would occur at harvest time. Thus, any mutations causing recognizable deviations from type would tend to be rapidly eliminated.

SUMMARY

Doubled maize monoploids would be expected to be completely homozygous since they arise from a single monoploid gamete. A detailed study was made of a series of doubled monoploids involving their S_3 through S_6 progenies. Significant differences between means were observed for each of the quantitative traits measured. Such significant differences were interpreted as resulting from some type of mutational change. The rate observed was 4.5 mutations per attribute per 100 gametes tested. The various factors that might influence the reliability of the observed mutation rate are discussed.

LITERATURE CITED

BRINK, R. A., and R. A. NILAN, 1952 The relation between light variegated and medium variegated pericarp in maize. Genetics **37**: 519–544

CHASE, SHERRET S., 1949 Monoploid frequencies in a commercial double cross hybrid maize, and in its component single cross hybrids and inbred lines. Genetics **34**: 328–332.

CROW, J. F., 1948 Alternative hypotheses of hybrid vigor. Genetics **33**: 477–487.

FORD, L. E., 1952 Some cytogenetic aspects of maize monoploids and monoploid derivatives. Ph.D. Thesis. Iowa State College. Ames, Iowa.

HALDANE, J. B. S., 1936 The amount of heterozygosis to be expected in an approximately pure line. J. of Genet. **32**: 375–391.

McCLINTOCK, BARBARA, 1933 The association of non-homologous parts of chromosomes in the mid-prophase of meiosis in *Zea mays*. Z. Zellforsch. u Mikroskop. Anat. **19**: 192–237.

1950 The origin and behavior of mutable loci in maize. Proc. Natl. Acad. Sci. U. S. **36**: 344–355.

1951 Chromosome organization and genic expression. Cold Spring Harbor Symposia Quant. Biol. **16**: 13–47.

1953 Induction of instability at selected loci in maize. Genetics **38**: 579–599.

RANDOLPH, L. F., 1932 The chromosomes of haploid maize, with special reference to the double nature of the univalent chromosomes in the early meiotic prophase. Science **75**: 566–567.