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Mass Selection for Prolificacy in Maize *[1]

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Summary. Results of 5 generations of selection for improved productivity in corn by selecting for prolificacy, a correlated trait, are reported. The regression for gain in yield per cycle of selection relative to the parental variety, Hays Golden, was 6.28%. This compares favorably with a previously reported gain from mass selection in the same variety using weight of grain per plant as the selection trait. The greater effectiveness of selection where prolificacy was the primary trait is believed due to higher selection intensity used as well as higher heritability.

Mass selection has been shown to be effective in modifying highly heritable traits in maize (SMITH 1909). In the early part of the present century, it was concluded generally not to be effective in the improvement of yield in adapted varieties although as pointed out by SPRAGUE (1955), no critical evaluation of the procedure was available from the early literature. Selection effectiveness for yield improvement in maize populations is dependent upon the presence of additive genetic variation for yield. HULL (1945) attributed the failure of mass and ear-to-row selection for yield in maize to the lack of additive genetic variation in varietal populations. He concluded that the genetic variation present was largely non-additive and therefore not subject to utilization in mass selection procedures. Subsequently, the characterizing and quantifying of relative amounts of genetic variation in open-pollinated varieties of maize became of utmost importance in providing guidelines for most efficient approaches in corn breeding.

COMSTOCK and ROBINSON (1948) outlined the use of certain mating systems in maize for the derivation of genetic variance components. A number of studies using these mating systems in maize varietal populations has been reported in recent years (ROBINSON et al. 1955, LINDSEY et al. 1962, LONNQUIST et al. 1966, WILLIAMS et al. 1965, COMPTON et al. 1965, GOODMAN 1965 and others). These studies generally revealed the presence of a considerable amount of additive genetic variation for yield. Selection based upon individual plant or among various types of cross progenies was therefore expected to be successful in improving yielding ability of maize populations. Recent reports have shown this to be so.

Improvement of maize populations through selection of parents based upon testcross progeny evaluation (recurrent selection) has shown substantial progress (LONNQUIST 1961, PENNY et al. 1963). Mass selection for yield under cultural practices providing reasonable control over environmental variation has also been successful (GARDNER 1961, JOHNSON 1963, LONNQUIST 1966, LONNQUIST et al. 1966). These results have substantiated reports of a considerable amount of additive genetic variance for yield in maize populations.

Yield improvement in maize populations undergoing various types of selection at the Nebraska Experiment Station has resulted in correlated changes including greater height, increased maturity and prolificacy. The latter observation resulted in an interest in the possibility of utilizing this trait in selection for increased productivity. RICHEY (1922) reviewed studies of early workers who had reported observations on the value of prolificacy for increasing the productive potential in maize. No reports are available however, of selection experiments carried

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out using prolificacy as the primary trait in selection for yield. Quantitative genetic studies in maize carried out in recent years, however, have shown generally, a relatively high correlation between ear number and yield (ROBINSON et al. 1951, GOODMAN 1965, STUBER et al. 1966, LONNQUIST et al. 1966 and Nebraska unpub. data). Since ear number is a component of grain yield, one might expect such a correlation to exist. In view of the early observations on the apparent relationship between ear number and yield, together with the more recently reported correlations between these traits, it seemed worthwhile to use prolificacy as the primary trait in selection and relate progress in productivity to such selection.

Material and methods

The Hays Golden variety was chosen for this study. It is adapted to the area where the research was carried out, having been maintained at the Nebraska Experiment Station since its collection from south-central Nebraska about 1943. Also, the variety has been used in a mass selection program based upon yield per plant since 1955 (GARDNER 1961). Thus the results obtained could provide a basis for comparison of the two types of selection.

An isolated block of approximately 4000 to 5000 plants has been planted each year. During the first 4 years, the rows were 1 m apart with hills 1 m apart in the rows. A total of 3 seeds were planted in each hill. After emergence the hills were thinned to 2 seedlings per hill. The method was subsequently changed so that the hills were .5 m apart in the row, 2 seeds being planted in each hill and the seedlings later thinned leaving 1 plant per hill. The change was necessitated by an increase in tillering which occurred presumably as a result of the selection for prolificacy. Since the tillers bore ears, it was difficult to relate the tillers to the appropriate plant where 2 plants occurred together in the same hill.

At harvest one ear from each of approximately 200 plants having more than 1 ear was taken. This constituted a selection intensity of about 5%. Hays Golden variety, like most of the varieties in the central U.S.A. cornbelt, had been selected for many years for a single, large-ear plant type. Prolificacy in the original variety is relatively rare, and when it occurs the development of the second ear is usually very poor. In the first season of selection for prolificacy any plant having 2 ears, even though the second was poorly developed, was harvested. Subsequently, there has been no problem in finding plants with 2 or more well-developed ears. Selection of those plants with well-developed ears of about equal size and otherwise apparently free from diseases and on standing stalks have been selected. An equal number of seeds is taken from each of the harvested ears to provide the total needed to plant the next year's isolation.

Progress in productivity from selection for prolificacy has been measured in replicated yield trials using at least 10 replications each year and at populations of about 34,500 plants per hectare. The original variety has been included as a check and the yields of the selected populations are presented as per cent of the check. Each cycle of selection is included in the yield trials for 3 consecutive years.

The check variety is regrown every 2 or 3 years in an isolated plot consisting of about 4000 plants. At harvest time about 250 plants are harvested from the center rows of the isolation with no selection except for smut-free plants bearing ears. Of the sample harvested, equal numbers of seeds are taken from each ear to provide a balanced composite with sufficient seed to replant the isolation when necessary. A somewhat larger balanced composite is made up in a similar manner for use in yield trials.

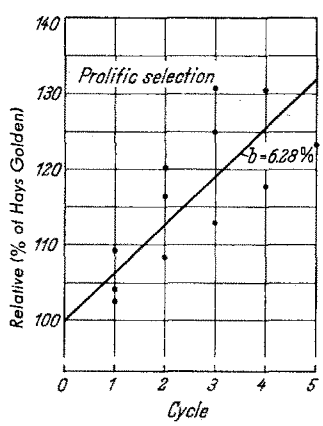

Fig. 1. Yield response (linear regression) to mass selection for prolificacy relative to Hays Golden variety.

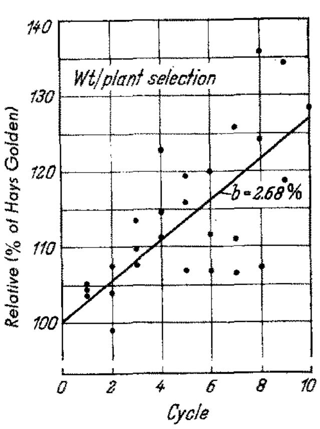

Fig. 2. Yield response (linear regression) to mass selection for grain yield per plant relative to Hays Golden variety.

Results and discussion

The gain in yield as determined in performance trials carried out during 3 years following each cycle of selection beginning in 1962 is shown graphically in Figure 1. Relative to the parent variety, Hays Golden, the average gain in productivity per cycle for the first 5 generations of selection is 6.28%. This compares favorably with the gain of 3.8% per generation reported by GARDNER (1961) for the first 5 generations in the same variety using mass selection based upon weight of grain per plant. The latter program has been continued and after 10 generations of selection the regression of relative gain on cycle of selection is 2.68% per generation (Figure 2). Thus, four generations of selection for prolificacy resulted in a level of productivity attained by 10 generations of selection for yield per plant in the same variety.

Mass selection based upon weight of grain (ear corn) per plant has resulted in a marked increase in maturity as measured by moisture in the grain at harvest (1.58% per generation). Even though the harvested ears are kept in the seed house for a period of time and presumably are air dried to an equilibrium moisture state before weighing, the heavier ears are undoubtedly those from later plants and possibly having slightly higher moisture content. The change in maturity accompanied by higher yields in the prolific selection series is much less (.64% per generation). Whether this difference in the two series continues, remains to be seen. It does, however, point up the fact that some improvement in productivity is possible without greatly affecting maturity.

The apparently greater effectiveness of selection for prolificacy in increasing productivity is no doubt due in part to the greater selection intensity applied.

Mass selection based upon weight per plant has been subjected to a selection intensity of 10%. Prolific selection has undergone a selection intensity of about 5%. The latter type of selection is much simpler to carry out and the trait is less subject to environmental variation. Thus with less effort a larger number of plants can be observed in selecting the desired total harvested sample.

Prolificacy may be indicative of greater plant vigor. Moreover, two or more ears on the main culm may allow for greater photosynthetic efficiency since there should be less congestion in the movement of photosynthate from the leaf areas to the storage organs (ears). Also in prolific plants, any impairment of movement in a given shank region because of insect damage or disease provides alternate pathways for continued movement to the starch deposition regions (ears).

The increase in tillering in plants selected for prolificacy is also an indication of plant vigor. Tillers as such have always been selected against in the midwest where they believed to result in greater moisture loss because of increased leaf area. They can contribute to productivity, however, where they produce grain. Where conditions are favorable to greater plant growth and plant populations are not such as to fully utilize available fertility and moisture supplies the tendency to develop grain bearing tillers may act as an adjustment mechanism for obtaining optimum yields. Problems with increased lodging on the part of grain bearing tillers may exist, however, although there is reason to believe this problem can be overcome by selection for greater stalk strength.

Prolificacy is of interest as a breeding tool. The development of several ears on each plant can provide the breeder with what becomes an approach to a multiflowered plant, not in a strict sense of the word but at least an important deviation from the single eared type. This modification permits the utilization of mating systems not previously utilized. Since the gain in yield through selection for prolificacy is rather substantial the opportunities for simultaneous selection for other important agronomic traits seems good. Yield improvement will be of little interest if other important attributes are ignored. Total agronomic improvement as well as productivity (net worth) should be readily possible if available technics are utilized.

Heritability of yield per plant in maize is relatively low. Only limited information on the relative heritabilities of yield and ear number is available. The results, however, reflect higher heritability for ear number than for yield (ROBINSON et al. 1949 and Nebraska unpublished). Also, as pointed out earlier, the correlation between these two traits has been relatively high. Thus the necessary requirements for successful improvement in productivity by selection for the correlated trait, prolificacy, exist.

The use of a correlated secondary character as the primary trait in selection (ears per plant) to improve the character of interest (yield) has been termed indirect selection (FALCONER 1960). It has been pointed out that indirect selection may be more effective if the secondary character has a substantially higher heritability and the genetic correlation between the two is high. The possibility of being able to apply a substantially higher selection intensity to the secondary character is also a critical factor. The character ears per plant can be measured with precision. Yield, on the other hand, is highly subject to environmental variations, and differences in moisture content may be a more serious influence on weight differences than is commonly realized. As FALCONER (1960) points out, the most effective progress may be obtained where both the desired and the secondary character are used in combination. Although grain weights were not taken in the present study, attention was given to apparently higher grain yields in the prolific plants selected. It would seem that a component of yield which can be measured with less work and error (ears per plant) than the primary trait (yield) and which is highly correlated with the primary trait will be useful as an aid to improvement in yield.

Zusammenfassung

Die Ergebnisse einer über 5 Generationen durchgeführten Selektion auf Erhöhung der Ertragsfähigkeit bei Mais werden mitgeteilt. Es wurde auf Fruchtbarkeit (Anzahl gut entwickelter Kolben), ein korreliertes Merkmal, ausgelesen. Die Regression für den Ertragszuwachs je Selektionszyklus betrug, bezogen auf die elterliche Sorte 'Hays Golden', 6,28%. Das stimmt gut mit einem früher schon berichteten Anstieg nach Massenselektion der gleichen Sorte überein, wo als Selektionsmerkmal das Korngewicht je Pflanze diente. Das bessere Ergebnis der Selektion auf Fruchtbarkeit wird auf die angewendete größere Selektionsintensität und die höhere Heritabilität zurückgeführt.

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Genetic Diversity and Heterosis in *Nicotiana* *

I. Interspecific Crosses [1]

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Summary. Two flue-cured varieties of *N. tabacum* were crossed to putative progenitor species and to distantly related species. Heterosis for yield, plant height, and number of leaves was largest for crosses to progenitor species, particularly to *N. otophora* and *N. tomentosiformis*. The magnitude of this heterosis appeared to be greater than estimates presented in the literature for crosses among varieties of *N. tabacum*. An additional study presented some evidence for the genomic basis of heterosis in crosses of *N. tabacum* with *N. tomentosiformis* and *N. sylvestris*.

Introduction

A number of studies have been conducted in *Nicotiana* to obtain estimates of heterosis in F_1 hybrids. This heterosis, when measured as general vigor of the plant, is similar to luxuriance described by DOBZHANSKY (1952). Throughout this paper, the point of reference will be the mean of both parents, and heterosis will pertain to the deviation of F_1 from mid-parent.

Early reports on results of hybridization in *N. tabacum* L. pointed out the lack of heterosis in the varieties and strains which existed at that time. DARWIN (1876) made special note of crosses among varieties of *N. tabacum* by describing the lack of vigor in crosses as a curious case. SETCHELL *et al.* (1922) summarized results of intervarietal crosses in *N. tabacum* as follows: "When we are dealing with complex differences, the F_1 is commonly intermediate in character expression between the two parents. Not only is this true as respects the F_1 plant as a whole but it is also true for individual characters".

In recent years there has been a large amount of data on heterosis presented with a wide variety of strains of *N. tabacum*. Examples of these studies are given by RAVE (1934), OKA *et al.* (1959), MURTY *et al.* (1962), POVILAITIS (1964), OKA and EGUCHI (1965), MURTY (1965), CHAPLIN (1966), MARANI and SACHS (1966), MATZINGER *et al.* (1960), MATZINGER and MANN (1962), MATZINGER *et al.* (1962), MANN *et al.* (1962), and AYCOCK *et al.* (1963). In general, heterosis values for various characters ranged from no heterosis to only modest amounts. However, in a few cases the F_1 hybrid exceeded both parents. In many of these studies, increased heterosis was attributed to increased genetic diversity, although many crosses of varieties with apparently diverse origin did not exhibit heterosis.

Interspecific hybridization within *Nicotiana* has been practiced extensively, however, there is little information on comparisons of the interspecific hybrids with the parent species for growth characteristics in replicated trials. Results of early observations on differences among crosses in interspecific hybridization are summarized by KOSTOFF (1941 to 1943). When crosses were made between *N. tabacum* and other species, the crosses to *N. sylvestris* Speg. and Comes and *N. rustica* L. were very vigorous, whereas the crosses to more distantly related '*N. sanderae*' or *N. alata* Link and Otto produced dwarf hybrids. A large number of flue-cured varieties of *N. tabacum* were compared with their crosses to *N. sylvestris* by MANN and WEYBREW (1958). Although *N. sylvestris* was not included in the test, the relative performance of the hybrids compared with the flue-cured parents indicated that appreciable heterosis was being exhibited in the crosses. ASHTON (1946) summarized reports of heterosis in many of the self-pollinated crops, including tobacco. His survey indicated some evidence that greater heterosis was exhibited from interspecific crosses than intraspecific crosses.

The present study was designed to measure the heterotic response when flue-cured varieties of *N. tabacum* were crossed to species of *Nicotiana* with varying degrees of phylogenetic diversity. *N. tabacum* ($n = 24$) is an amphidiploid of two 12-chromosome species. The probable progenitors are *N. sylvestris* (genome designation, S′S′) and a member of the Tomentosae section, either *N. otophora* Grisebach, favored by GOODSPEED (1954), or *N. tomentosiformis* Goodspeed favored by GERSTEL (1960). The genomic designation of the Tomentosae section representative is T′T′. The species representatives in the crosses were these three candidates as progenitors of *N. tabacum*, and two more distantly related diploid species, *N. glauca* Graham and *N. glutinosa* L. In addition, three varieties of *N. tabacum* were crossed to KOSTOFF's amphiploid 4X (*N. sylvestris* × *N.*

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

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