Recurrent Selection for Smut Resistance in Corn*

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Summary. The effectiveness of recurrent selection vs. continuous inbreeding in improving smut resistance of a very susceptible flint corn was studied. Two cycles of recurrent selection were performed, and S_6 generation was reached in the inbreeding series.

The common smut, *Ustilago maydis*, is one of the most destructive diseases of corn in Poland. Early, open pollinated flints are particularly susceptible. These varieties are of little importance and will be soon replaced by hybrids. They may, however, be of value as sources of inbreds because of their earliness, adaptation to local conditions and flinty character. Hybrids of flint × dent type are known to be superior in higher lattitudes and the same proved to be true in trials with Polish varietal hybrids reported by CZAPIEWSKA and CZAPIEWSKI (1956), BACZYŃSKI (1956), BACZYŃSKI and KRÓLIKOWSKI (1958) and KRÓLIKOWSKI et al. (1961). An extensive program of developing inbreds from local varieties was started in Poland in 1953 and 1954 (RUEBENBAUER, 1956; BOJANOWSKI, 1956; BOJANOWSKI and JAKACKI, 1962).

It was learned soon that the frequency of satisfactorily vigorous inbreds derived from local flints was low and a great proportion of them had to be discarded (KRÓLIKOWSKI, 1964). This was partly due to a pronounced inbreeding depression, but smut also played an important rôle in it. The author had the opportunity to see at the Plant Breeding Station Mikulice in 1961 a series of S_1 and S_2 inbreds derived from an open-pollinated early flint Złota Górecka which were all heavily affected and some virtually destroyed by the fungus. Similarly, almost all inbreds derived from a local flint population Wawrzeńczycka planted at the Plant Breeding Station Czulice in 1961 were appallingly smutted. No smut resistant inbreds were also developed from an open-pollinated flint variety Stanowicka, although some 2,500 selfed progenies were derived in the course of breeding program carried out by F. DZIEGIELEWSKI (unpublished). These inbreds were mostly very susceptible and some of them had to be discarded even in late generations, after being tested for combining ability.

Hence, smut susceptibility has been a major obstacle in exploiting Polish local flints as sources of inbreds.

It was believed prior to the era of hybrid corn that breeding was ineffective in controlling smut. JONES (1918) found significant differences in smut resistance among inbreds. Then, owing to the work of several investigators (GARBER and QUISENBERRY, 1925; HAYES et al., 1924; IMMER, 1927; and STRINGFIELD and BOWMAN, 1942) it was demonstrated that selection for smut resistance among inbreds was very effective and resistant hybrids were soon developed. Smut has no longer been a serious problem in the American Corn Belt.

* Dedicated to Dr. GEORGE F. SPRAGUE on the occasion of his 65th birthday.

The situation is different in Poland. Polish breeders have many resistant inbreds to their disposal, but if breeding programs were to be limited to these materials, the entire gene pool of local flints would have to be abandoned. Therefore, improving smut resistance appears to be a prerequisite for utilizing local flints as sources of inbreds.

The inheritance of smut resistance is by far not clear. There are, however, many data indicating its complex nature (IMMER, 1927; HOOVER, 1932; BURNHAM and CARTLEDGE, 1939; and SABOE and HAYES, 1941). This complexity may account for the ineffectiveness of mass selection, as well as for the extremely low frequency of resistant inbreds derived from susceptible populations. Therefore, recurrent selection as a method designed to increase the frequency of desirable genes (SPRAGUE and BRIMHALL, 1950; SPRAGUE, MILLER and BRIMHALL, 1952; and JENKINS, ROBERT and FINDLEY, 1954) should be more effective in improving smut resistance than continuous inbreeding and selection.

An experiment aiming at a comparison of effectiveness of these two systems in developing resistant inbreds from a susceptible source was started in 1960.

Experimental

Experiments were performed in smut nurseries of the Dept. of Genetics, Warsaw Agricultural University, Ursynów in the years 1960—1965 and at the Plant Breeding Station Pustków near Wrocław in 1966. Plants were dusted with chlamydospores at 4—5 leaves stage and again when they were about knee-high. This technique provided for epiphytosis when weather conditions were favorable to the growth of the fungus, otherwise, however, it produced little if any effect.

Smut intensity was high in 1960, 1961 and 1963, medium in 1962, 1964 and 1966, and very low in 1965. The seasons of 1962 and 1965 were cold and rainy, while those of 1963 and 1964 were warm and dry.

Smut damage to the plants was determined in percentage of affected plants. According to IMMER and CHRISTENSEN (1928) and JOHNSON and CHRISTENSEN (1935) smut galls located on ears and on stalks above ears are more destructive than those located on other parts of plants, losses in yield being dependent upon the number and size of galls. Therefore, in our experiments smut infection on ears and stalks above ears was recorded separately and is referred to as "harmful" in order to single it out from "total". Besides, an arbitrary scoring system was developed by the author, taking into account both the percentage of smutted plants and the amount of damage. This system was used up to 1964 but was then abandoned because a very close correlation was found between the score and the percentage data (.93 for "harmful" and .90 for "total").

Table 1. *Mean percentage of smutted plants (H — "harmful", T — "total") in inbred families of the first cycle.*

Year and generation	No. of family	Number of inbreds	Mean percentage of smutted plants H	T	F variance ratio for family means
1961 S_1	752	1	7	38	
	754	1	4	48	
	814	1	10	28	
	823	1	11	47	
	828	1	7	50	
1961 S_2	752	5	3	51	
	754	5	8	38	
	814	4	24	38	H — 1.66
	823	1	0	9	T — 2.42
	828	4	7	25	
	Stanowicka		45	72	
1963 S_4	752	8	2	46	
	814	32	8	29	H — 8.45*
	828	13	0.4	0.4	T — 17.61*
	Stanowicka		31	70	
1964 S_5	752	12	0.5	1	
	814	37	0.1	0.6	H — 1.28
	828	13	0.04	0.4	T — 0.30
	Stanowicka		7	18	
1965 S_6	752	10	0.3	0.3	
	814	13	0.3	0.3	H — 0.61
	828	7	0	0	T — 0.61
	Stanowicka		7	8	
1966 S_6	752	3	8	8	
	814	15	1.4	2.6	H — 1.58
	828	6	5	5	T — 0.83
	Stanowicka		23	27	

** Significant at 1% level.

Table 2. *Mean percentage of smutted plants in five groups of S_4 inbreds tracing back to five S_2 individuals, all originating from a single S_1 plant of the 814 family, 1963.*

Designation of parental S_3 inbred	No. of S_4 inbreds	Mean per cent of smutted plants "harmful"	"total"
710/62	10	13	27
711/62	3	1	18
712/62	7	25	55
713/62	8	0.3	25
714/62	4	5	13
Mean	32	8	29

Analysis of variance (BLISS' transformation)

Source of variance	d.f.	Infection "harmful"	"total"
Total		7065	6890
Groups	4	3266	2453
Inbreds within groups	27	3799	4437
$F =$		5.79**	3.74*

* Significant at 5% level. — ** Significant at 1% level.

Experimental materials were planted in hills spaced 80×50 cm and thinned to one plant per hill, thus making a population of 25,000 plants per hectare. Unpublished results of experiments performed by F. DZIEGIELEWSKI and by J. BOJANOWSKI and J. LITWIŃSKA showed that low population density and thinning to one plant per hill provided for smut infection.

A very smut-susceptible, open-pollinated early yellow flint variety Stanowicka was chosen as experimental material. Two separate breeding programs were started from the same source: continuous inbreeding and recurrent selection. Smut resistance was the sole criterion of selection. No selection for vigor was applied unless inbreds could be propagated.

In 1960 300 S_1 progenies were planted in single rows. Five plants were selfed in each row. Since no one row was smut-free, 10 least smutted ones were selected. In 1961 the 10 selected S_1 progenies were planted with remnant seed and intercrossed diallelically. Five of them, however, became heavily smutted in the fall and were discarded, together with diallel crosses involving them. Designations of the 5 selected inbreds were: 752, 754, 814, 823, 828.

Continuous inbreeding and selection among 1st-cycle inbreds was started from the same S_1 progenies. In 1961 35 S_2 inbreds were planted and smut percentage was recorded. Inbreds derived from the discarded S_1's were eliminated. Besides, no seed was set on selfed plants tracing back to No. 754 and 823. Consequently, only 3 groups of S_3 selfs were obtained, tracing back to No. 752, 814 and 828. In 1962 stands were so poor in S_3 progeny rows that no reliable data could be recorded. Attempts were made to secure a sufficient number of selfed progenies.

In 1963 smut percentage of 48 S_4 inbreds was recorded. The same was done in 1964 with S_5 and in 1966 with S_6. The number of inbreds decreased, being 30 in 1965 and 25 in 1966. All 1966 plantings were made with remnant seeds.

Data on smut percentage in the continuous inbreeding series are given in Table 1, including the values of F for the variance among inbred families. The analysis of variance among groups of S_4 inbreds within the 814 inbred family is presented in Table 2.

In 1966 mean weight of ears per plant was determined to provide a tentative measure of vigor (Table 4).

Diallel crosses among 5 selected S_1 inbreds constituted the source material for the second cycle of recurrent selection. One of the crosses was missing, hence 9 F_1 hybrids were obtained. Smut percentage of these hybrids and of Stanowicka variety was determined on 30-plant, 2-row plots in 3 replicates in 1962. Data were not critical because of losses in stands due to cold and rainy weather. The same F_1's were selfed in 1962 and smut percentage of 72 2nd-cycle S_1 progenies belonging to 9 groups designated from I to IX was determined in 1963. Self pollinations were also made in S_1 inbreds. Groups V and VII were discarded because of high smut percentage, while I and IX were lost because of the failure in seed setting under the 1963 drought.

In 1964 57 S_2 and 59 S_1 inbreds were planted for smut recording, intercrossing and further selection. Seed setting in 1964 was also poor.

In 1965 26 S_1, 22 S_2 and 54 S_3 inbreeds were planted and smut percentage was recorded.

Since smut intensity was low in 1964 and still lower in 1965, it was not possible to judge whether any progress was made within groups towards resistance from S_1 to S_3.

In 1965 weather conditions were just disastrous for corn. Flowering was delayed about 5 weeks and no hand pollinations were made. Only remnant seed was planted in 1966.

Smut percentage of 21 S_2 and 51 S_3 inbreds of the 2nd cycle was recorded in 1966 in Pustków.

Data on smut percentage of initial F_1 hybrids and all 2nd-cycle inbreds are presented in Table 3, including the values of F for variance among groups of inbreds tracing back to the same F_1.

Mean weight of ears per plant was also determined (Table 4).

In 1965 smut percentage of 26 hybrids among 15 2nd-cycle S_1 inbreds and 3 hybrids among 3 1st-cycle S_5 inbreds was determined on 25-plant rows in 3 replicates; Stanowicka variety was used as a check. Smut intensity was extremely low and only the total percentage of smutted plants was recorded.

Table 3. *Mean percentage of smutted plants (H — "harmful", T — "total") in initial F_1's and in inbreds of the second cycle.*

Year and generation	Group No. and pedigree	Number of inbreds	Mean percentage of smutted plants H	T	F variance ratio for group means
1962 F_1	I 752×754		8	28	
	II 752×814		5*	23	
	III 752×823		1.3**	35	
	IV 752×828		4*	25	
	V 754×814		6	17	
	VI 754×828		2**	10**	
	VII 814×823		16	36	
	VIII 814×828		0**	0.4**	
	Stanowicka		13	35	
1963 S_1	I as above	9	18**	51	
	II	8	17	52	
	III	8	5**	30**	
	IV	8	9**	23**	H — 7.04**
	V	9	39	53	T — 7.67**
	VI	8	7**	15**	
	VII	6	31	47	
	VIII	12	1.4**	11**	
	Stanowicka		31	70	
1964 S_1, S_2	II	13	6	18	
	III	17	0.3**	4**	
	IV	22	3	10	H — 4.11**
	VI	15	1	2**	T — 9.20**
	VIII	47	1**	2**	
	Stanowicka		7	18	
1965 S_1, S_2 S_3	II	9	2	3	
	III	12	0**	0**	
	IV	11	0.4**	0.4**	H — 6.68**
	VI	8	0.1**	0.1**	T — 5.04**
	VIII	64	0.02**	0.1**	
	Stanowicka		7	8	
1966 S_1, S_2 S_3	II	2	26	26	
	III	6	7**	9**	
	IV	11	16	17	H — 4.25**
	VI	6	14	14	T — 3.95**
	VIII	54	5**	6**	
	Stanowicka		23	27	

* Significant at 5% level. — ** Significant at 1% level.
Marks of significance in the columns of smut percentage refer to differences between group means and the source variety Stanowicka.

Table 4. *Mean weight of ears per plant of the 1st and 2nd cycle inbreds and of the source variety, 1966.*

Pedigree	Cycle	Generation	No. of inbreds	Ear weight per plant mean	range
752	1	S_6	3	114	105—126
814	1	S_6	14	117	137—214
828	1	S_6	6	15	5— 37
II 752×814	2	S_3	2	106	64—150
III 752×823	2	S_3	6	80	17—158
IV 752×828	2	S_2, S_3	11	67	17—115
VI 754×828	2	S_2, S_3	6	31	4—140
VIII 814×828	2	S_2, S_3	47	61	10—145
Stanowicka	—	—	—	354	—

Table 5. *Total percentage of smutted plants in F_1 hybrids among S_5 inbreds of the first cycle and S_1 inbreds of the second cycle, together with a comparative score of vigor, 1965.*

Entry No.	Pedigree of parental inbreds	% plants smutted	Score of vigor
38	752×814	2*	—
39	752×828	4	—
40	814×828	2*	0
2	VIII×VIII	0**	—
3	VIII×VIII	5*	0
5	VIII×VIII	3*	—
6	VIII×VIII	0**	—
7	VIII×VIII	3*	—
8	VIII×VIII	0**	—
9	VIII×VIII	0**	—
10	VIII×VIII	0**	—
11	VIII×VIII	1**	—
15	VIII×III	9	0
16	VIII×III	4*	—
17	VIII×III	3*	0
18	VIII×III	11	0
19	VIII×III	0**	0
20	VIII×III	1**	0
21	VIII×III	0**	0
22	VIII×III	5*	—
23	VIII×III	11	0
24	VIII×III	4*	0
25	VIII×III	1**	—
26	IX×II	1**	0
1	III×VI	4*	0
4	III×VI	3*	0
12	III×VI	1**	+
13	II×VI	2**	+
14	II×VI	5*	+
	Stanowicka	11	0

Difference from Stanowicka is significant.
* at 5% level. — ** at 1% level.

Table 6. *Percentage of smutted plants and ear weight per plant of the source variety Stanowicka and a of mixture of F_1 hybrids among S_1 inbred of the second cycle.*

	Percentage of smutted plants "harmful"	"total"	Ear weight per plant (in grams)
Stanowicka	23.7	27.1	183
Mixture of F_1's	5.6	6.2	182
Difference	18.1*	20.9*	1

* Significant at 0,1% level.

Hybrids were visually compared with Stanowicka as to general vigor by classifying them "plus", "zero" (no apparent difference) or "minus". The results are given in Table 5.

In 1966 smut percentage and ear weight of the recovered 2nd cycle population and the source population Stanowicka was determined on 30-plant, 2-row plots in 6 replicates. The recovered population was a mixture of 3 F_1 hybrids among 5 2nd-cycle S_1 inbreds tracing back to 2 initial groups, namely III and VIII (i.e. to initial 1st-cycle inbreds 752, 814, 823 and 828). This mixture was not a proper sample of the entire gene pool of the 2nd-cycle inbreds, but it was the only material saved after a series of unfavorable seasons. The results are given in Table 6.

Discussion

Data presented in Tables 1 and 4 illustrate the low effectiveness of continuous inbreeding and selection in developing resistant inbreds from a susceptible variety. Only 3 inbreds out of 300 were left after 2 generations. All of them, particularly No. 752, are not fully resistant. The most resistant inbred No. 828 is almost subvital and would be of no practical use.

In spite of masking effect of seasonal variability of smut prevalence it can be seen from Table 1 that the resistance of all 3 inbred families was improved in the course of inbreeding.

Differences among inbred families, non-significant in 1961, became significant in 1963 when intra-family variance decreased. Significant variance among groups of S_4 inbreds within the 814 family (Table 2) indicates that smut resistance may still undergo segregation in S_2. The lack of significant variance among families in 1964, 1965 and 1966 may be attributed to the improvement of their resistance or to low smut prevalence, or to the joint effect of both factors.

The 814 inbred, although not fully resistant, is phenotypically better than others, its combining ability being unknown.

The results indicate, therefore, that smut resistance can be improved by selection under selfing, but if a rigorous screening for smut resistance would be applied to certain materials, there would be little if any opportunity to select for other characters.

Recurrent selection, as it was stated by SPRAGUE (1955), "appears to be applicable to all situations in which a reasonably accurate phenotypic evaluation is possible." It is being used for improving disease resistance (JENKINS et al., 1954), and hence could be reasonably expected to be applicable to smut resistance. The results obtained in the recurrent selection series indicate, however, that some difficulties may be encountered.

The evaluation of smut reaction based on single rows of 20 or 30 individuals is not accurate. Testing large numbers of inbreds in replicated trials would be labor-consuming and would also reduce the amount of remnant seed.

Since the symptoms of the disease occur late in the summer, which renders impossible any selection prior to flowering, 3 seasons are required for one cycle of recurrent selection for smut resistance.

The effectiveness of selection depends very much upon smut prevalence in a given season. In continuous inbreeding, susceptible lines escaping infection in one season may be eliminated in later generations. In recurrent selection, such inbreds become involved in diallel crossing, thus bringing about a waste of effort if some of them reveal their susceptibility late in the second year of the cycle. In cases of two subsequent years of low smut intensity susceptible escapes become incorporated to the gene pool of the recovered population.

On the other hand, recurrent selection has the advantage over continuous inbreeding in that diallel crossing of selected inbreds provides information on their cross-performance in relation to smut resistance. Such empirical test may be of importance owing to the fact that smut resistance is not consistently dominant, intermediate or recessive. KYLE (1930) found that in some cases F_1 was more susceptible than either parent, which might be attributed to the heterotic increase of growth rate of meristematic tissues. The author's own unpublished data indicate that apparently smut-free inbreds may differ in prepotency of transmitting resistance to their cross-progeny.

Data concerning the performance of F_1 hybrids among 1st- and 2nd-cycle inbreds show that improvement of resistance of these inbreds can not be attributed merely to inbreeding depression. It is true that in 1965 trial hybrids among 2nd-cycle inbreds tracing back to the same initial group were less smutted and also less vigorous than others, but, on the other hand, this particular group VIII (814×828) was the most resistant throughout the entire experiment. As it can be seen after the numbers of inbreds in particular groups (Table 3), selection for smut resistance favored inbreds of the group VIII, and generally the 828 genotype. Unfortunately, the low vigor of 828 makes a great proportion of the 2nd-cycle inbreds of little practical interest.

It should be pointed out, however, that a mixture of F_1 hybrids among 2nd-cycle inbreds tracing back to 4 initial S_1's differed from Stanowicka only in smut percentage, its vigor being unchanged.

Data presented in this paper, although too scarce to be generalized, seem to indicate that progress towards smut resistance may be slower under recurrent selection than under continuous inbreeding. On the other hand, recurrent selection enables to avoid narrowing the genetic basis of source material in which rigorous screening for smut resistance is necessary.

The author holds an opinion that the frequency of genes conditioning smut resistance in Stanowicka, and presumably in some other early flints, is too low to make any program of direct selection successful. Selection should be, therefore, preceded by crossing with some, preferably heterogenous, source of resistance. A breeding program of this type was started with Stanowicka at the Plant Breeding Station Pustków in 1962.

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Zusammenfassung

Mit dem Ziel der Verbesserung der Brandresistenz wurde die Wirksamkeit rekurrenter Selektion gegenüber fortgesetzter Inzucht an einem sehr anfälligen Hartmais untersucht. Die rekurrente Selektion wurde in zwei Zyklen durchgeführt, bei der Inzuchtserie wurde die S_6-Generation erreicht.

References

1. BACZYŃSKI, Z.: Sprawozdanie z doświadczenia z mieszańcami międzyodmianowymi kukurydzy założonego w Stacji Hodowlano-Badawczej IHAR Stare Olesno w 1955 r. Biul. IHAR **11**, 122—148 (1956). — 2. BACZYŃSKI, Z., i Z. KRÓLIKOWSKI: Wyniki doświadczenia z mieszańcami międzyodmianowymi kukurydzy. Biul. IHAR **4**, 56—63 (1958). — 3. BOJANOWSKI, J.: Perspektywy rozwoju hodowli kukurydzy w Polsce. Nowe Rolnictwo **10**, 766—771 (1956). — 4. BOJANOWSKI, J., and A. JAKACKI: General information on corn breeding in Poland. Bull. 2nd Meeting of the Maize and Sorghum Section of Eucarpia, Rome, 20—25 (1962). — 5. BURNHAM, C. R., and J. L. CARTLEDGE: Linkage relations be-

tween smut resistance and semisterility in maize. J. Am. Soc. Agron. **31**, 924–933 (1939). — 6. CZAPIEWSKA, A., i T. CZAPIEWSKI: Doświadczenie z mieszańcami miedzyodmianowymi kukurydzy. Biul. Hodowli i Selekcji Roślin No. **5–6**, 14–32 (1956). — 7. GARBER, R. J., and K. S. QUISENBERRY: Breeding corn for resistance to smut (*Ustilago zeae*). J. Am. Soc. Agron. **17**, 132–140 (1925). — 8. HAYES, H. K., E. C. STAKMAN, F. GRIFFEE and J. J. CHRISTENSEN: Reaction of selfed lines of maize to *Ustilago zeae*. Phytopath. **14**, 268–280 (1924). — 9. HOOVER, M. M.: Inheritance studies of the reaction of selfed lines of maize to smut (*Ustilago zeae*). West Virginia Agr. Exp. Sta. Bull. **253** (1932). — 10. IMMER, F. R.: The inheritance of reaction to *Ustilago zeae* in maize. Minn. Agr. Exp. Sta. Tech. Bull. **51** (1927). — 11. IMMER, F. R., and J. J. CHRISTENSEN: Determination of losses due to smut infections in selfed lines of corn. Phytopath. **18**, 599–602 (1928). — 12. JENKINS, M. T., A. L. ROBERT, and W. R. FINDLEY, JR.: Recurrent selection as a method of concentrating genes for resistance to *Helminthosporium turcicum* leaf bligth in corn. Agron. Journ. **46**, 89–94 (1954). — 13. JOHNSON, I. J., and J. J. CHRISTENSEN: Relation between number, size, and location of smut insections to reduction in yield of corn. Phytopath. **25**, 223–233 (1935). — 14. JONES, D. F.: Segregation of usceptibility to parasitism in maize. Am. Jour. Bot. **5**, 295–300 (1918). — 15. KRÓLIKOWSKI, Z., Z. BACZYŃSKI i F. KRUPA: Synteza wyników doświadczen z mieszancami odmianowymi i polskimi odmianami kukurydzy. Biul. IHAR **6**, 9–24 (1961). — 16. KRÓLIKOWSKI, Z.: Genetic value of a maize population as initial material for developing inbred lines. Genetica Polonica **5**, 161–187 (1964). — 17. KYLE, C. H.: Relation between the vigor of the corn plant and its susceptibility to smut (*Ustilago zeae*). Jour. Agric. Res. **41**, 211–231 (1930). — 18. RUEBENBAUER, T.: Dotychczasowe osiągnięcia hodowli kukurydzy oraz plan prac badawczych na najbliższe lata. Biul. IHAR **11**, 14–20 (1956). — 19. SABOE, L. C., and H. K. HAYES: Genetic studies of reactions to smut and of firing in maize by means of chromosomal translocations. J. Am. Soc. Agron. **33**, 463–470 (1941). — 20. SPRAGUE, G. F.: Corn Breeding. In: Corn and Corn Improvement, p. 221–283. New York, N.Y.: Academic Press Inc. 1955. — 21. SPRAGUE, G. F., and B. BRIMHALL: Relative effectiveness of two systems of selection for oil content of the corn kernel. Agron. Jour. **42**, 83–88 (1950). — 22. SPRAGUE, G. F., P. A. MILLER, and B. BRIMHALL: Additional studies of the relative effectiveness of two systems of selection for oil content of the corn kernel. Agron. Jour. **44**, 329–331 (1952). — 23. STRINGFIELD, G. H., and D. H. BOWMAN: Breeding corn hybrids for smut resistance. J. Am. Soc. Agron. **34**, 486–494 (1942).

Results of Non-Selective Inbreeding in Maize*

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Summary. The results reported here indicate that selection, as practiced by maize breeders during the development of inbred lines, has markedly reduced the potential morphological variability of Corn Belt germ plasm. It is suggested that a number of traits which appear to a greater degree in "elite" lines than in those resulting from non-selective inbreeding could be the result of selection for genes or chromosomal segments derived from the introgression of maize and teosinte. Yet lines exhibiting maximum teosinte influence would not likely survive the screening imposed by visual selection.

Evidence is presented which suggests that visual selection as practiced during inbreeding has little, if any, direct influence on yield in hybrid combinations.

With respect to the inheritance of combining ability, results from these experiments support the assumption that high × high general combiners, on the average, tend to be higher yielding than any other set of combinations of high, medium, or low general combiners. It is, however, difficult to account for the relatively high yields of high × low general combiners on the basis of additive gene action alone.

It is suggested that in material as heterogeneous as open pollinated Corn Belt varieties, as much genetic diversity can come from within varieties as from between varieties, particularly if the varieties themselves have undergone extensive introgression during the course of their evolution.

Introduction

An interest in the origin and evolution of Corn Belt maize led the author, some years ago, to the assumption that a study of the comparative morphology of a typical cross section of Corn Belt inbreds might provide additional information relative to the identity of the putative parents of this most important segment of maize germ plasm. It was primarily for this reason that such a study was undertaken. It soon became apparent, however, that if the origin of Corn Belt maize even approximated that which had been postulated, many of the morphological types which should have been recovered from inbreeding Corn Belt varieties were not present in the cultures of modern corn breeders. It was assumed, therefore, that either the postulated origin of Corn Belt maize was in error, or more plausibly, that only a segment of the total phenotypic variability of Corn Belt germ plasm had survived the rigors of selection as practiced by maize breeders.

It was partly to provide answers to these questions and partly to develop a group of non-selected lines for use in experiments in quantitative inheritance that a random inbreeding scheme was started in the mid-1950's.

Materials and Methods

Seed from approximately 100 open pollinated ears of each of four varieties were selected as the original sources for inbreeding. The four varieties were Reids Yellow Dent, Krug, Lancaster and Midland. Seed from the 100 ears was bulked within each varietal source, and 600 kernels were taken at random from each variety. These were planted in blocks by variety, and at flowering, an effort was made to self each plant of each variety, irrespective of its agronomic qualities. These included lodged plants, diseased plants, and many other types which would normally be rejected by the breeder. Natural selection, of course, took its toll. A certain number of plants were lost in each generation due to the spread in time of silking and pollen shedding, and due to male sterility, insect attack, ear molds, etc.

At harvest, all ears were saved and approximately equal numbers of kernels were chosen from each ear, sufficient to make a bulk sample of 600 kernels.

* Dedicated to Dr. GEORGE F. SPRAGUE on the occasion of his 65th birthday.