MASS SELECTION IN MAIZE COMPOSITES BY MEANS OF SELECTION INDICES

F. DE WOLFF

MASS SELECTION IN MAIZE COMPOSITES
BY MEANS OF SELECTION INDICES

Dit proefschrift met stellingen van

FRANS DE WOLFF,

Landbouwkundig ingenieur, geboren te Leiden, 2 augustus 1940,
is goedgekeurd door de promotor, Dr. Ir. J. H. van der Veen,
hoogleraar in de Erfelijkheidsleer.

De Rector Magnificus van de Landbouwhogeschool,
J. M. POLAK

Wageningen, 9 november 1971.

MASS SELECTION IN MAIZE COMPOSITES BY MEANS OF SELECTION INDICES

(with a summary in Dutch)

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWWETENSCHAPPEN
OP GEZAG VAN DE RECTOR MAGNIFICUS, MR. J. M. POLAK,
HOOGLERAAR IN DE RECHTS- EN STAATSWETENSCHAPPEN
VAN DE WESTERSE GEBIEDEN
TE VERDEDIGEN TEGEN DE BEDENKINGEN VAN EEN
COMMISSIE UIT DE SENAAT
VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN
OP VRIJDAG 4 FEBRUARI 1972 TE 16 UUR

DOOR

FRANS DE WOLFF

STELLINGEN

I

Het toetsen van selekties in 'hill plots' heeft als nadeel dat het toetsen plaats vindt onder milieu-omstandigheden welke afwijken van de normale veldomstandigheden. Dit nadeel kan worden ondervangen door gebruik te maken van de regressie van de F_{n+1} generatie op de F_n generatie, waarbij de F_n generatie wordt getoetst in 'hill plots', terwijl de F_{n+1} generatie wordt getoetst onder de normale veldomstandigheden.

BAKER, R. J. and D. LEISLE (1970). Comparison of hill and rod row plots in common and durum wheats. Crop Sci. 10: 581–583

II

De resultaten van selektieproeven uitgevoerd met twee gerst populaties wettigen de veronderstelling dat het gebruik van een selektie-index van praktisch nut is bij de selektie voor een hogere gerst opbrengst.

RASMUSSON, D. C. and R. Q. CANNEL (1970). Selection for grain yield and components of yield in barley. Crop Sci. 10: 51–54

III

Het rendement van 'full-sib' familie selektie kan aanzienlijk worden verhoogd door toevoeging van een generatie, verkregen uit zelfbevruchting in de te toetsen 'full-sib' families.

SPRAGUE, G. F. (1966). Quantitative genetics in plant improvement. In: Kenneth J. Frey (ed.) Plant Breeding. Iowa State Univ. Press, Ames, Iowa. p. 315–347.

IV

De z.g. 'modified ear-to-row selection' methode is ongeacht de omstandigheden een ondoelmatige methode.

LONNQUIST, J. H. (1964). A modification of the ear-to-row procedure for the improvement of maize populations. Crop Sci. 4: 227–228.

V

Resistentie voor het in 1970 in Nigeria geïdentificeerde fysio van *Helminthosporium maydis* wordt bepaald door het cytoplasma.

Dit proefschrift.

VI

Waarnemingen in Mokwa, Nigeria, toonden aan dat het aantal dagen dat de mais nodig heeft om tot bloei te komen niet of nauwelijks verschilt bij vroege of late uitplant. De grote verschillen welke werden waargenomen door Van Eijnatten in Ibadan, Nigeria, berusten waarschijnlijk op een onvoldoende nauwkeurige uitvoering van de proeven. Ook is het verschil tussen Ibadan en Samaru met betrekking tot de tijd welke de mais nodig heeft om tot bloei te komen aanzienlijk kleiner dan door deze auteur is opgegeven.

EIJNATTEN, C. L. M. van (1965). Towards the improvement of maize in Nigeria. Thesis, Wageningen.

VII

Bij het gewasonderzoek dat momenteel wordt uitgevoerd in Ethiopië is het van belang de potentiële opbrengsten van de verschillende gewassen te kwantificeren.

WESTPHAL. E. (1971). Ethiopische voedingsgewassen: een inventariserend onderzoek. Landb. Tijdschr. 83: 188–191.

VIII

Het verdient aanbeveling om de produktie en afzet van sheanuts in Nigeria te stimuleren.

RUYSSEN, B. (1957). Le Karité au Soudan. Agron. Trop. 12: 142–172, 278–306, 414–440.

IX

De huidige aandacht voor de aanpassingsmoeilijkheden van arbeiderskinderen bij het bestaande onderwijs onderstreept de grote problemen waarmee het onderwijs wordt gekonfronteerd in de ontwikkelingslanden.

GUSUALDI, Michele, c.s. (1970). Die rotschool van u. A. W. Bruna en Zoon, Utrecht, Antwerpen.

X

Het onderzoek in de geneeskunde gericht op zeer kostbare methodieken moet worden afgeremd.

aan Ans

CONTENTS

1. INTRODUCTION

In recent years there has been a renewed interest in mass selection. Mass selection or individual selection is selection on the basis of the individual phenotype. Mass selection was long thought unsuccessful as a method to improve the yield of maize, although there were few critical data available to support this view (SPRAGUE, 1955). Results from quantitative genetic studies on open-pollinated varieties of maize showed that there still existed considerable amounts of additive genetic variance for yield in these varieties (GARDNER, 1963). The genetic variance for yield should often be large enough to warrant a mass selection programme. GARDNER (1961) developed a method for mass selection in which a high level of environmental control is maintained to maximize the heritability. With ten cycles of selection in the variety Hays Golden, he realized an average yield improvement per cycle of 2.68 percent (LONNQUIST, 1967). After six cycles of selection no decline was noticed yet in the additive variance available for yield (LONNQUIST et al., 1966).

Using a tropical variety of maize, JOHNSON obtained a 4.8 percent improvement per cycle over seven cycles of selection (JOHNSON, 1963; ANON., 1968).

HALLAUER and SEARS (1969) used mass selection to improve the yield of two varieties of maize. Five and six cycles of selection failed to give significant responses. Among the reasons for the failure of the selection, they noted the low additive variance available for yield and the low selection pressure. By excluding the stemlodged plants from selection, the selection intensity became 27.4 instead of 7.5 percent. They noted that there might have been a positive correlation between yield and stemlodging, which in itself would explain the poor results sufficiently. The advantages of mass selection, in comparison to selection methods based on progenies are:

1. Its relative simplicity.
2. It takes only one generation per cycle, where most of the selection methods based on progenies take more than one generation per cycle.
3. It allows for the screening of large numbers of plants, from which again large numbers may be selected, thereby maintaining the initial genetic variability with little danger of fixation and inbreeding.

A disadvantage of mass selection is its slow progress per cycle or per unit of time. The relative efficiency of mass selection versus methods using progenies depends on the size of the heritability, the higher the heritability the more favourable becomes mass selection (FALCONER, 1960).

Mass selection is the most obvious method for the initial stage of a population improvement programme. The high additive genetic variance existing in a new population makes mass selection a relatively efficient method of selection. The many generations grown within a limited span of time allow for a rapid breaking up of linkage blocks. The selection among large numbers at frequent intervals allows for the realisation of a large number of the many potential genotypes,

while the great number of individuals selected is a safeguard against the premature loss of genetic variability (SPRAGUE, 1966).

The application of mass selection is often limited by the low realized heritability. The realized heritability from mass selection may be increased by determining the value of each individual phenotype by means of a selection index. The selection index should give proper weights to the different traits recorded from the individual, so as to maximize the correlation between the phenotypic value and the breeding value of the individual (SMITH, 1936; HAZEL, 1943).

The present study has been undertaken at Mokwa, Nigeria. Although in Nigeria maize is known as a food crop since long, the standard of maize production is still very low (VAN EIJNATTEN, 1965). The major problems of maize production are the low yield potential of the crop and the susceptibility of the crop to lodging. When these two factors may be combined in one selection index, it should be possible to select simultaneously for an increase in yield and for an increase in resistance to lodging.

2. INDEX SELECTION, A REVIEW OF LITERATURE

2.1. The theory of the selection index

The theory of the selection index was developed by Smith (1936) and Hazel (1943). Worked examples of index selection were given by Robinson et al. (1951) and Brim et al. (1959). A review on index selection was published by a group of authors (Autorenkollektiv, 1967).

The object is the selection of plants with a superior breeding value. When there are n traits of economic importance, the breeding value of each trait, H_i, may be weighed by its relative economic value a_i. The aggregate breeding value of a plant is thus given by:

$$H = \sum_{i=1}^{n} a_i H_i \tag{1}$$

Thus H is the additive genetic part of the genotypic value of the plant, which may be referred to shortly as the genetic value or the breeding value of the plant.

However, as we are unable to measure the genetic value of a plant, we have to base the selection on the phenotypic value of the plant. The phenotypic value of a plant may be given as:

$$I = \sum_{i=1}^{n} b_i X_i \tag{2}$$

where b_i is the weighing factor and X_i the phenotypic value for the ith trait. The correlation between the phenotypic value, I, and the genetic value, H, is:

$$r(I, H) = \frac{\text{cov}(I, H)}{\sqrt{\sigma^2_I \cdot \sigma^2_H}} \tag{3}$$

When the genetic and environmental effects are additive and independently distributed (which means that there is no genotype – environment interaction nor a correlation between genotype and environment), and when there is linkage equilibrium, formula (3) may be written as:

$$r(I, H) = \frac{\sigma^2_H}{\sqrt{\sigma^2_H \cdot \sigma^2_I}} \tag{4}$$

or:

$$r(I, H) = \frac{\sigma^2_H}{\sigma^2_I} \times \frac{\sigma_I}{\sigma_H} \tag{5}$$

The ratio between the genetic variance, σ^2_H, and the phenotypic variance, σ^2_I, is denoted by the heritability in the narrow sense, h^2, so that:

$$r(I, H) = h^2 \times \frac{\sigma_I}{\sigma_H} \tag{6}$$

It follows that:

$$h^2 = r\,(I, H) \cdot \frac{\sigma_H}{\sigma_I} \tag{7}$$

The response to selection is given by (see FALCONER, 1960):

$$\frac{R}{\sigma_p} = \frac{S}{\sigma_p} \cdot h^2 \tag{8}$$

where:
R = response to selection
σ_p = standard deviation of the phenotypic value
S = selection differential
h^2 = heritability

The standardised selection differential S/σ_p is called the selection intensity, to be denoted by k. The response to selection may thus be written as:

$$R = k \cdot h^2 \cdot \sigma_p \tag{9}$$

From (7) and (10) it follows that:

$$R = k \cdot r\,(I, H) \frac{\sigma_p}{\sigma_I} \cdot \sigma_H \tag{10}$$

Noting that σ_p and σ_I do both represent the standard deviation of the phenotypic value, formula (10) simplifies to:

$$R = k \cdot r\,(I, H) \cdot \sigma_H \tag{11}$$

The response to selection is maximized by maximizing the correlation between the phenotypic and the genetic value, $r\,(I, H)$. This is realized when the weighing factors b_i of formula (2) are calculated as the solution to the following set of n equations (see e.g. BRIM et al., 1959):

$$\sum_{i=1}^{n} b_i\,P_{i, j} = \sum_{i=1}^{n} a_i\,G_{i, j}\ (\text{for } j = 1, 2, \ldots, n) \tag{12}$$

in which respectively $P_{i, j}$ and $G_{i, j}$ stand for the phenotypic and genetic covariance between the ith and the jth trait, or when $i=j$, the phenotypic and genetic variance of the ith trait.

The total response to index selection is equal to the weighed sum of the responses for each of the separate traits (see BRIM et al., 1959):

$$R_{total} = \sum_{i=1}^{n} a_i\,R_i \tag{13}$$

The expectation of the total response is:

$$R_{total} = k \cdot \sqrt{\sum_{i=1}^{n} b_i\,A} \tag{14}$$

where

$$A = \sum_{j=1}^{n} a_j G_{l,j} \quad \tag{15}$$

The total response is hereby expressed in the same units as used for the standard deviation of the phenotypic value, σ_I. The expectation of the response for the ith trait is:

$$R_i = \frac{k \cdot \sqrt{\sum_{j=1}^{n} b_j G_{l,j}}}{R_{total}} \tag{16}$$

When there is only one trait, for instance yield, which has to be improved by selection, the equations from which the weighing factors b_i are calculated are simplified to:

$$\sum_{i=1}^{n} b_i P_{i,j} = G_{y,j} \ (\text{for } j = 1, 2, \dots, n) \tag{17}$$

in which $G_{y,j}$ stands for the genetic covariance between the jth trait and yield. The expected response to index selection becomes in this case:

$$R_y = k \cdot \sqrt{\sum_{j=1}^{n} b_j G_{y,j}} \tag{18}$$

which of course may also be written as:

$$R_y = k \cdot \sqrt{\sum_{i=1}^{n} b_i G_{i,y}} \tag{19}$$

In the selection index yield itself may or may not be included as one of the characters on which the selection is based.

It is often difficult to estimate the relative economic values of different traits. PESEK and BAKER (1969b, 1970) presented a method to calculate a selection index using the desired levels for the improvement of the different traits, instead of their relative economic values. Their index is not an optimal solution for the selection index. A more serious criticism is that the desired levels have to be set also for traits of no direct value. PESEK and BAKER proposed to set the level for improvement in such cases at zero, but this implies that these traits are not to be altered by selection, which may limit the response obtained in other traits.

The expected response to selection for different estimates of the relative economic values may be easily compared when employing the method presented by HENDERSON (1963). He first calculated selection indices for the separate improvement of each trait. Then he weighed these selection indices according to the relative economic values of the traits concerned, and added them up to

obtain the selection index for the simultaneous improvement of all traits of economic value.

$$I = \sum_{i=1}^{n} a_i I_i \qquad (20)$$

The resulting index was identical with the selection index found when the improvement of all traits was considered simultaneously.

The larger the number of traits that are considered in the selection index, the larger the expected response to selection will be. However, it is impractical to consider more than a few traits. Within a large group of traits there should be several subgroups of correlated traits. Each trait of such a subgroup may be taken as an expression of the same characteristic, like for instance maturity or vigor. Most of the information which may be obtained from such a subgroup of traits should be realized by choosing one major trait out of such a group. Likewise, most of the information concerning the value of an individual should be realized using only a few of such major traits. As we do not know the true parameters of the population, the selection index is calculated using estimates for the genetic and phenotypic variances and covariances of the population. The larger the number of traits that are involved in the selection index, the larger becomes the influence of errors inherent to the estimates (COCHRAN, 1951). The optimal solution to the selection index therefore will be an index based on only a few major traits.

Several authors presented formulas for the standard error of the selection index and for the standard error of the expected response to selection, based on the error of the estimates of the population parameters (NANDA, 1949; WILLIAMS, 1962). When the expected response to index selection is only slightly superior to the response to single trait selection, index selection may be less efficient than single trait selection, due to the error involved in the estimates.

A simulation study on the influence of sampling errors was carried out by HARRIS (1963, 1964). He considered the case of two traits of equal heritability and equal economic importance. The covariance between the two traits due to common environment was taken to be zero. Within these limits he used fifteen different population types, with the heritability taking the values 0.2, 0.5, and 0.8, and the genetic correlation between the two traits taking the values –0.5, 0.0, 0.2, 0.5, and 0.8. For each population type he used fifteen different sample sizes, while he did the simulation procedure nineteen times for each combination of population type and sample size. The simulation procedure led to the following conclusions. The influence of sampling errors decreased with an increase in sample size. The influence of sampling errors also decreased, when increasing either the heritability or the genetic correlation or both. For most combinations of sample size and population type the expected response to index selection was slightly overestimated.

It is often necessary to calculate a new selection index for each population, because each population has its own specific set of parameters. HANSON and JOHNSON (1957) used the data from different populations to calculate a general

selection index. They determined the phenotypic weights b_i such that the average genetic gain was maximized.

The parameters of a population should alter as a result from index selection. Index selection should lower the heritability and the genetic correlation of the characters represented in the selection index. An interesting case is when the traits to be improved by selection are negatively correlated. Index selection should be a relatively efficient method of selection under such conditions. However the two traits may be improved simultaneously only in as far as the negative correlation is not due to pleiotropic gene action. As shown by HARRIS (1963, 1964) the influence of sampling errors should be large with negatively correlated traits.

A simulation study to compare index selection and tandem selection in self-pollinated crops showed index selection to be superior (PESEK and BAKER, 1969a). Selection experiments with Drosophila comparing index selection with tandem selection and with selection using independent culling levels were inconclusive (SEN and ROBERTSON, 1964; RASMUSON, 1964). A theoretical examination of these three methods of selection showed that index selection should be more efficient than either of the other methods (HAZEL and LUSH, 1942; YOUNG, 1961). The use of independent culling levels may be advantageous when selection on one or more traits is possible before flowering, making selection on these traits possible on both the male and the female parent (YOUNG, 1961). The independent culling levels are applied between the selection on characters observable before flowering versus the selection on characters observable after flowering. YOUNG and WEILER (1961) developed a graphical method to estimate the optimum combination of culling levels for such situations. Like the selection index, the optimum level of culling levels is determined by the relative economic values and the phenotypic and genetic variances and covariances of the different traits.

2.2. THE PARAMETERS OF THE POPULATION

2.2.1. *Phenotypic correlations*

Between 1890–1920 corn shows became popular in the U.S.A. Score cards, with emphasis on traits correlated with yield, were used to select the prize winning ear samples. These samples were supposed to be valuable sources of seed. Later studies showed that selection on the phenotypic performance without environmental control produced little if any progress (McCALL and WHEELER, 1913; CUNNINGHAM, 1916; LOVE and WENTZ, 1917; RICHEY, 1922; KIESSELBACH, 1922). In recent years phenotypic correlations with yield were again reported (MURTY and ROY, 1957; WEILING, 1964; SINGH, 1966; SHARMA et al., 1968). However, knowing the phenotypic correlations without knowing the genetic correlations does not serve any purpose.

2.2.2. *Correlations between inbred lines and their F 1 crosses*

When hybrid maize first became popular, several workers looked for traits in inbred lines which could serve as indicators for hybrid performance (JORGENSON and BREWBAKER, 1927; NILSSON-LEISSNER, 1927; JENKINS, 1929). As could be expected, hybrid yield was not found to be closely correlated with any of the traits of the inbred parent lines. Better correlations were obtained when the lines were tested for general combining ability (JENKINS, 1929; HAYES and JOHNSON, 1939; SPRAGUE, 1952).

STRUBE (1967) constructed several selection indices for the selection of inbred lines for general combining ability.

2.2.3. *Estimation of the genetic and phenotypic variances and covariances*

The genetic variance of open-pollinated varieties may be estimated from:
1. a parent-offspring relation;
2. a sib relation.

2.2.3.1. Parent-offspring relation

LUSH (1940) measured the heritability as twice the regression of offspring on one parent. The genetic variance is given by twice the covariance between one parent and the mean of its offspring, or by twice the covariance between the midparent value and the mean of its offspring (FALCONER, 1960). Likewise, the genetic covariance between two traits I and J is equal to:

$$\text{genetic covariance } (I, J) = 2 \text{ cov } (I_1, I_2) \tag{21}$$

when subscript 1 stands for traits from one parent or from the mean of the two parents, and subscript 2 for traits from the mean of the offspring. HAZEL (1943) gave the genetic covariance between I and J as:

$$\text{genetic covariance } (I, J) = 2 \sqrt{\text{cov } (I_1, J_2) \text{ cov } (I_2, J_1)} \tag{22}$$

When estimating the genetic covariance according to the above expression an optimal use is made of all information available from the parent-offspring relationship.

ROBINSON et al. (1949) and WILLIAMS et al. (1965) estimated the heritability of several traits in maize from the regression of offspring on one parent.

The selection index may be estimated directly from the parent-offspring relationship, without first estimating the population parameters. The selection index is given by twice the multiple regression of the value of the offspring on the characters of the parents. When only one character, for instance yield, is to be improved by selection, the value of the offspring is given by its yield. When improving several traits simultaneously, the value of the offspring is given by the weighed sum of these traits, with the traits weighed according to their relative economic values.

2.2.3.2. Sib relation

To estimate the genetic variance from a sib relationship it is convenient to use the analysis of variance. The estimation of variance components from the ana-

lysis of variance was discussed by CRUMP (1946) and EISENHART (1947). COM-STOCK and ROBINSON (1948, 1952a) presented several mating designs to estimate the additive genetic and the dominance variance from a combination of full-sib and half-sib families. Other mating designs are also possible. The simplest case is a one-factor mating design, which is a design with only one component of variance for progenies (COCKERHAM, 1963). A one-factor mating design using half-sib progenies is adequate when we are only interested in the additive genetic variance (COMSTOCK and ROBINSON, 1952b; DUDLEY and MOLL, 1969).

COCKERHAM (1963) listed the conditions which should be satisfied when estimating the genetic variance of open-pollinated varieties:
a. Regular diploid and solely mendelian inheritance;
b. no environmental correlations among relatives;
c. no linkage;
d. relatives are not inbred;
e. relatives may be considered to be random members of some non-inbred population.

Condition (a), solely mendelian inheritance might not be completely valid when using maternal half sibs because of maternal inheritance which may occur through the cytoplasm. Within old, established varieties one would not expect any cytoplasmic differences to exist. However cytoplasmic differences may be present in composites of diverse and recent origin (FLEMING et al., 1960; SINGH, 1962; SINGH, 1965; CRANE and NYQUIST, 1967; HUNTER and GAMBLE, 1968; GARWOOD and LAMBERT, 1968; BHAT and DHAWAN, 1969; GARWOOD et al., 1970).

Condition (b), no environmental correlation among relatives is also not completely valid when using maternal half sibs because of maternally induced correlations between relatives (maternal effects), since the mother plant is a major component of the embryonic environment.

Condition (c), no linkage, is often stated as linkage equilibrium. The condition of linkage equilibrium is often not completely valid in populations of recent origin, which have gone through only a few cycles of random mating (DUDLEY and MOLL, 1969). Even at linkage equilibrium linkage still causes a positive bias in the estimation of the genetic variance (COCKERHAM, 1956, 1963).

The conditions (d) and (e) may be satisfied by using proper experimental techniques.

The genetic correlation among half sibs is 0.25 (FISHER, 1918). The genetic variance between half-sib families is equal to one quarter of the total genetic variance. COCKERHAM (1954) pointed out that the genetic variance between half sibs contains also small quantities of epistatic variance.

When open-pollinated ears are used as the source of half-sib families each family will contain a number of full-sib family groups. Provided there are many pollen parents available at the time of pollination, the number of full-sib families within a half-sib family should be large in comparison to the size of the full-sib families. This should make the fraction of the genetic variance due to full-sib family groups within half sibs negligible.

Under open pollination one might expect some assortative mating to occur. Assortative mating should lead to an overestimation of the genetic variance (LINDSEY et al., 1962). However with a polygenic trait and a high environmental variation this bias is negligible.

Determination of the genetic variance from experiments conducted in only one environment will generally lead to an overestimation, because the genetic variance will be confounded with the genotype by environment interaction (COMSTOCK and MOLL, 1963; COCKERHAM, 1963). The genotype by environment interaction may be estimated when the experiments are carried out in a random sample of environments. SPRAGUE and FEDERER (1951) were among the first to estimate the variety by location and the variety by year interaction.

COCKERHAM (1963) presented the expectations of the mean squares for a combined analysis of progenies in a number of environments as given in table 1.

The error component of variance of table 1 may be written as (COCKERHAM, 1963):

$$\sigma^2 = \frac{\sigma^2_w}{w} + \sigma^2_e \tag{23}$$

where:

σ^2_w = variance among individual plants within plots;
w = the number of plants per plot;
σ^2_e = between plot component of environmental variance.

When the analysis of variance is carried out for w individual plants per plot, the expectation of the mean squares will be as presented in table 2.

An estimate of the total phenotypic variance is given by:

$$\sigma^2_p = \sigma^2_w + \sigma^2_e + \sigma^2_{ge} + \sigma^2_g \tag{24}$$

When individual selection is carried out within plots the appropriate phenotypic variance does not contain the 'between plot' component of variance:

$$\sigma^2_p \text{ (within plots)} = \sigma^2_w + \sigma^2_{ge} + \sigma^2_g \tag{25}$$

TABLE 1. Combined analysis of progenies in l environments.

Source	D.f.	Expectations of the mean squares
Environments	$(l - 1)$	
Replications	$l(r - 1)$	
Progenies	$(n - 1)$	$\sigma^2 + r\sigma^2_{ge} + r \cdot l\sigma^2_g$
Progenies × environments	$(l - 1)(n - 1)$	$\sigma^2 + r\sigma^2_{ge}$
Error	$l(r - 1)(n - 1)$	σ^2
Corrected total	$l \cdot r \cdot n - 1$	

l = number of environments
r = number of replications within environments
n = number of progenies
σ^2 = error component of variance
σ^2_{ge} = variance component due to genotype × environment interaction
σ^2_g = progeny component of variance

TABLE 2. Analysis of variance for w plants per plot.

Source	D.f.	Expectations of the mean squares
Environments	$(l - 1)$	
Replications	$l(r - 1)$	
Progenies	$(n - 1)$	$\sigma^2_w + w\sigma^2_e + w \cdot r\sigma^2_{ge} + w \cdot r \cdot l\sigma^2_g$
Progenies × environments	$(n - 1)(l - 1)$	$\sigma^2_w + w\sigma^2_e + w \cdot r\sigma^2_{ge}$
Between plots	$l(r - 1)(n - 1)$	$\sigma^2_w + w\sigma^2_e$
Within plots	$n \cdot l \cdot r (w - 1)$	σ^2_w
Corrected total	$n \cdot l \cdot r \cdot w - 1$	

The variance components are given as variances of single plants. When progenies are half-sib families the progeny component of variance σ^2_g is equal to one-quarter of the additive genetic variance.

An estimate of the additive genetic variance is given by:

$$\sigma^2_a = 4\,\sigma^2_g \tag{26}$$

The phenotypic and genetic covariances between two traits are estimated in a way much like the variances. Instead of the mean squares the mean products between the two traits are calculated. In the expectations of the mean products components of covariance take the place of components of variance (COMSTOCK and ROBINSON, 1952b; MODE and ROBINSON, 1959).

The expectations of the mean squares presented in table 1 and 2 may be used to estimate the response to selection obtained from selection methods based upon progeny means. EBERHART (1969) presented a general formula for the expected response to selection using such methods:

$$R = \frac{k \cdot p \cdot \sigma^2_{g'}}{y \left\{ (\sigma^2_e + \sigma^2_w/w)/(r \cdot l) + \sigma^2_{ge}/l + \sigma^2_g \right\}^{1/2}} \tag{27}$$

where:

p = amount of parental control (see below)

$\sigma^2_{g'}$ = additive variance between progenies. When using half-sib progenies, the additive variance between progenies, $\sigma^2_{g'}$ is equivalent to the progeny component of variance, σ^2_g.

y = number of years required per selection cycle.

The formula may also be written as:

$$R = \frac{k \cdot p \cdot \sigma^2_{g'}}{y \left\{ (\sigma^2 + r\,\sigma^2_{ge} + r \cdot l\,\sigma^2_g)/(r \cdot l) \right\}^{1/2}} \tag{28}$$

where σ^2 is the error component of variance as given by (23). We notice that $(\sigma^2 + r\,\sigma^2_{ge} + r \cdot l\,\sigma^2_g)$ is equivalent to the expectation of the progeny mean square as given in table 1.

The amount of parental control, p, depends on the seed source which is used

to represent the selected progenies (EBERHART, 1969). With selection based on the performance of half-sib progenies there are three possibilities:

1. The most simple one is modified ear-to-row selection as proposed by LONNQUIST (1964). In this scheme one of the replications of the yield trials is grown in isolation, and the best plants are selected from the best ear-rows within this replication. The selection of the best ear-rows is based on the performance in all replications. Seed bulked from all progenies is interplanted as a pollinator between the ear-rows, which are detasseled. Thus, testing and recombination are taking place at the same time, so that this scheme takes only one generation per cycle. As the selected ears are open-pollinated, the selection is practised on the female parent only, and the amount of parental control, p, is 0.5.

2. Half-sib selection or as it is called half-sib testing or ear-to-row selection, uses remnant seed of the selected half-sib families, thereby practising full parental control, $p = 1$. Half-sib selection takes two generations per cycle, one generation for testing and one generation for the recombination between the selected families.

3. Half-sib progeny selection or recurrent selection for within population general combining ability. This scheme uses selfed seed from the male parents of the half-sib progenies, so that the amount of parental control is twice as high as in half-sib selection, $p = 2$. The selection takes three generations per cycle. In the first generation plants designated as males are selfed and crossed to a number of females. Each male group of crosses is bulked so as to give the half-sib progenies representing the males. The yield trials are grown during the second generation, while the selfed seed of the selected males is recombined during the third generation.

Modified ear-to-row selection, half-sib selection and half-sib progeny selection take respectively one, two and three generations per cycle. However, for all these three methods a minimum of one year per selection cycle, $y = 1$, is required under Mokwa conditions, because progeny trials may be conducted only during the main cropping season.

The above formula for the expected response to selection does not account for any effect of individual selection, although the selection methods do normally include some individual selection. For instance using half-sib selection one may practise individual selection within progenies when recombining the selected families. However the effect of such individual selection is limited for several reasons:

1. Individual selection is often applied during the off-season in the nursery, using a low selection intensity.

2. The selection is practised within progenies, exploiting only part of the additive genetic variance of the population.

3. The criteria used for individual selection often differ from the criteria used for selecting the best progenies. For instance while the progenies may be selected only on the basis of their yield performance, individual selection may take also other factors into account, like resistance to lodging, ear and plant height, disease resistance, etc. (EBERHART, 1967).

12

2.3. APPLICATION OF THE SELECTION INDEX

2.3.1. *Index selection as applied in different crops*

An extensive literature on index selection exists in the field of animal breeding. Here we confine ourselves to index selection as applied to plant breeding.

Selection indices have been calculated for:

alfalfa	(ELGIN et al., 1970);
cabbage	(SHARMA and SWARUP, 1964);
cotton	(PANSE and KHARGOKAR, 1949; MANNING, 1956, 1963; MILLER et al., 1958);
maize	see paragraph 2.3.2., page 14;
oats	(WALLACE et al., 1954);
rice	(ABRAHAM et al., 1954);
sorghum	(SWARUP and CHAUGALE, 1962);
soybean	(JOHNSON et al., 1955; BRIM et al., 1959; TANG, 1963; CALDWELL and WEBER, 1965; BYTH et al., 1969);
sunflower	(SCHULZE, 1962);
tobacco	(MURTY and PAVATE, 1962);
wheat	(SMITH, 1936; SIMLOTE, 1947; SIKKA and JAIN, 1958; PARODA and JOSHI, 1970; PESEK and BAKER, 1970).

In all these examples the selection indices were calculated for the selection based upon *progeny means.*

Several workers calculated selection indices for selection among varieties (SMITH, 1936; SIMLOTE, 1947; ABRAHAM et al., 1954; SIKKA and JAIN, 1958; SWARUP and CHAUGALE, 1962; MURTY and PAVATE, 1962). A general selection index to screen varieties can never be very accurate, because there may be large differences in the population parameters of different varieties. But especially in varietal selection it is often necessary to distinguish small differences. Index selection is therefore not a suitable method for selection among varieties.

Index selection in most cases was only slightly superior to single trait selection for the desired character. The highest expected response to index selection was reported by SHARMA and SWARUP (1964), who presented a selection index for cabbage with an expected response, which was sixty percent higher than the response to single trait selection for yield. Unfortunately no data on the realized response have been given. MILLER et al. (1958) calculated several selection indices for cotton. When the lines were tested in only two replications, they obtained a selection index with an expected efficiency of one hundred and thirty-four percent, but when testing was carried out more extensively, the efficiency of index selection versus direct selection for yield decreased. This is because an increase in the amount of testing produces a larger increase in the efficiency of direct selection for yield than in the efficiency of index selection, so that the efficiency of index selection decreases relative to the efficiency of direct selection for yield. Again no data have been given on the realized response to index selection.

MANNING (1956, 1963) applied index selection in a cotton breeding program-

me. In each generation of selection he calculated from the selfed progenies a new selection index specific for that season. He applied the selection index to select the best entries out of the progeny trials, from which the selection index had been calculated. MANNING realized in twelve generations of index selection an increase in yield of about thirty percent. The cumulative expected response from twelve generations of index selection was fifty percent, while the expected response to single trait selection for yield was fourty-four percent.

CALDWELL and WEBER (1965) and BYTH et al. (1969) working with soybean compared specific, average and general selection indices. The specific, average and general selection indices were calculated respectively from data derived from the population under selection, pooled data from a number of related crosses and pooled data from unrelated populations. The specific index was superior to both the average and the general selection index (CALDWELL and WEBER, 1965). However a general selection index was superior to a specific index when genotype by environment interaction was important (BYTH et al., 1969).

Working with alfalfa, ELGIN et al. (1970) found that a 'base index', in which the traits were weighed only according to their economic value, was equally efficient as a selection index.

2.3.2. *Index selection as applied in maize*

Comparatively little is known about index selection in maize. ROBINSON et al. (1951) used the data from the F_2 generation of a single cross hybrid, to demonstrate the calculation of a selection index. They considered the case of a selection index to be used in the selection of half-sib progenies, when the progenies were tested in non-replicated plots. As an example they presented a selection index which included the plant height, the number of ears per plant, and the yield. In their example the expected genetic advance from index selection was thirty percent superior to the expected genetic advance from selection on yield alone. However they did not advocate index selection as a method to improve the yield of maize, because the increase in selection efficiency should not warrant the extra effort of calculating and applying a selection index.

CHAUDRI (1964) calculated a selection index for a synthetic population of maize based on yield and ear characters. An index including five traits gave an increase in expected genetic advance of only fourteen percent compared to single trait selection for yield.

LAIBLE (1964) and LAIBLE and DIRKS (1968) introduced an Ear Number Weight Index (ENWI), which they defined as the quotient of the total grain yield per plant and the yield of the largest ear. They calculated selection indices for several single cross combinations, based on yield and number of ears per plant, or based on yield and ENWI. Their conclusion was that index selection gave only modest gains over single trait selection for yield.

As noted in paragraph 2.2.2. STRUBE (1967) constructed a selection index for the selection of inbred lines.

RUEBENBAUER and WEGRZYN (1963) used a 'quotient index'. They took the

quotient of the value of a trait and its mean value in the whole population. They then obtained the index value of an individual as the sum of the quotients of all traits considered in the selection. The 'quotient index', while more convenient to use, should produce results almost similar to those obtained from a selection index.

None of these maize workers have given data on the realized response to index selection.

The selection indices which have been calculated for maize as well as for other crops were all based on single or replicated plots as units of selection. In most cases the value of index selection was questionable. With the yield measured from single or replicated plots, one has already a rather precise estimate of the genetic value of an entry. The more extensively the entries are tested, the smaller will be the additional information about the genetic value of the entries which may be obtained from a selection index (SMITH, 1936; ABRAHAM et al., 1954; MILLER et al., 1958). With individual or mass selection, yield by itself will provide a poor estimate of the genetic value of the individual. A selection index, which makes maximum use of all information available from a single plant, should provide a much better estimate of the genetic value of the plant.

Results of an experiment by WILLIAMS et al. (1965) may serve as an example. Using an open-pollinated variety they considered the selection of full-sib families, when testing was carried out for two years in four replications. Indirect selection for yield by selecting on the ear diameter was expected to be twenty-seven percent less efficient than direct selection for yield. On the other hand from their data it can be seen that individual selection for ear diameter is expected to be eight percent more efficient in improving yield than individual selection for yield. A selection index including ear diameter and yield should give a nineteen percent higher expected response than single trait selection for yield.

LONNQUIST (1967) found that individual selection of multiple eared plants was more efficient in improving yield than individual selection for yield. TORREGROZA and HARPSTEAD (1967) obtained a yield improvement of fourteen percent after five cycles of mass selection for multiple ears. In both cases individual selection by means of a selection index based on yield and number of ears per plant should have been more efficient than either single trait selection for yield or single trait selection for multiple ears.

3. SIMULTANEOUS SELECTION FOR YIELD AND LODGING RESISTANCE IN MAIZE, A REVIEW OF LITERATURE

As said in chapter 1 the main problems of maize production in Nigeria were the low yield level of the crop and the susceptibility of the crop to lodging. When seeking to improve both traits simultaneously it is important to know whether there is any correlation between yield and resistance to lodging. We will first consider the improvement of each trait separately, after which we will study the possibility of simultaneous improvement of yield and resistance to lodging.

3.1. SELECTION FOR YIELD

In comparison to other traits yield has a low heritability (GARDNER, 1963). Numerous workers have looked for traits which they could use in indirect selection for yield. Most of the correlations with yield reported in literature were phenotypic correlations (see paragraph 2.2.1., page 7). More recent publications gave also genetic correlations with yield (ROBINSON et al., 1951; LINDSEY et al., 1962; LAIBLE, 1964; GOODMAN, 1965; STUBER et al., 1966; CHAUDRI, 1964; WILLIAMS et al., 1965; HALLAUER and WRIGHT, 1967; HALLAUER, 1968; ANON., 1969).

It is difficult to compare the figures given by different authors because the correlations depend on cultural practices and on the kind of population studied. Altering the spacing between plants may result in different correlations (ANON., 1969). GOODMAN (1965) compared an adapted and exotic composite. In the adapted composite he found high correlations with yield for several traits, while he found the same correlations to be small and often negative in the exotic composite. In general fairly high genetic correlations with yield were reported with the number of ears per plant, plant and ear height and date of flowering, while somewhat lower correlations with yield were reported for ear characters.

3.2. SELECTION FOR LODGING RESISTANCE

Lodging depends largely on environmental conditions. It has a low heritability. A quantitative measurement of lodging is not possible. One can only distinguish qualitatively in lodging and non-lodging. These two factors make it difficult to select directly for lodging resistance (THOMPSON, 1963).

It is possible to distinguish between two types of lodging (THOMPSON, 1963).
1. Stemlodging, i.e. the stalk is broken below the ear.
2. Rootlodging, i.e. the plants are leaning more than thirty degrees from the vertical, but they are not broken below the ear.

3.2.1. *Selection for resistance to stemlodging*

An indication of the resistance to stemlodging is obtained by measuring the strength of the stalk. The stalk strength was measured by recording the resistance to breaking (DURRELL, 1925; FOLEY, 1962) or by recording the resistance of the stalk to penetration or crushing (McROSTIE and MACLACHLAN, 1942). ZUBER and GROGAN (1961) determined the crushing strength and the rind thickness of the stalk. They cut a 2-inch section from the third internode above the ground and placed it upright in a hydraulic press. They recorded the pressure required to crush the stalk section. Using the fragments of the crushed stalk section they could then easily determine the rind thickness. They measured the rind thickness with a micrometer callipers in 0,001 cm.

Both crushing strength and rind thickness were highly correlated with resistance to stemlodging, while the weight of a 2-inch stalk section gave a somewhat lower correlation with resistance to stemlodging (ZUBER and GROGAN, 1961; THOMPSON, 1963). The crushing strength and the rind thickness could be measured from any internode of the stalk. The highest correlations with resistance to stemlodging were obtained when using one of the lower internodes (THOMPSON, 1964). The 'genotype by environment interactions' for crushing strength, rind thickness, and weight of a 2-inch stalk section were rather low. In selecting for stalk strength it would normally be sufficient to obtain data from a single environment (THOMPSON, 1963; ZUBER and LOESCH JR., 1966).

The diameter, the internode length and the breaking strength of the stalk gave low correlations with resistance to stemlodging (ZUBER and GROGAN, 1961; THOMPSON, 1964).

THOMPSON (1970) determined the 'dry specific gravity' of stalk sections as the quotient of dry weight and fresh volume. He found that the dry specific gravity and the dry weight were both highly correlated with resistance to stemlodging.

3.2.2. *Selection for rootlodging resistance*

Several workers recorded the pulling strength with which the plant was uprooted as a measure of rootlodging resistance (HOLBERT and KOEHLER, 1924; WILSON, 1930; SNELL, 1966).

CRAIG (1968) used the ratio of pulling strength and ear height as a measurement for the root strength.

VAIDYA et al. (1962) took the weight of the plant multiplied by the plant height and divided by the root weight as an indicator of rootlodging resistance.

Both the root volume and the dry weight of the roots could be used as indicators for rootlodging resistance (MUSICK et al., 1965; NORDEN, 1966).

3.3. CORRELATION BETWEEN YIELD AND LODGING RESISTANCE

Whether simultaneous selection for yield and lodging resistance will be successful depends on the genetic correlation between these characters. By the

heavier weight of the ears, increased yields present a greater mechanical stress to the plant. Increased yields may also exhaust the plant, leaving an inadequate amount of photosynthetic products for the stalk and the roots (CAMPBELL, 1964; DAYNARD et al., 1969). There is indeed some evidence that the stalk may be depleted from soluble carbohydrates during ear formation. Soluble carbohydrates were moved from the stalk to the ear when photosynthesis was reduced by shading or defoliation (SAYRE et al., 1931; HOYT and BRADFIELD, 1962; MORTIMORE and WARD, 1964; DUNCAN et al., 1965; ALLISON and WATSON, 1966; LIEBHARDT et al., 1968). A transfer of soluble carbohydrates from the stalk was also observed under conditions of warm cloudy weather (DUNCAN et al., 1965) or when plants suffered from potash deficiency (LIEBHARDT et. al., 1968) or under high population stress (MORTIMORE and WARD, 1964). A number of workers noticed a translocation of carbohydrates under normal growing conditions (SAYRE et al., 1931; VAN REEN and SINGLETON, 1952; HOYT and BRADFIELD, 1962; MÜHLING, 1963; FOCKE et al., 1966; JOHNSTON et al., 1966; DAYNARD et al., 1969; GENTER et al., 1970). Others however did not observe a decrease in the sugar content of the stalk during grain formation (SAYRE, 1948; CAMPBELL, 1964; ALLISON and WATSON, 1966).

CAMPBELL (1964) found a negative correlation between the sugar level of the stalk and yield. He suggested that as long as the plant is not killed by adverse conditions, a high sugar level in the stalk at maturity may prolong the life of the stalk tissue and so maintain the strength of the stalk.

The sugar level of the stalk at maturity was correlated with the resistance to stalk and root rot (MORTIMORE and WARD, 1964).

SINGH et al. (1969) studying inbred lines, found little if any genetic correlation between yield and the characters indicating stalk strength: crushing strength, rind thickness and weight of a 5-cm stalk section. They noted however that one would not expect a competition between yield and stalk strength within low yielding inbred lines. Studying a number of adapted and introduced varieties, SINGH (1970) found a positive correlation between yield and the characters indicating stalk strength. From this he concluded that selection for stalk strength should have a positive effect on yield. However, these data should be interpreted with some caution because the correlations may be explained also by assuming that the adapted varieties were satisfactory both in yield level and stalk strength, while the introduced varieties, not adapted to the new environment, might have shown both low yields and weak stalks.

Selection for resistance to stemlodging resulted in a decrease in yield, number of ears per plant and ear height. This would indicate a negative correlation between yield and resistance to stemlodging (THOMPSON, 1963).

If the reserves of the plant are depleted during grain formation it would not only effect the stalk strength, but also the root strength. However the relation between yield and root strength is more complex because a large, strong root system would favour the uptake of nutrients and water and so favour the yield potential of the plant.

Positive correlations were reported between yield and pulling resistance, root

volume, number of brace roots, and dry weight of the roots (HAYES and JOHNSON, 1939; NORDEN, 1966).

Two cycles of selection for root strength gave no significant differences in yield (CRAIG, 1968).

One would expect the two types of lodging, stem- and rootlodging, to be negatively correlated, because under a situation of stress one type of lodging has to occur. Increasing the resistance to one type of lodging will make the plant more susceptible to the other type of lodging. In agreement with this THOMPSON (1963) found positive correlations between the amount of rootlodging and the characters indicating stalk strength: crushing strength and rind thickness.

Of course real progress in resistance to lodging is only obtainable when selection is carried out for general resistance to lodging, including both stem- and rootlodging.

4. THE SELECTION INDEX,
RESULTS FROM EXPERIMENTS, I

Experiments were conducted to test selection indices calculated from a parent-offspring relationship.

4.1. RATIONALE OF THE EXPERIMENT

Estimating the selection index from a parent-offspring relationship has several advantages. The multiple regression of the mean value of the offspring on the characters of the parent plants gives a direct estimate of the selection index, independent of any genetic interpretation. The experimental procedure is rather simple. The plant characters have to be recorded only from the parent generation. The parent plants may be planted in any convenient pattern, as long as the plants are grown under the conditions that are common to actual selection. Parent plants with incomplete records may be discarded from the experiment, because selection among the parents does not bias the multiple regression of offspring on parents. The mean value of the offspring is determined in progeny trials. When the selection is aimed at the improvement of the crop within a certain set of environments, the progeny trials should be conducted in a random sample of these environments.

4.2. MATERIAL

Two composites were used in the experiment, namely Samaru Composite 2 and Colombian Composite. The history of these composites is the following: working in Samaru, Nigeria, in 1966 DR. O. J. WEBSTER made several composites by mixing seed from variety hybrids. Samaru Composite 1 consisted of a mixture of equal amounts of seed from variety hybrids between Mexico 5 and the entries:

    Biu Yellow
    Yotoco × Diacol V 351
    (USA 342 × Diacol V 206) × Diacol 254
    Composite III Amarillo Centro America
    Ven. 16 × ETO

Samaru Composite 2 was a mixture of seed from variety hybrids between the entries:

    Biu Yellow
    Yotoco × Diacol V 351
    (USA 342 × Diacol V 206) × Diacol 254
    (Cub. 325 × USA 342) × Diacol 254

(Yotoco × Diacol V 351) × Diacol 254
Compuesto Caribe Amarillo
D.V. 101 × D.V. 351
Ven. 16 × ETO
D.V. 351

Samaru Composite 3 consisted of a mixture of equal amounts of seed from variety hybrids between Biu Yellow and Composite III Amarillo Centro America, and between Biu Yellow and Mexico 5.

Biu Yellow was an advanced generation of a cornbelt hybrid, and contained a certain proportion of cytoplasmic male sterility. Biu Yellow possessed a good combining ability in crosses with varieties from tropical origin. The other entries were introductions from Colombia and Mexico. With the exception of Mexico 5, the entries had been maintained in Nigeria by repeated cycles of hand pollination, so that a considerable loss might have taken place in the genetic variability of the entries.

Comparing the entries involved in the three Samaru Composites we notice that the composites formed related populations, containing a number of entries in common.

The three original seed mixtures were multiplied at Samaru during the 1966–1967 dry season by random mating. In 1967 the first generation, 'G 1', of each of the three composites was grown in isolation at Mokwa and left to open pollination. The 'G 2' generations of the three composites were interplanted at Mokwa during the early season of 1968, thereby using a recurrent pattern of two rows planted to a composite. This planting system allowed a fair amount of intercrossing to occur between the composites, while individual selection was possible within each composite. About two hundred and fifty ears were selected and bulked from each composite. The 'G 3' generations of the three, now partially intercrossed composites were grown during the late season of 1968 in a similar pattern as used for the 'G 2' generations. Equal amounts of seed of the ears harvested from the 'G 3' generations were bulked to form the Colombian Composite.

4.3. METHODS

To study the parent-offspring relationship the 'G 2' generation of Samaru Composite 2 had been planted on 13th August 1967 as a late-season crop on an isolated field at the Mokwa experimental farm. The crop received 26 kg P_2O_5 per ha, applied as superphosphate a few days before planting, and 100 kg nitrogen per ha, applied as sulphate of ammonia in equal doses two and six weeks after planting. The seeds were hand planted, planting two seeds per stand. The stands were spaced 30 cm within the row and 91 cm between rows. Two weeks after planting the stands were thinned to one plant each.

The following individual plant characters were recorded from two hundred plants, which together formed one complete row in the field:

1. The days to silking, that is the number of days from planting till the emergence of the silks.
2. The number of ears with silks.
3. The number of leaves above the main ear, which generally is the top ear of the plant.
4. The number of green leaves at the time of silking.
5. The plant height, measured two weeks after silking from ground level to the flag of the top leaf of the plant, in cm.
6. The ear height, measured two weeks after siking from ground level to the node from which the main ear developed, in cm.
7. The square diameter of the stalk, in 0.01 cm². The diameter was recorded about two weeks after silking, at about 10–30 cm above the ground, measuring the narrowest part of an internode with a vernier callipers in 0.01 cm.
8. The product of length and width of the leaf growing from the node from which the main ear developed, in 0.1 dm². The width of the leaf was measured at its widest point.
9. The length of the main ear, in 0.1 cm.
10. The circumference of the main ear, measured at its widest point, in 0.1 cm.
11. The number of seed rows on the main ear.
12. The weight of dry grain.

Also recorded were the number of ears harvested per plant. In almost all cases the main ear was the only seed producing ear of the plant, the character 'number of ears harvested' was therefore not used in the statistical analysis of the results.

The plants were left to open pollination. The crop suffered from a lack of rain towards the end of the season. From the two hundred plants a number had to be discarded because they broke off before reaching maturity. In addition some selection among the remaining plants was necessary because a minimum of one hundred and twenty seeds per plant was needed for the progeny test.

The individual progenies of one hundred and twenty-one plants were tested in a yield trial conducted at the Mokwa experimental farm during the early season of 1968. The yield trial was laid out using a double (simple) lattice design with four replications as given by FEDERER (1955). The design was chosen in order to correct, if necessary, for environmental heterogenity ('adjustments for incomplete blocks'). The plot size was one row of fifteen stands. The experiment was planted on 26th April 1968. The cultural practices used for the experiment were the same as before. Plot yields were recorded as the weight of the ears immediately after harvesting. For various practical reasons the weight of undried ears per plot had to be used as a measurement of yield. However it could be safely assumed that there were no large differences in threshing percentage and moisture content of the ears between progenies. Adjustments for incomplete blocks turned out to be unnecessary. Consequently, the design chosen has no further bearing on the analysis of the experiment.

The experimental data were used to determine several selection indices. The

selection indices were estimated from the multiple regression of the progeny yields on the characters of the parents.

An identical experiment was performed with Colombian Composite. The parent generation consisted of thirty-six plants, grown during the late season of 1969. The progenies of the thirty-six plants were tested in the early season of 1970. A more detailed description of this second experiment, and also the reason for the limited number of progenies, will be given in chapter 5.

4.4. RESULTS

The response to selection is estimated according to expression (11), page 4, as:

$$\hat{R} = k \cdot \hat{r} (I, H) \cdot \hat{\sigma}_H \tag{29}$$

where:

$\hat{R}$ = estimated response to selection
k = selection intensity
$\hat{r}(I, H)$ = estimate for the correlation between the phenotypic and the genetic value
$\hat{\sigma}_H$ = estimate for the standard deviation of the genetic value.

As can be seen from the formula the response to selection depends on the correlation between the phenotypic and the genetic value. The genetic value or breeding value of a plant may be estimated as twice the mean deviation of its progeny from the population mean. As the phenotypic value of a plant we may use its yield or any other measurement obtained from the plant. In the latter case yield is to be improved by means of indirect selection. Not included in the formula is the amount of parental control p as given in par. 2.2.3.2., page 11. When including p the formula for the response to selection becomes:

$$\hat{R} = p \cdot k \cdot \hat{r} (I, H) \cdot \hat{\sigma}_H \tag{30}$$

When selecting after flowering the selection is practised on the seed parent only, which means that the amount of parental control p is 0.5.

Table 3 for Samaru Composite 2 and table 4 for Colombian Composite give for each of the characters recorded from the parent plants respectively:
1. The correlation between that character and the mean progeny yield.
2. The improvement in yield obtained as an indirect response to selection for that character, with the improvement in yield expressed as a percentage of the mean yield.
3. The same improvement in yield now expressed as a percentage of the response to direct selection for yield (character twelve).

Within Samaru Composite 2, as shown by table 3, there were three traits which each gave a better prediction of the yield of the progeny than yield itself. These were the characters: circumference of the ear, days to silking, and plant

TABLE 3. The plant characters of Samaru Composite 2

Character	(a)	(b)	(c)
1. days to silking	0.24	$k \times 2.3$	115
2. number of ears with silks	0.13	$k \times 1.2$	60
3. number of leaves above the ear	0.11	$k \times 1.1$	53
4. number of green leaves	0.11	$k \times 1.1$	54
5. plant height	0.24	$k \times 2.3$	112
6. ear height	0.18	$k \times 1.7$	84
7. square diameter, stalk	0.09	$k \times 0.9$	43
8. length × width, leaf	0.12	$k \times 1.2$	59
9. length main ear	0.15	$k \times 1.5$	72
10. circumference main ear	0.27	$k \times 2.6$	127
11. number of seed rows, main ear	0.00	$k \times 0.0$	0
12. weight of dry grain (yield)	0.21	$k \times 2.0$	100

(a) = the correlation between the character and the mean progeny yield;
(b) = the improvement in yield expressed as a percentage of the mean yield;
(c) = the improvement in yield expressed as a percentage of the response to direct selection for yield;
k = selection intensity.

height. Within Colombian Composite, table 4, there was only one such a character, the circumference of the ear.

The multiple regression of the progeny yield on the characters of the parent plants was calculated for each of the two populations. An estimate for the selection index is given according to expression (2), page 3, by:

$$I = \sum_{i=1}^{n} \hat{b}_i \, \hat{X}_i \qquad (31)$$

where $\hat{b}_i$ is an estimate for the weighing factor and $\hat{X}_i$ an estimate for the phenotypic value for the ith trait. Selection indices for the two populations were estimated by taking the weighing factor for the ith trait b_i as twice the partial regression coefficient of the progeny yield on the phenotypic value $\hat{X}_i$ (see par. 2.2.3.1., page 8).

As it is not feasible to use a selection index based on twelve characters, some procedure is needed to select a subset of characters which will give an optimal prediction of the progeny yields. The solution to this problem can be found only by actually trying out all possible combinations of two, three and more characters. However with a large number of characters such a procedure is hardly feasible, even when using an electronic computer (SNEDECOR and COCHRAN, 1967).

SNEDECOR and COCHRAN (1967) present two different approaches to the problem of how to find a subset of independent variables (the plant characters) which will give an optimal prediction of the dependent variable (the progeny yield). These are the step up method and the step down method. According to the step down method we first calculate the multiple regression using all inde-

TABLE 4. The plant characters of Colombian Composite

Character	(a)	(b)	(c)
1. days to silking	0.17	$k \times 1.5$	44
2. number of ears with silks	0.07	$k \times 0.6$	18
3. number of leaves above the ear	0.10	$k \times 0.9$	27
4. number of green leaves	0.04	$k \times 0.4$	12
5. plant height	0.29	$k \times 2.6$	75
6. ear height	0.18	$k \times 1.6$	46
7. square diameter, stalk	0.28	$k \times 2.5$	72
8. length × width, leaf	0.24	$k \times 2.2$	63
9. length, main ear	0.17	$k \times 1.5$	44
10. circumference, main ear	0.55	$k \times 5.0$	143
11. number of seed rows, main ear	−0.13	$-k \times 1.2$	−35
12. weight of dry grain (yield)	0.38	$k \times 3.5$	100

(a) = the correlation between the character and the mean progeny yield;
(b) = the improvement in yield expressed as a percentage of the mean yield;
(c) = the improvement in yield expressed as a percentage of the response to direct selection for yield;
k = selection intensity.

pendent variables. The character which then gives the smallest contribution to the expected response to selection is omitted from the set of independent variables, after which the multiple regression is calculated again for the remaining set of independent variables. By repeating this procedure the characters may be eliminated from the selection index one by one.

In the step up method the problem is approached from the other side. First the character which by itself will give the largest expected response to selection is sought, then a second character is looked for which will give the largest additional expected response to selection. The procedure may be repeated until the selection index includes all the characters available.

The two methods will not necessarily select the same set of characters, and neither method guarantees finding the same variables as the exhaustive method of investigating every subset. Striking differences appear mainly when the independent variables are highly correlated. The differences are not necessarily alarming, because when intercorrelations are high different subsets can give almost equally good predictions (SNEDECOR and COCHRAN, 1967).

Selection indices for Samaru Composite 2 were estimated using the step down method. The selection indices are given in table 5. The selection indices including more than seven characters have not been given. Selection indices for Colombian Composite were estimated both according to the step down method, as presented in table 6, and according to the step up method, table 7. Again, the selection indices including more than seven characters have not been given.

In each selection index given in the tables 5, 6 and 7 one character has been underlined, this is the character which is omitted from the selection index in the next step down procedure (tables 5 and 6), or which has been included in the index during the last step up procedure (table 7).

TABLE 5. Selection indices for Samaru Composite 2, estimated according to the step down method

	R'^2	$S_{\hat{y}}$	D.f.	b_i/Sb_i	estimated expected response		realized response		Quotient index, realized response
					I	II	I	II	II
$I = + 0.65\,\hat{x}_1 +$ $+ 1.42\,\hat{x}_2 +$ $+ 2.64\,\hat{x}_3 +$ $- 3.97\,\hat{x}_6 +$ $+ 1.07\,\hat{x}_{10} +$ $- 0.47\,\hat{x}_{11} +$ $+ 1.37\,\hat{x}_{12}$	0.205	2.368	113	0.686	$k \times 4.4$	217	$k \times 5.1$	148	83
$I = + 0.61\,\hat{x}_1 +$ $+ 1.58\,\hat{x}_2 +$ $+ 3.33\,\hat{x}_3 +$ $- 4.05\,\hat{x}_6 +$ $+ 1.24\,\hat{x}_{10} +$ $- 0.49\,\hat{x}_{11}$	0.202	2.363	114	1.047	$k \times 4.3$	215	$k \times 5.0$	144	61
$I = + 0.58\,\hat{x}_1 +$ $+ 1.21\,\hat{x}_2 +$ $+ 1.49\,\hat{x}_3 +$ $+ 1.20\,\hat{x}_{10} +$ $- 0.46\,\hat{x}_{11}$	0.194	2.364	115	0.771	$k \times 4.3$	211	$k \times 5.3$	152	58
$I = + 0.61\,\hat{x}_1 +$ $+ 1.30\,\hat{x}_2 +$ $+ 1.30\,\hat{x}_{10} +$ $- 0.48\,\hat{x}_{11}$	0.190	2.360	116	1.445	$k \times 4.2$	209	$k \times 5.3$	153	39
$I = + 0.58\,\hat{x}_1 +$ $+ 1.38\,\hat{x}_{10} +$ $- 0.45\,\hat{x}_{11}$	0.176	2.371	117	1.714	$k \times 4.1$	201	$k \times 5.2$	149	40
$I = + 0.56\,\hat{x}_1 +$ $+ 1.04\,\hat{x}_{10}$	0.155	2.390	118	3.440	$k \times 3.8$	188	$k \times 4.7$	135	82

The underlined character in each selection index is omitted from the selection index in the next step down procedure (table 5 and 6), or it has been included in the index during the last step up procedure (table 7). R'^2 = squared multiple correlation coefficient between the dependent variable and its linear regression on the independent variables; $S_{\hat{y}}$ = standard error of the deviations from regression; D.f. = degrees of freedom; b_i/Sb_i = test statistic for the underlined character for the test on the parameter $\beta_i = 0$. The estimated expected and the realized response to selection are given: I, as a percentage of the mean yield and II, as a percentage of the response to truncation selection for yield. k = selection intensity; $\hat{x}_1$ = days to silking; $\hat{x}_2$ = number of ears with silks; $\hat{x}_3$ = number of leaves above the main ear; $\hat{x}_4$ = number of green leaves at the time of silking; $\hat{x}_5$ = plant height, in m; $\hat{x}_6$ = ear height, in m; $\hat{x}_7$ = square diameter of the stalk, in cm²; $\hat{x}_8$ = product of length and width of the leaf growing from the node from which the main ear develops, in dm²; $\hat{x}_9$ = length main ear, in cm; $\hat{x}_{10}$ = circumference main ear, in cm; $\hat{x}_{11}$ = number of seed rows on the main ear; $\hat{x}_{12}$ = weight of dry grain (yield), in 100 g.

TABLE 6. Selection indices for Colombian Composite, estimated according to the step down method

	R'^2	$S_{\hat{y}}$	D.f.	b_i/Sb_i	Response to index selection				Quotient index, realized response
					estimated expected response		realized response		
					I	II	I	II	II
$I = + 0.18\,\hat{x}_1 +$ $+ 1.70\,\hat{x}_2 +$ $- 2.10\,\hat{x}_5 +$ $+ 2.70\,\hat{x}_6 +$ $+ 0.27\,\hat{x}_9 +$ $+ 1.92\,\hat{x}_{10} +$ $- 0.57\,\hat{x}_{11}$	0.561	1.020	28	0.669	$k \times 6.8$	197	$k \times 3.3$	166	120
$I = + 0.17\,\hat{x}_1 +$ $+ 1.65\,\hat{x}_2 +$ $+ 0.93\,\hat{x}_6 +$ $+ 0.22\,\hat{x}_9 +$ $+ 1.85\,\hat{x}_{10} +$ $- 0.54\,\hat{x}_{11}$	0.554	1.010	29	0.433	$k \times 6.8$	195	$k \times 3.4$	170	112
$I = + 0.17\,\hat{x}_1 +$ $+ 1.66\,\hat{x}_2 +$ $+ 0.17\,\hat{x}_9 +$ $+ 1.90\,\hat{x}_{10} +$ $- 0.56\,\hat{x}_{11}$	0.551	0.996	30	0.773	$k \times 6.7$	195	$k \times 3.4$	170	102
$I = + 0.18\,\hat{x}_1 +$ $+ 1.30\,\hat{x}_2 +$ $+ 1.94\,\hat{x}_{10} +$ $- 0.63\,\hat{x}_{11}$	0.542	0.990	31	1.384	$k \times 6.7$	193	$k \times 3.4$	169	92
$I = + 0.98\,\hat{x}_2 +$ $+ 1.93\,\hat{x}_{10} +$ $- 0.70\,\hat{x}_{11}$	0.514	1.004	32	1.210	$k \times 6.5$	188	$k \times 2.9$	143	78
$I = + 1.90\,\hat{x}_{10} +$ $- 0.66\,\hat{x}_{11}$	0.491	1.011	33	3.555	$k \times 6.4$	184	$k \times 2.8$	139	66

For explanation see table 5.

TABLE 7. Selection indices for Colombian Composite, estimated according to the step up method

	R'^2	S_j^2	D.f.	b_i/Sb_i	estimated expected response I	II	realized response I	II	Quotient index, realized response II
$I = + 1.90\,\hat{\chi}_{10} - 0.66\,\hat{\chi}_{11}$	0.491	1.011	33	3.555	$k \times 6.4$	184	$k \times 2.8$	139	66
$I = - 0.15\,\hat{\chi}_8 + 2.19\,\hat{\chi}_{10} - 0.86\,\hat{\chi}_{11}$	0.522	0.995	32	1.439	$k \times 6.6$	190	$k \times 2.8$	138	64
$I = + 0.13\,\hat{\chi}_1 - 0.15\,\hat{\chi}_8 + 2.18\,\hat{\chi}_{10} - 0.80\,\hat{\chi}_{11}$	0.537	0.995	31	0.986	$k \times 6.7$	192	$k \times 3.2$	156	67
$I = + 0.17\,\hat{\chi}_1 + 1.07\,\hat{\chi}_2 - 0.12\,\hat{\chi}_8 + 2.15\,\hat{\chi}_{10} - 0.78\,\hat{\chi}_{11}$	0.560	0.986	30	1.251	$k \times 6.8$	196	$k \times 3.3$	162	74
$I = + 0.16\,\hat{\chi}_1 + 1.51\,\hat{\chi}_2 - 0.14\,\hat{\chi}_8 + 0.23\,\hat{\chi}_9 + 2.15\,\hat{\chi}_{10} - 0.71\,\hat{\chi}_{11}$	0.575	0.985	29	1.022	$k \times 6.9$	199	$k \times 3.4$	169	80
$I = + 0.17\,\hat{\chi}_1 + 1.47\,\hat{\chi}_2 - 0.22\,\hat{\chi}_4 - 0.15\,\hat{\chi}_8 + 0.22\,\hat{\chi}_9 + 2.20\,\hat{\chi}_{10} - 0.71\,\hat{\chi}_{11}$	0.581	0.996	28	0.618	$k \times 6.9$	200	$k \times 3.5$	171	79

For explanation see table 5.

The tables 5, 6 and 7 give for each selection index the following statistical properties of the multiple regression from which the selection index was determined:
1. The squared multiple correlation coefficient R'^2 between the dependent variable and its linear regression on the independent variables.
2. The standard error of the deviations from regression $S_{\hat{y}}$ with degrees of freedom, d.f.
3. For the underlined character in the selection index is given the test statistic b_i/Sb_i for the test on the parameter $\beta_i = 0$. On the basis of the test statistic may be decided whether the character should be omitted from the selection index (SNEDECOR and COCHRAN, 1967).

The tables 5, 6 and 7 give for each selection index also the following information on the response to index selection:
4. An estimate of the expected response to index selection, expressed both as a percentage of the mean yield and as a percentage of the response to truncation selection for yield.
5. The realized response to index selection, again expressed both as a percentage of the mean yield and as a percentage of the response to truncation selection for yield.
6. The realized response to selection when using a quotient index based upon the same set of characters as is used in the selection index. The response is expressed as a percentage of the response to truncation selection for yield.

The expected and realized responses to index selection were calculated using formula (30), page 23. The realized response to selection could not be determined from the data of the own population, as these had been used to obtain an estimate for the expected response to selection. One possibility was to test the selection indices, i.e. to assess their predicted value on a separate group of plants from the same composite which had not been used in the estimation of the selection indices. However these were not available. As the two composites were related populations the selection indices estimated for Samaru Composite 2 could be tested using the plants of Colombian Composite, and vice versa.

The quotient index, proposed by RUEBENBAUER and WEGRZYN (1963), was used as an example of an index, in which the traits are weighed according to some estimation procedure. In the quotient index method the traits are weighed by taking for each trait the quotient of the single-plant value and the mean value of the whole population.

Samaru Composite 2, table 5. The realized response to index selection expressed as a percentage of the mean yield of Colombian Composite was larger than the estimated expected response to index selection, but when expressed as a percentage of the response to truncation selection for yield the realized response was lower than the estimated expected response. This is because the response to truncation selection for yield in Colombian Composite is much higher than the same response in Samaru Composite 2. However the main point is that the realized response to index selection was always larger than the realized response to truncation selection for yield. The response to index

selection was also larger than the response obtained from a quotient index. The quotient index method was less efficient than truncation selection for yield.

Colombian Composite, table 6 and 7. The step down and the step up method did not result in the same formulae for the selection index. These discrepancies are of course not unexpected, they are not very relevant in the present context since the expected and realized responses given in the two tables do not differ very much. The realized response was always lower than the predicted response, but less so when the response was expressed as a percentage of the response to truncation selection for yield. These relations are symmetrical to the relations found for Samaru Composite 2. Again, like in Samaru Composite 2 the realized response to index selection was always larger than the realized response to truncation selection for yield. It was also larger than the response obtained from a quotient index. The quotient index method was in most cases less efficient than truncation selection for yield.

4.5. DISCUSSION

4.5.1. *Discussion of methods*

Some selection was necessary among the plants of the parent generation. This could hardly be avoided as there are always some sterile plants or plants with only a few seeds. The selection among the parent plants should bias the genetic covariance, calculated from the parent-offspring relationship, and the phenotypic variances and covariances, calculated from the parent plants. However the selection has no effect on the size of the regression of offspring on parents (FALCONER, 1960). As the selection index is estimated from the multiple regression of the yield of the offspring on the characters of the parents, the selection index is not biased by the selection among the parent plants.

The populations used in the experiments, Samaru Composite 2 and Colombian Composite, were both from recent origin. The progenies of Samaru Composite 2 and Colombian Composite had gone through respectively three and five cycles of open pollination. Although most of the linkage blocks should have been broken up, the populations should not have reached a linkage equilibrium yet, which should somewhat bias the conclusions drawn from the parent-offspring relationship.

As noted in par. 4.1., page 20, when the selection is aimed at the improvement of the crop within a certain set of environments, the offspring should be tested in a random sample of these environments. The progenies of Samaru Composite 2 however were tested at only one location. This should result in an upward bias of the expected response to index selection.

4.5.2. *Discussion of results*

The characters which gave the best prediction of the genetic value of a plant were within Samaru Composite 2 (table 3) circumference of the ear, days to silking, plant height, and yield, in that order. From table 5 however we see that

the plant height comes only as the fifth character in the selection index, while yield appears as the seventh character in the index. This is because most of the information supplied by the characters plant height and yield is already available in the selection index through the characters circumference of the ear and days to silking, since the latter two characters are correlated to the former ones (see also par. 2.1., page 6).

Similarly for Colombian Composite we notice in table 4 that the character yield is the second best character in predicting the genetic value of a plant. However, yield does not appear in the selection indices given in the tables 6 and 7 because yield is highly correlated with the character circumference of the ear, which appears as the first character in the selection index.

Although in both populations the correlation between the progeny yield and the character: 'number of seed rows on the main ear' is very low, the character appears as the second or third trait in the selection index. The number of seed rows becomes important in combination with the character: 'circumference of the ear'. The circumference of the ear is highly correlated both with the progeny yield and with the number of seed rows. The combination appearing in the selection index of the circumference of the ear with a positive sign and the number of seed rows with a negative sign indicates that the selection should be directed towards increasing the width of the seed rows.

Large differences in both directions existed between the expected and the realized responses to index selection. Two reasons may be given to explain these differences:
1. Sampling errors were involved both in the calculation of the selection indices and in the calculation of the realized responses to selection.
2. The test population, used to measure the realized responses differed from the population for which the selection indices were calculated.

Comparing the figures of table 3 and 4 we notice that there were rather large differences between the populations. While the response to truncation selection for yield within Samaru Composite 2 was: $k \times 2.0$ percent, the same figure for Colombian Composite was: $k \times 3.5$ percent. Similar differences also existed for other characters.

The responses obtained from index selection were rather encouraging, despite the lack of precision in the selection indices. The realized response to index selection was always larger than the realized response to truncation selection for yield, with differences ranging between thirty-five and seventy-one percent. Optimal responses were obtained from selection indices including about four traits. The use of more traits produced hardly any further increase in the realized response to selection or none at all.

The realized response from a quotient index was in most cases considerably less than the realized response from a selection index. These results do not agree with the findings of RUEBENBAUER and WEGRZYN (1963), who found that a quotient index was only slightly less efficient than a selection index. In the present study the quotient index method was in most cases also less efficient than truncation selection for yield.

The quotient index method was used as an example of an index in which the weights of the different traits are estimated according to some rule of thumb. The success of any 'estimated' index should depend on whether the right characters are included in the index. For example, for the populations under study it is clear that the circumference of the ear is much more important than the length of the ear in determining the yield. Any index to be constructed for these populations should put emphasis on the circumference rather than on the length of the ear. This example shows that even when employing an 'estimated' index, it is still necessary to have some estimates for the population parameters, so as to know which are the main characters determining yield.

4.5.3. *Selection under special conditions*

It may be advantageous to select under environmental conditions which differ from the normal environment of the crop. For instance, to speed up a selection programme, selection may be practised also during the off-season. Another possibility is to create environmental conditions such as to maximize the genetic variance and the single-plant heritability. Such an environment is probably realized by choosing conditions which favour an optimal development of individual plants, using a wide spacing and ample amounts of fertilizer (ANON., 1969). The parent-offspring relationship is then used to measure the relationship between the phenotypic value, as obtained in the modified selection environment, and the genetic value as obtained from the progeny means, when the progenies are measured under normal cropping conditions.

The situation at Mokwa may serve as an example. The rainy season at Mokwa lasts from April till October. Within this time it is just possible to grow two crops of maize. The main crop is planted at the beginning of the season, in April-May, and harvested 100–110 days later in August-September. A second crop may still be planted until about mid-August to be in time before the end of the rains. With irrigation facilities a third crop may be grown during the dry season.

The efficiency of mass selection may be greatly increased when it becomes possible to select two or three times a year, instead of only just once during the main season. The experiments show that the yield of the early planted main crop may be improved by selection in a late-season crop. In both experiments the parent generations were grown as late-season crops, while the progenies were tested during the main season. The response to truncation selection for yield when selecting the top ten percent, $k = 1.755$, was, when selecting within Samaru Composite 2, 3.5 percent, and, when selecting within Colombian Composite, 6.1 percent. The realized response to individual selection could be further increased by thirty-five to seventy-one percent by using a selection index.

A third cycle of selection is possible during the dry season. The environment during the dry season differs greatly from the normal cropping environment. Truncation selection for yield during the dry season therefore should not necessarily result in an improvement in yield of the crop grown in the main season. A selection index which would serve as an indicator of the genetic value

of the phenotypes resulting under dry-season conditions should be most valuable for selection in the dry season. There are however no experimental data to support this.

4.5.4. *A comparison with selection methods based upon progeny means*

Assuming that the realized response to individual index selection is the same irrespective of the time of the year in which the selection is practised, we may estimate the cumulative response to individual index selection over a one year period. With three cycles of selection per year and a ten percent selection intensity the response per year should be for Samaru Composite 2 between fifteen and nineteen percent, and for Colombian Composite between twenty-six and thirty percent.

The response to individual index selection may be compared with the response obtained from selection methods based upon progeny means. A general formula for the expected response to selection using such methods was presented in par. 2.2.3.2., page 11. The experimental data for Samaru Composite 2 and Colombian Composite may be used to calculate the expected response to selection for the different methods based upon half-sib progeny means. When selecting the top ten percent the expected response to selection within Samaru Composite 2 should be for:

modified ear-to-row selection	4.2%
half-sib selection	8.4%
half-sib progeny selection	16.8%

The same figures for Colombian Composite are:

modified ear-to-row selection	4.8%
half-sib selection	9.6%
half-sib progeny selection	19.2%

The differences in the expected response to selection between the three selection methods depend on the amount of parental control p within each of the three methods (see par. 2.2.3.2., page 11).

As noted in paragraph 2.2.3.2., page 12, the expected response to selection calculated for the different selection methods does not take into account any effect of individual selection which normally has its place within these selection methods. As noted, the effect of any such individual selection should be small.

When we compare the figures given for individual index selection (15–19% for Samaru Composite 2 and 26–30% for Colombian Composite) with these given for the three other methods of selection, we notice that for both populations individual index selection compares favourably to selection methods using progenies. The two populations used in this study were composites of recent origin, possessing a large amount of genetic variability. As noted in chapter 1, page 1, individual selection should be a relatively efficient method of selection when using such populations. Individual selection however should be less suitable for the improvement of long established, high performing populations, possessing only a limited amount of genetic variability.

5. THE SELECTION INDEX,
RESULTS FROM EXPERIMENTS, II

An experiment was conducted to estimate selection indices for the simultaneous improvement of yield and resistance to stem- and rootlodging. The selection indices were determined using the results from a sib analysis.

5.1. EXPERIMENTAL CONDITIONS AND CHARACTERS MEASURED

A late-season crop of Colombian Composite was planted on 22nd July 1969 on an isolated field at the Mokwa experimental farm. The crop received 52 kg P_2O_5 per ha, applied as superphosphate a few days before planting, and 100 kg nitrogen per ha, applied as calcium-ammoniumnitrate in equal doses two and six weeks after planting. The seeds were hand planted with two seeds per stand. Two weeks after planting the stands were thinned to one plant each. The stands were spaced 30 cm within the row and 91 cm between rows, giving a total of 35,880 stands per ha.

Individual plant characters were recorded from three hundred plants. These plants were chosen at random with the restriction that each plant had a bordering stand at either side. Apart from the twelve characters listed in paragraph 4.2. five other characters were measured, they were:
1. the total number of leaves;
2. the number of nodes with brace roots;
3. the length of the shank of the main ear, in 0.5 cm;
4. the number of seed-producing ears;
5. the hundred-seed weight, in 0.1 g.

Ad 1. The differentiation of the tassel terminates the differentiation of the leaves, so that the total number of leaves per plant may be recorded as soon as the tassel becomes visible. However the first four or five leaves which the plant develops have already disappeared at the time the tassel becomes visible. Therefore the leaves had to be counted as they developed. About two to three weeks after planting, when the plants had five to six leaves, a strip of brown paper was attached round the stem between the fourth leaf and the fifth leaf. Subsequently, brown paper strips were attached round the stem between the eighth and the ninth leaf and between the twelfth and the thirteenth leaf. The total number of leaves could be determined as soon as the tassel became visible, by counting the number of leaves above the uppermost strip of brown paper.

Ad 2. The number of nodes with brace roots was determined a few days before harvesting, by recording the rank number of the uppermost node with brace roots. The rank number could be known because the rank number of the nodes corresponds to the rank number of the leaves.

Ad. 3. The ear is mounted on a short stalk, the shank of the ear, which

branches from the main stalk. The length of the shank was measured from the main stalk to the inplanting of the seeds.

Ad. 4. A seed-producing ear was recorded as such, when it produced at least 2 g of dry grain.

Ad 5. The hundred-seed weight was determined by weighing hundred seeds taken from the main ear.

After harvesting the ears it was tried to determine several stalk characters from the plants remaining in the field. It was not possible however to obtain reliable measurements from these plants, because about ninety percent of the plants were infested by stemborers while towards harvest the stalks of the plants were also attacked by termites.

The progenies of one hundred and forty-four out of the three hundred plants were tested in a progeny test conducted in 1970. In choosing the one hundred and forty-four plants some selection for yield was necessary, as a minimum of two hundred and eighty-eight seeds was needed for the progeny test.

To limit the block size the experiment was conducted using the procedure proposed by COMSTOCK and ROBINSON (1952a). The one hundred and forty-four progenies were divided in twelve groups of twelve progenies each, and each group was laid out separately in a randomized block design. The progenies were tested in four different environments with two replications per environment, giving a total of eight replications. Thus in each environment there were two replications of twelve blocks, each with twelve plots. The four environments consisted of two locations, the Mokwa experimental farm and a field cleared near the Mokwa residential area at a distance of 8 km from the farm. Two different environments were created at each location by using two dates of planting. The planting dates were at the Mokwa experimental farm 23rd May and 18th June, and at the field near the residential area 11th May and 6th June. The dates of planting had to be chosen rather late in the season, because in 1970 the rains were about three weeks later than normal.

The size of the plots was one row of eighteen stands. The first and the last stand of each plot were taken as border plants, so that the net plot size consisted of sixteen stands. The stands were spaced 30 cm within the row and 91 cm between rows, giving a total of 35,880 stands per ha. The seeds were hand planted with two seeds per stand. About two weeks after planting the stands were thinned to one plant each.

The field located near the residential area was cleared from grass and small shrubs during the preceding dry season, after which the field received eight cartloads farmyard manure per ha. Both the field at the experimental farm and the field near the residential area received 78 kg P_2O_5 as superphosphate and 67 kg K_2O as muriate of potash before planting. On both fields the crop received 100 kg nitrogen per ha as calcium-ammoniumnitrate in three times, one quarter of it two weeks after planting and the remaining quantity in equal doses five and eight weeks after planting. When some of the seedlings showed signs indicating zinc deficiency, the crop was sprayed twice with a solution of zinc sulphate, thereby applying a total of 224 g zinc sulphate per ha. To control

termites, the fields were treated before planting with dieldrin, using 1.5 kg per ha. Stemborers were controlled with two applications of 17 kg five percent thiodan granules per ha, given five and eight weeks after planting.

Within each plot two plants were chosen at random. As there were eight replications, a total of sixteen plants were chosen from each progeny. The plants were used to determine the individual plant characters. At this stage it was decided to alter the list of seventeen characters which had been used in studying the parent generation. Several characters were added to the list of characters, among these were the stalk characters which could not be recorded from the parent plants. Included also was the leaf angle, following reports of PENDLETON et al. (1968) on the influence of leaf angle on yield. The character number of green leaves at the time of silking was no longer used. Following reports of FRANCIS et al. (1969) the length and width of the leaves were recorded using leaf eight instead of using the leaf growing from the node from which the main ear developed. The complete list of characters recorded from the plants reads as follows:

A. Records taken before flowering
1. The days to shooting, that is the number of days from planting till the appearance of the tassel. The other characters observed before flowering were recorded when the tassel had just become visible.
2. The total number of leaves.
3. The length of leaf number eight when counting the leaves from the top leaf downwards, in cm.
4. The largest width of leaf number eight, in 0.1 cm.

B. Records taken during and after flowering
5. The days to silking, that is the number of days from planting till the emergence of the silks.
6. The number of ears with silks.
7. The number of leaves above the main ear, which usually was the top ear of the plant.
8. The leaf angle of leaf number three, when counting the leaves from the top leaf downwards. The leaf angle was measured using a piece of cardboard, 1 dm square. The cardboard was held in a vertical position above the leaf, with one side against the stem of the plant. The cardboard was then lowered so that it just touched the midrib of the leaf. Thus the point where the cardboard touched the leaf was at one dm distance from the stem. The length of the leaf in 0.01 dm, measured from the stem to the point where it touched the cardboard, was used as a measurement of the leaf angle. This measurement was equal to $1/\sin \alpha$, when α was the angle in degrees between stem and leaf.
9. The plant height, measured from ground level to the flag of the top leaf, in cm.
10. The ear height, measured from ground level to the node from which the main ear arises, in cm.

The latter three records were collected about two weeks after silking.

C. Records taken at harvest
11. The number of nodes with brace roots.
12. The number of seed-producing ears.
13. The length of the shank of the main ear, in 0.5 cm.
   Also recorded was the fact whether the plant was stemlodging or rootlodging or neither.

D. Ear characters, recorded after harvesting
14. The length of the main ear, in 0.1 cm.
15. The circumference of the main ear, measured at its widest points, in 0.1 cm.
16. The number of seed rows on the main ear.
17. The seed weight of the main ear, in g.
18. The seed weight of the second ear, in g.
19. The total seed weight, in g.
20. The hundred-seed weight, in 0.1 g.
21. The threshing percentage, calculated as the ratio of the total seed weight and the total weight of dry ears before threshing.

E. Straw characters, recorded after harvesting the ears
   After harvesting the ears the plants were uprooted with a lever divice in the way described by Craig (1968). The strength needed to uproot the plant was measured with a spring balance attached to the lever. The uprooted plants were divided in roots and straw by cutting the stalk at ground level. The straw which included the shank and the husks of the ear, was weighed. The roots were washed and the water shaken off. The roots were then left to dry for about half an hour in the sun before weighing them. A 5-cm stalk section was cut from the second internode above the ground. Using this stalk section the diameter of the stalk was measured in both directions with a vernier callipers in 0.01 cm. Next, the stalk section was dried for one week at 40°C, and weighed. The crushing strength was determined with a hydraulic press. The stalk section was placed standing upright in the press, and the amount of pressure needed to crush the stalk section, that is when the stalk would suddenly collapse, was recorded in pounds and converted to kg. Using the fragments of the crushed stalk section, the rind thickness was measured with a vernier callipers in 0.01 cm.
   The following straw characters were collected:
22. The pulling strength, that is the strength needed to uproot the plant, in kg.
23. The weight of the straw, in g.
24. The weight of the roots, in g.
25. The square of the diameter of the stalk, calculated as the product of the diameters measured in both directions, in 0.01 cm².
26. The dry weight of a 5-cm stalk section of the second internode, in 0.01 g.
27. The crushing strength of the stalk, in kg.
28. The rind thickness of the stalk, in 0.01 cm.

In addition, the following records were collected on a net plot basis:
1. The number of plants.
2. The yield of dry grain. The weight of freshly harvested ears was converted to dry weight of grain by multiplying the weights with a conversion factor. The conversion factor was determined separately for each environment, using a sample of about 10 kg freshly harvested ears.
3. The number of stemlodged plants, that is plants broken below the main ear.
4. The number of rootlodged plants, that is plants leaning more than thirty degrees from the vertical, but not broken below the ear. A distinction was made between plants only leaning and plants completely bent down, touching the ground. The first were counted as half rootlodging, while the latter were counted as fully rootlodging.

The observations on stem- and rootlodging were used as measurements for resistance to stem- and rootlodging. Resistance to stemlodging and resistance to rootlodging were therefore defined as follows. Plants not recorded as stemlodging were classified as resistant to stemlodging, while stemlodged plants were classified as non-resistant to stemlodging. Plants recorded as non-rootlodging, as half, and as fully rootlodging were classified respectively as resistant, half resistant, and non-resistant to rootlodging.

5.2. OBSERVATIONS AND PROCEDURES

Part of the experiment was virtually destroyed by a leaf disease, caused by *Helminthosporium maydis.* Prior to 1970 Colombian Composite itself and also the lines contributing to the composite were known to be resistant to *Helminthosporium maydis.* CRAIG identified the disease suddenly occurring in 1970 as caused by race T of *H. maydis* which apparently had not been present in Nigeria prior to 1970 (CRAIG, 1971). The first symptoms of the disease were shown some time before flowering by the lower leaves of the plant, small oval shaped spots, tan coloured in the centre, with a brown margin, and round the spots a discoloured translucent zone. Very soon all the leaves, husks and leafsheaths were attacked, showing spots ranging up to 25 mm in length and up to 8 mm in width. Spots joined together to form large areas of dead tissue till at about two to four weeks after silking when the leaves had died off completely, resulting in a reduction in yield of fifty percent and more. Also the ears showed symptoms of the disease, with blackened seeds mainly at the eartips.

The one hundred and forty-four half-sib progenies could be classified in two distinct groups, one hundred and seven progenies were susceptible to the disease, resulting in a near complete failure of the crop, while thirty-seven progenies carried complete resistance to the disease. This led to the provisional conclusion that resistance to the disease depended on a factor located in the cytoplasm, while the ratio between susceptible and resistant progenies of almost 3:1 is believed to be accidental.

This conclusion was confirmed by other observations. A number of resistant

38   *Meded. Landbouwhogeschool Wageningen 72-1 (1972)*

varieties had been crossed with Colombian Composite as the seed parent. All these crosses, which carried cytoplasm from Colombian Composite, were susceptible to the disease. In still another experiment one hundred and forty-four sets of reciprocal crosses had been made, using two hundred and eighty-eight plants of Colombian Composite. Each set of reciprocal crosses was bulked, giving one hundred and forty-four full-sib progenies. Of these progenies fifty-nine were completely resistant and thirty-one were completely susceptible to the disease, while the remaining fifty-four progenies consisted of both resistant and susceptible plants. These numbers do deviate somewhat from the expected p^2 to $2pq$ to q^2 ratio, the reason for this is that in a number of cases only one of the two reciprocal crosses set seed. This inflates the number of completely resistant and completely susceptible families.

Returning now to the half-sib progeny test, the one hundred and seven susceptible progenies had to be discarded so that there remained thirty-seven progenies. Part of the data of one progeny was lost, so that finally the data from only thirty-six half-sib progenies remained. With sixteen plants per progeny (two plants per plot in eight replications), there were records available from $16 \times 36 = 576$ plants.

Eight of the 576 plants were sterile, while a few other plants produced only a few seeds. These plants constituted a problem because several ear characters could not be recorded from these plants. Rather than entering zero for all these measurements, it was thought more desirable to use the minimum value which had been observed for these respective characters. Thus the minimum value recorded for the hundred-seed weight, 12.3 g, was taken as the hundred-seed weight for the seventeen plants, from which the hundred-seed weight could not be otherwise determined. Likewise, the minimum value of 8.0 cm for the circumference of the ear had to be used sixteen times, the minimum value of 5.1 cm for ear length, and the minimum value of 10 for the number of seed rows, had to be used four times, while the minimum value of 5.0 cm for the earshank had to be used twice.

From thirty plants the pulling strength could not be measured, because they broke off near the surface when uprooting them with the lever. Estimates for the missing values were obtained by calculating the pulling strength from the regression of pulling strength on root weight.

From the 576 plants under observation there were seventeen plants from which the label was lost or which broke off or died *before* flowering. Consequently these plants were substituted each by a third plant randomly chosen within the same plot. The total number of leaves and the number of nodes with brace roots could not be recorded anymore from these later plants, while for thirteen of them it was also too late to record the shooting date. Estimates for the missing data were calculated from the regression on a correlated character. As correlated characters were used the plant height for the total number of leaves, the days to silking for the days to shooting, and the root weight for the number of nodes with brace roots. Although other, more precise statistical methods could have been employed to overcome the difficulty of missing values,

the procedure of estimation by using the regression on a correlated character was thought to be sufficiently adequate for the purpose.

In the original experimental layout there were two times twelve, which is twenty-four blocks, each consisting of twelve plots per environment. With data from only thirty-six progenies there remained however only two times thirty-six, which is seventy-two plots per environment. In analysing the results, each environment was now taken as a single block, disregarding the earlier subdivision in twenty-four blocks. This introduced some bias as the treatments were not randomly distributed within each environment.

The data were analysed according to the analysis of variance presented in table 2, page 11. Analyses of variance were carried out for each single character, and analyses of covariance were carried out for all possible pairs of characters. The expectations of the mean squares and the mean products were used to obtain estimates for the various components of variance and covariance. In a number of cases negative estimates were obtained for the variance component for the genotype by environment interaction or for the variance component between plots or for both, while a negative estimate was also obtained for the progeny component of variance for the character seed weight of the second ear. Whenever a negative estimate was obtained for a variance component, the component was taken to be zero.

The variance and covariance components were used to obtain estimates for the genetic variances and covariances, the within plot phenotypic variances and covariances, and the total phenotypic variances and covariances. The total phenotypic variance is estimated according to expression (24), page 10, as:

$$\hat{\sigma}^2_p = \hat{\sigma}^2_w + \hat{\sigma}^2_e + \hat{\sigma}^2_{ge} + \hat{\sigma}^2_g \tag{32}$$

where:

$\hat{\sigma}^2_w$ = estimate for the variance among individual plants within plots
$\hat{\sigma}^2_e$ = estimate for the between plot component of variance
$\hat{\sigma}^2_{ge}$ = estimate for the variance component due to genotype by environment interaction
$\hat{\sigma}^2_g$ = estimate for the progeny component of variance

The phenotypic variance within plots is estimated according to expression (25), page 10, as:

$$\hat{\sigma}^2_p \text{ (within plots)} = \hat{\sigma}^2_w + \hat{\sigma}^2_{ge} + \hat{\sigma}^2_g \tag{33}$$

The phenotypic variance within plots is equal to the total phenotypic variance minus the between plot component of variance. Likewise the phenotypic covariance within plots does not contain the between plot component of covariance. In presenting the results, we will first confine ourselves to the total phenotypic variances and covariances. The phenotypic variances and covariances will therefore stand for the total phenotypic variances and covariances, unless indicated otherwise.

The characters of economic importance, yield, resistance to stemlodging and resistance to rootlodging, were recorded in two different ways:

40

/

1. From single plants, single-plant measurements were obtained from two plants per plot, just as for the other plant characters.
2. From the net plots, for each plot the plot total was divided by the number of plants per plot to obtain the single-plant mean value for that plot.

The analysis of variance for each of the three characters may be carried out using either the single-plant measurements of the single-plant mean value as the value for each plant. The analysis of variance is carried out for two plants per plot. When using the single-plant mean values the same value has to be assigned to both plants within a plot, which means that it is not possible to estimate the within plot component of variance. However, the estimates obtained for the other variance components, including the progeny component of variance, should be better than the estimates obtained from single-plant measurements, because the single-plant mean value uses information derived from whole plots. Likewise the analysis of covariance between yield (or resistance to stem- or rootlodging) and any other character may be carried out in two different ways, by using for yield either the single-plant measurements or the single-plant mean values. The single-plant mean value for yield should give a better estimate for the progeny component of covariance than the single-plant measurement for yield. In order to make an optimal use of the information available the genetic covariances with yield were estimated using the single-plant mean values for yield, while the phenotypic covariances with yield were estimated using the single-plant measurements for yield. The same procedure was followed for the other two characters of economic importance, resistance to stemlodging and resistance to rootlodging.

5.3. PRESENTATION OF RESULTS AND CALCULATION OF SELECTION INDICES

Some of the results are summarized in table 8. For each character are given:
1. An estimate for the single-plant heritability h^2.
2. Estimates for the genetic and phenotypic correlations with the three characters of economic importance, yield, resistance to stemlodging and resistance to rootlodging.

The single-plant heritability h^2 was calculated as the ratio between the genetic variance and the phenotypic variance. As noted above, the genetic variances for yield and resistance to stem- and rootlodging could be estimated from the single-plant mean values. This means that the single-plant heritabilities for these three characters were estimated with greater accuracy than the single-plant heritabilities for the other plant characters. The genetic correlations with the three characters of economic importance were calculated as the genetic correlations with the single-plant mean values for these characters. However the phenotypic correlations with these three characters were calculated as the phenotypic correlations with the single-plant measurements for these characters. The genetic correlations between yield and resistance to stemlodging, between yield and resistance to rootlodging, and between resistance to stemlodging and

TABLE 8. The single-plant heritability, and the genetic and phenotypic correlations with yield, resistance to stemlodging, and resistance to rootlodging, as estimated for the different characters

	(a)	(b)	(c)	(d)	(e)	(f)	(g)
1. days to shooting	0.75	0.40	−0.15	−0.08	−0.07	−0.21	−0.06
2. total number of leaves	0.84	0.18	0.10	−0.19	−0.03	−0.34	−0.08
3. length of leaf eight	0.46	0.57	0.26	0.04	0.11	−0.06	0.02
4. width of leaf eight	0.32	0.85	0.33	0.22	0.01	0.17	−0.06
5. days to silking	0.80	0.12	−0.42	0.08	0.05	−0.25	−0.04
6. number of ears with silks	0.26	−0.26	0.23	−0.89	−0.07	−0.18	−0.06
7. number of leaves above the main ear	0.44	0.34	−0.06	0.26	0.06	0.25	0.06
8. leaf angle	0.57	0.32	0.06	0.27	0.01	0.36	0.07
9. plant height	0.26	0.72	0.28	−0.21	0.06	−0.63	−0.11
10. ear height	0.43	0.64	0.31	−0.31	0.04	−0.72	−0.20
11. number of nodes with brace roots	0.45	0.00	−0.01	0.21	0.04	0.05	0.06
12. number of seed-producing ears	0.07	0.55	0.38	−0.52	−0.06	0.30	−0.01
13. length of the shank of the main ear	0.46	0.31	0.34	0.20	0.10	0.18	0.03
14. length of the main ear	0.09	0.90	0.62	0.19	0.14	0.26	−0.10
15. circumference of the main ear	0.13	0.61	0.69	−0.01	0.13	−0.30	−0.16
16. number of seed rows on the main ear	0.54	−0.34	0.25	−0.24	−0.08	−0.19	−0.03
17. seed weight of the main ear	0.06	0.67	0.89	0.18	0.21	0.10	−0.15
18. seed weight of the second ear	−*	−*	0.38	−*	−0.09	−*	0.05
19. total seed weight (yield)	0.09	−	−	0.04	0.17	0.07	−0.12
20. hundred-seed weight	0.40	0.57	0.53	0.49	0.30	−0.08	−0.15
21. threshing percentage	0.14	−0.45	0.59	−0.22	0.01	−0.36	−0.09
22. pulling strength	0.12	0.89	0.27	1.05**	0.36	0.63	0.03
23. weight of straw	0.46	0.62	0.39	0.62	0.38	−0.33	−0.21
24. root weight	0.31	0.80	0.36	0.65	0.29	0.74	0.07
25. square diameter of the stalk	0.36	0.63	0.39	0.08	0.13	0.22	−0.05
26. dry weight of a 5-cm. stalk section	0.34	0.74	0.25	0.97	0.35	0.11	−0.13
27. crushing strength of the stalk	0.39	0.60	0.17	0.92	0.32	0.18	−0.12
28. rind thickness of the stalk	0.27	0.22	0.22	0.35	0.23	0.18	−0.15
resistance to stemlodging	0.15	0.04	0.17	−	−	0.61	−0.35
resistance to rootlodging	0.12	0.07	−0.12	0.61	−0.35	−	−

* A negative estimate was obtained for the genetic variance of the character seed weight of the second ear. ** The correlation was estimated to be larger than 1.0.

(a) = single-plant heritability, (b) = genetic correlation with yield, (c) = phenotypic correlation with yield, (d) = genetic correlation with resistance to stemlodging, (e) = phenotypic correlation with resistance to stemlodging, (f) = genetic correlation with resistance to rootlodging, (g) = phenotypic correlation with resistance to rootlodging.

resistance to rootlodging, could be estimated with greater precision than the other correlations by using each time for each pair of characters the single-plant mean values.

The parameters of the population may be used to estimate selection indices for yield improvement, using the formulae (2) and (17) from respectively page 3 and page 5.

$$I = \sum_{i=1}^{n} \hat{b}_i \hat{X}_i \tag{34}$$

$$\sum_{i=1}^{n} \hat{b}_i \hat{P}_{i,j} = \hat{G}_{y,j} \, (j = 1, 2, \ldots, n) \tag{35}$$

where:
$\hat{b}_i$ = estimate for the weighing factor for the ith trait
$\hat{X}_i$ = estimate for the phenotypic value for the ith trait
$\hat{P}_{i,j}$ = estimate for the phenotypic covariance between the traits i and j, or
       when $i = j$ an estimate for the phenotypic variance
$\hat{G}_{y,j}$ = estimate for the genetic covariance between the jth trait and yield.

An estimate of the selection index is given by formula (34), the weighing factors $\hat{b}_i$ in formula (34) may be calculated from the set of n equations given by expression (35). On the left-hand side the equations contain the phenotypic variances and covariances and on the right-hand side the genetic covariances with yield. Yield itself is one of the characters considered in the selection index, and for yield itself we obtain instead of a genetic covariance the genetic variance of yield.

The expected response to index selection may be calculated according to formula (19), page 5.

$$\hat{R}_y = p \cdot k \cdot \sqrt{\sum_{i=1}^{n} \hat{b}_i \hat{G}_{i,y}} \tag{36}$$

where:
$\hat{R}_y$ = estimated expected response to selection
p = amount of parental control, and
k = selection intensity.

A selection index for yield improvement was calculated with the selection index based upon twenty-seven characters. The character 'number of ears with silks' was not used in the construction of the selection indices, because a misleading estimate was obtained for the genetic covariance between yield and number of ears with silks, as will be explained further in the discussion.

Some procedure was needed to choose out of the twenty-seven characters a subset of characters which would give an optimal prediction of the value of a plant. The problem could not be solved by using the estimation procedures given by SNEDECOR and COCHRAN (1967) (see also par. 4.4., page 24), because the standard errors of the different estimates were not available. The following estimation procedure was followed instead: Starting with a selection index based on twenty-seven characters, the character which gave the lowest value for the product $\hat{b}_i \hat{G}_{i,y}$ was eliminated, after which the selection index was calculated anew for the remaining characters. The elimination procedure was repeated till there remained only one character in the selection index.

TABLE 9. Selection indices for the improvement of yield

Selection index	Estimated expected response to index selection	Selection index	Estimated expected response to index selection
$\hat{I} = + 1.21\ \hat{\chi}_1\ +$ $+ 4.88\ \hat{\chi}_4\ +$ $+ 0.237\ \hat{\chi}_{10}\ +$ $+ 3.42\ \hat{\chi}_{15}\ +$ $- 2.56\ \hat{\chi}_{16}\ +$ $+ 0.597\ \hat{\chi}_{20}\ +$ $- 0.553\ \hat{\chi}_{21}$	$k \times 5.9$	$\hat{I} = + 1.55\ \hat{\chi}_1\ +$ $+ 5.34\ \hat{\chi}_4\ +$ $+ 0.208\ \hat{\chi}_{10}\ +$ $\underline{+ 0.701\ \hat{\chi}_{20}}$	$k \times 5.0$
$\hat{I} = + 1.34\ \hat{\chi}_1\ +$ $+ 4.88\ \hat{\chi}_4\ +$ $+ 0.241\ \hat{\chi}_{10}\ +$ $\underline{+ 1.62\ \hat{\chi}_{15}\ +}$ $+ 0.936\ \hat{\chi}_{20}\ +$ $- 0.547\ \hat{\chi}_{21}$	$k \times 5.7$	$\hat{I} = \underline{+ 1.36\ \hat{\chi}_1\ +}$ $+ 5.98\ \hat{\chi}_4\ +$ $+ 0.233\ \hat{\chi}_{10}$	$k \times 4.6$
		$\hat{I} = + 5.88\ \hat{\chi}_4\ +$ $\underline{+ 0.273\ \hat{\chi}_{10}}$	$k \times 4.1$
$\hat{I} = + 1.32\ \hat{\chi}_1\ +$ $+ 5.32\ \hat{\chi}_4\ +$ $+ 0.260\ \hat{\chi}_{10}\ +$ $+ 1.04\ \hat{\chi}_{20}\ +$ $\underline{- 0.446\ \hat{\chi}_{21}}$	$k \times 5.6$	$\hat{I} = + 6.83\ \hat{\chi}_4$	$k \times 3.4$

The estimate for the expected response to index selection is expressed as a percentage of the mean yield. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_1$ = days to shooting; $\hat{\chi}_4$ = width of leaf eight, in cm; $\hat{\chi}_{10}$ = ear height, in cm; $\hat{\chi}_{15}$ = circumference of the main ear, in cm; $\hat{\chi}_{16}$ = number of seed rows on the main ear; $\hat{\chi}_{20}$ = hundred-seed weight, in g; $\hat{\chi}_{21}$ = threshing percentage.

Selection indices for yield improvement are presented in table 9 with the indices based on up to seven characters. The expected response to selection was estimated for selection after flowering, so that the amount of parental control p is 0.5. The estimate for the expected response to selection R_y is expressed as a percentage of the mean yield. As may be seen from the table, when eliminating the characters one by one, the characters remaining in the index are: the width of leaf eight, the ear height, the days to shooting, the hundred-seed weight, the threshing percentage, the circumference of the main ear and the number of seed rows on the main ear, in that order. Further comments on the characters appearing in the selection indices will be given in the discussion.

Selection indices for resistance to stemlodging and for resistance to root-lodging were calculated in a similar way as the selection indices for yield improvement. The selection indices for the improvement of resistance to respectively stem- and rootlodging are presented in the tables 10 and 11. In both tables the estimate for the expected response to selection $\hat{R}_y$ is given as a percentage of the mean amount of lodging. When eliminating the characters one by one, the characters remaining in the selection index for stemlodging resist-

TABLE 10. Selection indices for the improvement of resistance to stemlodging

Selection index	Estimated expected response to index selection	Selection index	Estimated expected response to index selection
$I = -0.0356\ \hat{\chi}_2 +$ $+ 0.0336\ \hat{\chi}_7 +$ $- 0.00137\ \hat{\chi}_9 +$ $+ 0.00227\ \hat{\chi}_{20} +$ $+ 0.0000644\ \hat{\chi}_{23} +$ $+ 0.906\ \hat{\chi}_{26} +$ $+ 0.000308\ \hat{\chi}_{27}$	$k \times 27.3$	$I = -0.0354\ \hat{\chi}_2 +$ $+ 0.00183\ \hat{\chi}_{20} +$ $+ 0.940\ \hat{\chi}_{26} +$ $+ 0.000320\ \hat{\chi}_{27}$	$k \times 25.1$
$I = -0.0420\ \hat{\chi}_2 +$ $+ 0.0294\ \hat{\chi}_7 +$ $+ 0.00193\ \hat{\chi}_{20} +$ $+ 0.0000168\ \hat{\chi}_{23} +$ $+ 0.846\ \hat{\chi}_{26} +$ $+ 0.000314\ \hat{\chi}_{27}$	$k \times 25.7$	$I = -0.0364\ \hat{\chi}_2 +$ $+ 0.988\ \hat{\chi}_{26} +$ $+ 0.000332\ \hat{\chi}_{27}$	$k \times 24.9$
$I = -0.0416\ \hat{\chi}_2 +$ $+ 0.0282\ \hat{\chi}_7 +$ $+ 0.00205\ \hat{\chi}_{20} +$ $+ 0.874\ \hat{\chi}_{26} +$ $+ 0.000216\ \hat{\chi}_{27}$	$k \times 25.7$	$I = +0.750\ \hat{\chi}_{26} +$ $+ 0.000350\ \hat{\chi}_{27}$	$k \times 22.1$
		$I = +0.000554\ \hat{\chi}_{27}$	$k \times 20.4$

The estimate for the expected response to index selection is expressed as a percentage decrease in the mean amount of stemlodging. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_2$ = total number of leaves; $\hat{\chi}_7$ = number of leaves above the main ear; $\hat{\chi}_9$ = plant height, in cm; $\hat{\chi}_{20}$ = hundred-seed weight, in g; $\hat{\chi}_{23}$ = weight of straw, in g; $\hat{\chi}_{26}$ = dry weight of a 5-cm stalk section, in g; $\hat{\chi}_{27}$ = crushing strength of the stalk, in kg.

ance are, as may be seen from table 10: the crushing strength, the dry weight of a 5-cm stalk section, the number of leaves, the hundred-seed weight, the number of leaves above the main ear, the straw weight and the plant height, in that order. The characters remaining in the selection index for rootlodging resistance are (table 11): the ear height, the root weight, the weight of straw, the length of leaf eight, the pulling strength, the leaf angle and the plant height, in that order.

Selection indices for the simultaneous improvement of yield and resistance to stem- and rootlodging may be calculated according to formula (12), page 4:

$$\sum_{i=1}^{n} \hat{b}_i\, P_{i,j} = \sum_{i=1}^{n} \hat{a}_i\, G_{i,j} \quad (j = 1, 2, \ldots, n) \tag{37}$$

where:

$\hat{a}_i$ = estimated relative economic value of the ith trait, and
$G_{i,j}$ = estimate for the genetic covariance between the traits i and j.

TABLE 11. Selection indices for the improvement of resistance to rootlodging

Selection index	Estimated expected response to index selection	Selection index	Estimated expected response to index selection
$I = -0.0273\,\hat{\chi}_3 +$ $+ 0.0810\,\hat{\chi}_8 +$ $- 0.000731\,\hat{\chi}_9 +$ $- 0.00227\,\hat{\chi}_{10} +$ $+ 0.00287\,\hat{\chi}_{22} +$ $- 0.000708\,\hat{\chi}_{23} +$ $+ 0.00234\,\hat{\chi}_{24}$	$k \times 20.0$	$I = -0.0314\,\hat{\chi}_3 +$ $- 0.00317\,\hat{\chi}_{10} +$ $- 0.000562\,\hat{\chi}_{23} +$ $+ 0.00266\,\hat{\chi}_{24}$	$k \times 19.0$
$I = -0.0288\,\hat{\chi}_3 +$ $+ 0.0814\,\hat{\chi}_8 +$ $- 0.00283\,\hat{\chi}_{10} +$ $+ 0.00279\,\hat{\chi}_{22} +$ $- 0.000717\,\hat{\chi}_{23} +$ $+ 0.00232\,\hat{\chi}_{24}$	$k \times 19.9$	$I = -0.00375\,\hat{\chi}_{10} +$ $- 0.000592\,\hat{\chi}_{23} +$ $+ 0.00258\,\hat{\chi}_{24}$	$k \times 18.4$
		$I = -0.00504\,\hat{\chi}_{10} +$ $+ 0.00146\,\hat{\chi}_{24}$	$k \times 15.1$
$I = -0.0310\,\hat{\chi}_3 +$ $- 0.00285\,\hat{\chi}_{10} +$ $+ 0.00283\,\hat{\chi}_{22} +$ $- 0.000723\,\hat{\chi}_{23} +$ $+ 0.00238\,\hat{\chi}_{24}$	$k \times 19.6$	$I = -0.00411\,\hat{\chi}_{10}$	$k \times 10.2$

The estimate for the expected response to index selection is expressed as a percentage decrease in the mean amount of rootlodging. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_3$ = length of leaf eight, in cm; $\hat{\chi}_8$ = leaf angle; $\hat{\chi}_9$ = plant height, in cm; $\hat{\chi}_{10}$ = ear height, in cm; $\hat{\chi}_{22}$ = pulling strength, in kg; $\hat{\chi}_{23}$ = weight of straw, in g; $\hat{\chi}_{24}$ = root weight, in g.

For all the characters except yield and resistance to stem- and rootlodging, the relative economic value a is set to zero. The value of resistance to lodging relative to yield depends on whether the crop is harvested mechanically or by hand, and on the desired quality of the grain. Resistance to stem- and rootlodging were regarded as of equal economic importance. The value of resistance to lodging relative to the value of yield was estimated by assuming that the grain harvested from lodged plants had only half the value from the grain harvested from erect plants, because of the increased labour involved in harvesting and also because of a deterioration in grain quality. In the current experiment the stem- and rootlodging percentages were both twenty-one. When the value of a crop in the absence of lodging is taken as 100, the value of a crop with twenty-one percent stemlodging is $100 - 21/2 = 89.5$. An increase in the resistance to stemlodging, resulting in a one percent decrease of the stemlodging percentage, brings the value of the crop to $100 - 20/2 = 90$, an increase in value of $(90 - 89.5)/89.5) \times 100$ percent $= 0.559$ percent. In the experiment the mean yield per plant was 120 g. An increase of 0.559 percent, is thus equivalent to an increase of the mean yield per plant of $(0.559/100) \times 120$ g $= 0.67$ g. The economic value of resistance to stemlodging, measured in percent-

age is therefore 0,67 relative to the economic value of yield measured in g.

The relative economic values estimated in this way depend both on the mean yield per plant and on the lodging percentages. The figures given for the mean yield and the lodging percentages may be taken as representative for a good maize crop at Mokwa. As can be seen from the above numerical example a rise in yield should result in an increase in the relative economic value of lodging resistance, while a decrease in lodging should result in a slight decrease in the relative economic value of lodging resistance.

The selection indices for the simultaneous improvement of yield and resistance to stem- and rootlodging were calculated using the relative economic values given above. The expected response to index selection could be calculated using the formulae (14), (15) and (16), page 4 and 5.

$$\hat{R}_{\text{total}} = p \cdot k \cdot \sqrt{\sum_{i=1}^{n} \hat{b}_i \hat{A}} \tag{38}$$

$$\hat{A} = \sum_{j=1}^{n} \hat{a}_j G_{i,j} \tag{39}$$

$$\hat{R}_i = \frac{p \cdot k \cdot \sqrt{\sum_{j=1}^{n} \hat{b}_j G_{i,j}}}{\hat{R}_{\text{total}}} \tag{40}$$

where:

$\hat{R}_{\text{total}}$ = estimate for the expected total response to index selection, and

$\hat{R}_i$ = estimate for the expected response to index selection for the ith trait.

In order to limit the number of characters included in the selection index the estimation procedure given above was followed. Starting with a selection index based on twenty-seven characters, the character which gave the lowest value for the product $\hat{b}_i \hat{A}$ was eliminated, after which the selection index was calculated anew for the remaining characters. The procedure was repeated till there remained only one character.

The selection indices for the simultaneous improvement of yield and resistance to stem- and rootlodging are presented in table 12, with indices based on up to seven characters. The expected response to selection was calculated for selection after flowering, so that the amount of parental control p is 0.5. The estimates for the expected total response to index selection $\hat{R}_{\text{total}}$ and for the expected response to yield are expressed as a percentage of the mean yield. The estimates for the expected improvement in resistance to stemlodging and in resistance to rootlodging are expressed as percentage decrease in the amount of stem- or rootlodging.

Table 12 shows that when the characters are eliminated from the index one by one, the characters remaining in the index are: the root weight, the crushing

TABLE 12. Selection indices for the simultaneous improvement of yield and of resistance to stem- and rootlodging. The relative economic weights of yield and of resistance to stem- and rootlodging are given in the text.

Selection index	Estimated expected response to index selection			
	total response	yield	resistance to stemlodging	resistance to rootlodging
$\hat{I} = + 4.98\,\hat{\chi}_4 +$ $+ 20.65\,\hat{\chi}_8 +$ $- 2.43\,\hat{\chi}_{16} +$ $+ 0.824\,\hat{\chi}_{20} +$ $- 0.388\,\hat{\chi}_{21} +$ $+ 0.0992\,\hat{\chi}_{24} +$ $+ 0.0406\,\hat{\chi}_{27}$	$k \times 8.3$	$k \times 5.0$	$k \times 20.1$	$k \times 15.1$
$\hat{I} = + 4.76\,\hat{\chi}_4 +$ $+ 20.13\,\hat{\chi}_8 +$ $- 3.29\,\hat{\chi}_{16} +$ $+ 0.402\,\hat{\chi}_{20} +$ $+ 0.107\,\hat{\chi}_{24} +$ $+ 0.0474\,\hat{\chi}_{27}$	$k \times 8.0$	$k \times 4.7$	$k \times 20.1$	$k \times 15.3$
$\hat{I} = + 4.96\,\hat{\chi}_4 +$ $+ 19.73\,\hat{\chi}_8 +$ $- 3.50\,\hat{\chi}_{16} +$ $+ 0.116\,\hat{\chi}_{24} +$ $+ 0.0510\,\hat{\chi}_{27}$	$k \times 7.9$	$k \times 4.6$	$k \times 19.7$	$k \times 16.6$
$\hat{I} = + 4.11\,\hat{\chi}_4 +$ $+ 18.31\,\hat{\chi}_8 +$ $+ 0.123\,\hat{\chi}_{24} +$ $+ 0.0548\,\hat{\chi}_{27}$	$k \times 7.4$	$k \times 4.1$	$k \times 19.2$	$k \times 15.5$
$\hat{I} = + 18.41\,\hat{\chi}_8 +$ $+ 0.145\,\hat{\chi}_{24} +$ $+ 0.0590\,\hat{\chi}_{27}$	$k \times 7.1$	$k \times 3.8$	$k \times 20.5$	$k \times 16.5$
$\hat{I} = + 0.156\,\hat{\chi}_{24} +$ $+ 0.0586\,\hat{\chi}_{27}$	$k \times 6.6$	$k \times 3.4$	$k \times 19.7$	$k \times 14.0$
$\hat{I} = + 0.207\,\hat{\chi}_{24}$	$k \times 5.6$	$k \times 3.1$	$k \times 12.6$	$k \times 17.5$

When the crushing strenght $\hat{\chi}_{27}$ is replaced by the dry weight of a 5-cm stalk section $\hat{\chi}_{26}$, the selection index based upon three characters becomes as follows:

$\hat{I} = + 18.54\,\hat{\chi}_8 +$ $+ 0.122\,\hat{\chi}_{24} +$ $+ 128.0\,\hat{\chi}_{26}$	$k \times 6.8$	$k \times 3.7$	$k \times 19.0$	$k \times 14.3$

The estimates for the total response to selection and for the response in yield are expressed as a percentage of the mean yield, the estimates for the response in resistance to stemlodging and rootlodging are expressed as a percentage decrease in the mean amount of stem- or rootlodging. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_4$ = width of leaf eight, in cm; $\hat{\chi}_8$ = leaf angle; $\hat{\chi}_{16}$ = number of seed rows on the main ear; $\hat{\chi}_{20}$ = hundred-seed weight, in g; $\hat{\chi}_{21}$ = threshing percentage; $\hat{\chi}_{24}$ = root weight, in g; $\hat{\chi}_{26}$ = dry weight of a 5-cm stalk section, in g; $\hat{\chi}_{27}$ = crushing strength of the stalk, in kg.

strength, the leaf angle, the width of leaf eight, the number of seed rows on the main ear, the hundred-seed weight and the threshing percentage, in that order.

Selection indices for the simultaneous improvement of yield and resistance to stem- and rootlodging were also determined with relative economic values for stem- and rootlodging taken as twice their earlier given values. These selection indices are presented in table 13.

Doubling the relative economic values for stem- and rootlodging resistance would automatically imply that a lodged plant does not contribute anything to the value of the crop. This is not likely to lead to erroneous results for it can be argued that, while a lodged plant still contributes to the yield, it causes a rise in the cost of harvesting of the whole crop. Furthermore, the lodging percentage of a crop is not a fixed percentage, but depends on the time of harvest. The longer harvesting is delayed, the higher the lodging percentages become. At Mokwa, with its serious lodging problem, the crop is harvested as soon as the ears have reached their full weights, and the lodging percentages given represent a minimum.

Table 13 shows that when eliminating the characters one by one, the characters remaining in the index are: the root weight, the crushing strength, the leaf angle, the number of seed rows on the main ear, the width of leaf eight, the number of leaves above the main ear, and the dry weight of a 5-cm stalk section, in that order.

Four of the twenty-seven characters were observed before flowering, these are the characters: days to shooting, total number of leaves, and length and width of leaf eight. Selection on any of these four characters may be carried out before flowering. In selection before flowering it is possible to select on both the male and the female parent, so that full parental control is maintained, $p = 1.0$. Selection indices for yield based on these four characters are given in table 14. The expected response to selection, expressed as a percentage of the mean yield, is given as the response to selection before flowering.

No experimental data are available to test the selection indices given in the tables nine to fourteen. However the data from the thirty-six parent plants can be used to test selection indices calculated from the sib analysis, provided the selection indices contain only characters which have been recorded also from the parent plants. From the seventeen characters recorded from the parent plants fifteen were recorded also from the offspring. The two characters which were not recorded from the offspring generation were the 'number of green leaves at the time of silking' and the 'product of length and width of the leaf growing from the node out of which the main ear developed'. A misleading estimate was obtained for one character, the 'number of ears with silks' as will be explained further in the discussion, so that there finally remained fourteen characters which had been recorded both from the parent generation as well as from the offspring. The fourteen characters were: total number of leaves, days to silking, number of leaves above the main ear, plant and ear height, number of nodes with brace roots, number of seed-producing ears, length of the earshank, length, circumference and number of seed rows of the main ear, total seed

TABLE 13. Modified selection indices for the simultaneous improvement of yield and of resistance to stem- and rootlodging. This table differs from table 12 in that now the relative economic weights for stem- and rootlodging resistance are doubled (see text).

Selection index	Estimated expected response to index selection			
	total response	yield	resistance to stemlodging	resistance to rootlodging
$I = + 4.29\ \hat{\chi}_4 +$ $+ 4.98\ \hat{\chi}_7 +$ $+ 30.32\ \hat{\chi}_8 +$ $- 4.57\ \hat{\chi}_{16} +$ $+ 0.153\ \hat{\chi}_{24} +$ $+ 28.41\ \hat{\chi}_{26} +$ $+ 0.0740\ \hat{\chi}_{27}$	$k \times 11.4$	$k \times 4.5$	$k \times 20.9$	$k \times 16.8$
$I = + 4.41\ \hat{\chi}_4 +$ $+ 5.15\ \hat{\chi}_7 +$ $+ 30.32\ \hat{\chi}_8 +$ $- 4.60\ \hat{\chi}_{16} +$ $+ 0.163\ \hat{\chi}_{24} +$ $+ 0.0797\ \hat{\chi}_{27}$	$k \times 11.4$	$k \times 4.5$	$k \times 20.7$	$k \times 17.3$
$I = + 4.43\ \hat{\chi}_4 +$ $+ 29.05\ \hat{\chi}_8 +$ $- 4.63\ \hat{\chi}_{16} +$ $+ 0.178\ \hat{\chi}_{24} +$ $+ 0.0824\ \hat{\chi}_{27}$	$k \times 11.3$	$k \times 4.5$	$k \times 20.6$	$k \times 16.9$
$I = + 29.02\ \hat{\chi}_8 +$ $- 4.30\ \hat{\chi}_{16} +$ $+ 0.201\ \hat{\chi}_{24} +$ $+ 0.0872\ \hat{\chi}_{27}$	$k \times 11.1$	$k \times 4.1$	$k \times 21.5$	$k \times 17.3$
$I = + 27.26\ \hat{\chi}_8 +$ $+ 0.249\ \hat{\chi}_{24} +$ $+ 0.0910\ \hat{\chi}_{27}$	$k \times 10.5$	$k \times 3.7$	$k \times 20.7$	$k \times 16.3$
$I = + 0.222\ \hat{\chi}_{24} +$ $+ 0.0902\ \hat{\chi}_{27}$	$k \times 9.8$	$k \times 3.5$	$k \times 19.9$	$k \times 13.7$
$I = + 0.299\ \hat{\chi}_{24}$	$k \times 8.2$	$k \times 3.1$	$k \times 12.6$	$k \times 17.5$

When the crushing strength $\hat{\chi}_{27}$ is replaced by the dry weight of a 5-cm stalk section $\hat{\chi}_{26}$, the selection index based upon three characters becomes as follows:

$I = + 27.42\ \hat{\chi}_8 +$ $+ 0.175\ \hat{\chi}_{24} +$ $+ 187.0\ \hat{\chi}_{26}$	$k \times 9.9$	$k \times 3.7$	$k \times 19.0$	$k \times 14.3$

The estimates for the total response to selection and for the response in yield are expressed as a percentage of the mean yield, the estimates for the response in resistance to stemlodging and rootlodging are expressed as a percentage decrease in the mean amount of stem- or rootlodging. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_4$ = width of leaf eight, in cm; $\hat{\chi}_7$ = number of leaves above the main ear; $\hat{\chi}_8$ = leaf angle; $\hat{\chi}_{16}$ = number of seed rows on the main ear; $\hat{\chi}_{24}$ = root weight, in g; $\hat{\chi}_{26}$ = dry weight of a 5-cm stalk section, in g; $\hat{\chi}_{27}$ = crushing strength of the stalk, in kg.

TABLE 14. Selection indices for the improvement of yield, with selection before flowering.

Selection index	Estimated expected response to index selection	Selection index	Estimated expected response to index selection
$I = + 1.53\ \hat{\chi}_1 +$ $\underline{- 0.398\ \hat{\chi}_2} +$ $+ 0.416\ \hat{\chi}_3 +$ $+ 6.14\ \hat{\chi}_4$	$k \times 9.2$	$I = \underline{+ 0.456\ \hat{\chi}_3} +$ $+ 6.02\ \hat{\chi}_4$	$k \times 8.0$
$I = + 1.48\ \hat{\chi}_1 +$ $\underline{+ 0.419\ \hat{\chi}_3} +$ $+ 6.04\ \hat{\chi}_4$	$k \times 9.2$	$I = + 6.83\ \hat{\chi}_4$	$k \times 6.7$

The estimate for the expected response to index selection is expressed as a percentage of the mean yield. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_1$ = days to shooting; $\hat{\chi}_2$ = total number of leaves; $\hat{\chi}_3$ = length of leaf eight, in cm; $\hat{\chi}_4$ = width of leaf eight, in cm.

weight, hundred-seed weight, and square diameter of the stalk. Selection indices for yield were calculated starting with these fourteen characters. The characters were eliminated from the selection index one by one, according to the elimination procedure given above. Selection indices based on up to seven characters are presented in table 15. In the table the expected and realized responses to index selection are expressed as percentages of the mean yield, while the realized responses are also given as percentages from the realized response to truncation selection for yield.

Selection indices for yield were also determined using out of the fourteen characters only the seven ear characters. These indices are given in table 16. As may be seen from table 15 and 16 the expected and realized responses were in good agreement with each other, while the realized responses to index selection were in almost all cases superior to the realized response to truncation selection for yield.

Up till now we have limited ourselves to selection indices based upon the total phenotypic variances and covariances. The selection indices are appropriate when the field used for selection is taken as a whole. The efficiency of individual selection may be increased by dividing the field in plots, and selecting within plots. As the within plot phenotypic variance should be lower than the total phenotypic variance, the subdivision in plots should result in a larger single-plant heritability (GARDNER, 1961).

Selection indices for selection within plots may be calculated by entering the within plot phenotypic variances and covariances in the formulae for the selection index. Selection indices for yield for selection within plots were calculated as presented in table 17, using the same set of seven ear characters as were used in constructing the selection indices presented in table 16. When comparing table 16 and 17, we may note that the expected response to index selection

TABLE 15. Expected and realized response to index selection

Selection index	Estimated expected response	Realized response	
		I	II
$I = + 0.654\ \hat{\chi}_5 +$			
$+ 4.37\ \hat{\chi}_7 +$			
$+ 0.282\ \hat{\chi}_{10} +$			
$+ 1.64\ \hat{\chi}_{15} +$			
$- 2.87\ \hat{\chi}_{16} +$			
$+ 0.414\ \hat{\chi}_{20} +$			
$+ 3.34\ \hat{\chi}_{25}$	$k \times 4.9$	$k \times 4.8$	138
$I = + 5.03\ \hat{\chi}_7 +$			
$+ 0.302\ \hat{\chi}_{10} +$			
$+ 1.44\ \hat{\chi}_{15} +$			
$- 2.94\ \hat{\chi}_{16} +$			
$+ 0.342\ \hat{\chi}_{20} +$			
$+ 3.14\ \hat{\chi}_{25}$	$k \times 4.8$	$k \times 4.5$	131
$I = + 4.91\ \hat{\chi}_7 +$			
$+ 0.320\ \hat{\chi}_{10} +$			
$- 2.23\ \hat{\chi}_{16} +$			
$+ 0.546\ \hat{\chi}_{20} +$			
$+ 3.30\ \hat{\chi}_{25}$	$k \times 4.8$	$k \times 4.4$	128
$I = + 0.284\ \hat{\chi}_{10} +$			
$- 2.33\ \hat{\chi}_{16} +$			
$+ 0.528\ \hat{\chi}_{20} +$			
$+ 4.00\ \hat{\chi}_{25}$	$k \times 4.5$	$k \times 4.4$	128
$I = + 0.264\ \hat{\chi}_{10} +$			
$+ 0.642\ \hat{\chi}_{20} +$			
$+ 3.57\ \hat{\chi}_{25}$	$k \times 4.0$	$k \times 5.2$	151
$I = + 0.310\ \hat{\chi}_{10} +$			
$+ 0.724\ \hat{\chi}_{20}$	$k \times 3.7$	$k \times 4.7$	136
$I = + 0.338\ \hat{\chi}_{10}$	$k \times 3.0$	$k \times 1.6$	46

The estimate for the expected response to index selection is expressed as a percentage of the mean yield. The realized response is given: I, as a percentage of the mean yield and II, as a percentage of the response to truncation selection for yield. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_5$ = days to silking; $\hat{\chi}_7$ = number of leaves above the main ear; $\hat{\chi}_{10}$ = ear height, in cm; $\hat{\chi}_{15}$ = circumference of the main ear, in cm; $\hat{\chi}_{16}$ = number of seed rows on the main ear; $\hat{\chi}_{20}$ = hundred-seed weight, in g; $\hat{\chi}_{25}$ = square diameter of the stalk, in cm².

TABLE 16. Expected and realized response to index selection, for selection indices based on ear characters only

Selection index	Estimated expected response	Realized response	
		I	II
$I = + 8.06\ \hat{\chi}_{12} +$ $+ 0.534\ \hat{\chi}_{13} +$ $+ 0.581\ \hat{\chi}_{14} +$ $+ 2.81\ \hat{\chi}_{15} +$ $- 2.90\ \hat{\chi}_{16} +$ $- 0.0568\ \hat{\chi}_{19} +$ $+ 0.361\ \hat{\chi}_{20}$	$k \times 3.5$	$k \times 3.4$	99
$I = + 5.54\ \hat{\chi}_{12} +$ $+ 0.474\ \hat{\chi}_{13} +$ $+ 0.311\ \hat{\chi}_{14} +$ $+ 2.22\ \hat{\chi}_{15} +$ $- 3.04\ \hat{\chi}_{16} +$ $+ 0.267\ \hat{\chi}_{20}$	$k \times 3.5$	$k \times 3.8$	110
$I = + 5.63\ \hat{\chi}_{12} +$ $+ 0.539\ \hat{\chi}_{13} +$ $+ 2.44\ \hat{\chi}_{15} +$ $- 3.08\ \hat{\chi}_{16} +$ $+ 0.290\ \hat{\chi}_{20}$	$k \times 3.4$	$k \times 4.0$	115
$I = + 0.598\ \hat{\chi}_{13} +$ $+ 2.57\ \hat{\chi}_{15} +$ $- 3.09\ \hat{\chi}_{16} +$ $+ 0.279\ \hat{\chi}_{20}$	$k \times 3.3$	$k \times 4.4$	127
$I = + 2.64\ \hat{\chi}_{15} +$ $- 3.04\ \hat{\chi}_{16} +$ $+ 0.355\ \hat{\chi}_{20}$	$k \times 3.2$	$k \times 4.8$	138
$I = + 3.57\ \hat{\chi}_{15} +$ $- 3.64\ \hat{\chi}_{16}$	$k \times 3.1$	$k \times 4.3$	126
$I = - 2.12\ \hat{\chi}_{16}$	$k \times 1.7$	$k \times 1.2$	35

The estimate for the expected response to index selection is expressed as a percentage of the mean yield. The realized response is given: I, as a percentage of the mean yield and II, as a percentage of the response to truncation selection for yield. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_{12}$ = number of seed-producing ears; $\hat{\chi}_{13}$ = length of the shank of the main ear, in cm; $\hat{\chi}_{14}$ = length of the main ear, in cm; $\hat{\chi}_{15}$ = circumference of the main ear, in cm; $\hat{\chi}_{16}$ = number of seed rows on the main ear; $\hat{\chi}_{19}$ = total seed weight (yield), in g; $\hat{\chi}_{20}$ = hundred-seed weight, in g.

TABLE 17. Selection indices for the selection within plots.

Selection index	Estimated expected response to index selection	Selection index	Estimated expected response to index selection
$\hat{I} = + 7.69\ \hat{\chi}_{12} +$ $+ 0.720\ \hat{\chi}_{13} +$ $+ 0.556\ \hat{\chi}_{14} +$ $+ 3.35\ \hat{\chi}_{15} +$ $- 3.20\ \hat{\chi}_{16} +$ $\underline{- 0.0673\ \hat{\chi}_{19} +}$ $+ 0.294\ \hat{\chi}_{20}$	$k \times 3.6$	$\hat{I} = \underline{+ 0.735\ \hat{\chi}_{13} +}$ $+ 2.83\ \hat{\chi}_{15} +$ $- 3.31\ \hat{\chi}_{16} +$ $+ 0.243\ \hat{\chi}_{20}$	$k \times 3.4$
		$\hat{I} = + 2.89\ \hat{\chi}_{15} +$ $- 3.28\ \hat{\chi}_{16} +$ $+ 0.333\ \hat{\chi}_{20}$	$k \times 3.3$
$\hat{I} = + 4.37\ \hat{\chi}_{12} +$ $+ 0.648\ \hat{\chi}_{13} +$ $\underline{+ 0.240\ \hat{\chi}_{14} +}$ $+ 2.55\ \hat{\chi}_{15} +$ $- 3.28\ \hat{\chi}_{16} +$ $+ 0.211\ \hat{\chi}_{20}$	$k \times 3.5$	$\hat{I} = \underline{+ 3.75\ \hat{\chi}_{15} +}$ $- 3.87\ \hat{\chi}_{16}$	$k \times 3.2$
		$\hat{I} = - 2.18\ \hat{\chi}_{16}$	$k \times 1.8$
$\hat{I} = \underline{+ 4.41\ \hat{\chi}_{12} +}$ $+ 0.689\ \hat{\chi}_{13} +$ $+ 2.71\ \hat{\chi}_{15} +$ $- 3.32\ \hat{\chi}_{16} +$ $+ 0.235\ \hat{\chi}_{20}$	$k \times 3.5$		

The estimate for the expected response to index selection is expressed as a percentage of the mean yield. Each subsequent selection index is obtained from the preceding one by eliminating the underlined character. k = selection intensity; $\hat{\chi}_{12}$ = number of seed-producing ears; $\hat{\chi}_{13}$ = length of the shank of the main ear, in cm; $\hat{\chi}_{14}$ = length of the main ear, in cm; $\hat{\chi}_{15}$ = circumference of the main ear, in cm; $\hat{\chi}_{16}$ = number of seed rows on the main ear; $\hat{\chi}_{19}$ = total seed weight (yield), in g; $\hat{\chi}_{20}$ = hundred-seed weight, in g.

shows hardly any increase when selecting within plots. This is the more striking as very small plots were used, comprising only sixteen plants.

The weighing factors of a selection index may be multiplied by a constant for ease of calculation. As an example we use the selection index given at the bottom of table 13.

$$\hat{I} = 27.4 \times \hat{X}_8 + 0.175 \times \hat{X}_{24} + 187 \times \hat{X}_{26} \qquad (41)$$

where:

$\hat{X}_8$ = leaf angle

$\hat{X}_{24}$ = root weight in g

$\hat{X}_{26}$ = dry weight of a 5-cm stalk section in g.

When multiplying the weighing factors with 5.72 the selection index becomes:

$$\hat{I} = \hat{X}_{24} + 1070 \times \hat{X}_{26} + 157 \times \hat{X}_8 \qquad (42)$$

When the root weight is recorded in kg instead of in g the selection index may be simplified to:

$$I'' = \hat{X}_{24} + \hat{X}_{26} + 0.15 \times \hat{X}_8 \tag{43}$$

5.4. DISCUSSION

5.4.1. *Discussion of some general aspects*

To estimate the genetic variance from an open-pollinated variety, the variety should be in linkage equilibrium (see also par. 2.2.3.2., page 9). The population under study, Colombian Composite, is from fairly recent origin. The half-sib progenies used in the experiment were taken from the population after five cycles of open pollination. Although most of the linkage blocks should have been broken up, there might have been still some linkage disequilibrium.

Apart from some selection for yield, the one hundred and forty-four progenies used in the experiment could be considered to be half-sib progenies of random individuals of a non-inbred population. The thirty-six progenies which remained after natural selection for resistance to *Helminthosporium maydis*, race T, did not represent a random sample from the population. However it is assumed that the thirty-six progenies can in all other aspects be regarded as a random sample of the population.

The progeny trials were conducted at four different environments, which consisted of two locations with each two dates of planting. At Mokwa, as in many tropical areas, one of the main factors determining the environment is the distribution of the rainfall. A variation in rainfall distribution is obtained by choosing two dates of planting at one location, a simple procedure to create different environments (EBERHART, 1967). The method has its limitations because the two environments so created do not represent a random sample of all possible environments within an area. A limitation in staff and funds led to the choice of two locations not very far apart. Although the object of the maize breeding work was to breed for a larger area, the environments used may only be taken as representative for the immediate surroundings of Mokwa.

As stated before the characters yield and resistance to stem- and rootlodging, which have to be improved by index selection, were measured with greater precision than the other characters. These characters possess a relatively low heritability, reason also why index selection was proposed. The right-hand side of the equations given by expression (37) contain the genetic covariances with yield and resistance to stem- and rootlodging. Single-plant measurements of these characters with a relatively low heritability would give inaccurate estimates for the genetic covariances, therefore we used the single-plant mean values of yield and of resistance to stem- and rootlodging instead to estimate the genetic covariances with these characters.

In index selection the selection is based on characters with a relatively high heritability which are either identical to or genetically correlated with the

characters to be improved by selection. Because the characters should have a high heritability, single-plant measurements of these characters should give sufficiently precise estimates for the phenotypic and genetic variances and co-variances of these characters. Any character with a low heritability is of no interest to index selection, and by eliminating the characters one by one only characters possessing a relatively high heritability will be retained in the selection index.

The population used in this study, Colombian Composite, contained a number of male sterile plants. As noted in paragraph 4.2., page 21, cytoplasmic male sterility was brought into the composite by using an advanced generation cornbelt hybrid as one of the entries in the composite. The incidence of male sterile plants made it impossible to use the days to tasseling, that is the number of days from planting till anthesis, as one of the characters in this study.

5.4.2. *Discussion of some single-plant characters*
Table 8 gives for thirty different characters estimates for the single-plant heritability and for the phenotypic and genetic correlations with the three characters of economic importance: yield, resistance to stemlodging, and resistance to rootlodging. High single-plant heritabilities were obtained for characters related to maturity, these are the days to shooting, the days to silking and the total number of leaves. Low heritabilities were obtained for the characters of economic importance, the characters yield, resistance to stem-lodging, and resistance to rootlodging. Low heritabilities were also obtained for components of yield such as length, circumference, and seed weight of the main ear, seed weight of the second ear, and number of seed-producing ears.

Length and width of leaf eight. FRANCIS and coworkers took the product of length and width of leaf number seven as an estimate for the leaf area of the plant. In their study leaf seven was on average the largest leaf of the plant (FRANCIS et al., 1969). In this study the measurements of leaf eight were used, where leaf eight was on average the largest leaf of the plant. The length and width of leaf eight could be determined before flowering. Both leaf measurements were genetically correlated with yield.

Leaf angle. The importance of light as a factor in crop production was stressed by DONALD. The lower leaves of the plant may be deficient in light even at high light intensities. The amount of light received by the lower leaves of the plant depends on the arrangement of the leaves. The plant makes an optimal use of the amount of light available when the upper leaves of the plant are arranged in a vertical or almost vertical position, so that a relatively large amount of light reaches the lower leaves of the plant (DONALD, 1963).

PENDLETON and coworkers (1967) obtained a significant increase in yield of maize when they used large reflectors to increase the amount of light reaching the lower leaves of the plant. In another experiment they used isogenic hybrids differing in only one character to study the effect of erect leaves. Hybrids with erect leaves gave a forty percent increase in yield as compared to the control (PENDLETON et al., 1968). These experiments were conducted under a high

standard of production, using high density plant populations. The experiments show that under such conditions light is an important limiting factor.

In tropical areas the light intensity is often rather low. At Mokwa the light intensity reaches a minimum during the middle of the wet season, in August, just at the time that the maize crop is forming its ears. The average amount of sunshine in August is only about three hours a day (THOMPSON, 1965).

The leaf angle was measured as $1/\sin \alpha$, when α is the angle in degrees between the stem and the third leaf of the plant. A positive genetic correlation was found between leaf angle and yield ($\hat{r} = 0.32$) despite the rather low standard of production, using a new unimproved population of maize and using a rather low density plant population of 35,880 plants per ha. This indicates that light should become a limiting factor of increasing importance when one seeks to increase the yield level of the crop. To make an optimal use of the light available the selection should be directed towards a plant type with erect leaves. The leaf angle had a rather high single-plant heritability ($\hat{h}^2 = 0.57$), so that the leaf angle might be successfully altered by individual selection. The leaf angle was genetically correlated with resistance to stemlodging ($\hat{r} = 0.27$) and with resistance to rootlodging ($\hat{r} = 0.36$).

Earshank. Towards harvesting, the ear will often hang down from the plant with the tip of the ear downwards. This position favours the drying of the ear, because rainwater will not penetrate inside the ear, instead it will easily drop from the husks. The longer the shank of the ear, the earlier the ear will tend to hang down, while ears with a short shank will stay in an erect position until harvest. A long earshank therefore is a desirable character. Individual selection for long earshanks should be successful because the character had a rather high single-plant heritability. It is thereby satisfactory to notice that the length of the earshank was positively correlated with yield and with resistance to stem- and rootlodging.

Number of ears with silks. A negative estimate was obtained for the genetic covariance between yield and the number of ears with silks. Most plants had either one or two ears with silks, so that rather surprisingly the results indicate that the selection for improved yields should be for single eared plants. These results however do not agree with the findings of chapter four, nor with the results for other characters. Positive estimates were obtained for the genetic covariances between yield and the number of seed-producing ears and between yield and the character seed weight of the second ear. Therefore, with probably a deceptive estimate for the covariance between yield and the character number of ears with silks, it was thought better not to include this character in the selection indices.

Number of seed-producing ears. A low single-plant heritability was obtained for the character number of seed-producing ears, which implies that individual selection for multiple-eared plants should result in a very low correlated response in yield. This is not in agreement with the results reported by LONNQUIST (1967) and TORREGROZA and HARPSTEAD (1967), where both obtained a good response in yield when selecting for a multiple-eared plant type.

The estimate for the heritability of the number of seed-producing ears is not very reliable, because there were only few data available for this character. The plants could be divided in only two categories, single- and double-eared plants, while only about ten percent of the plants produced two ears. Still, the number of seed-producing ears is probably not an important trait in the population under study. The majority of plants had two ears with silks, but seed set was obtained usually on only one ear. Although the plants had the genetic potential to develop two ears, phenotypically most plants were unable to develop more than one ear. LONNQUIST (1967) used in his experiment the variety Hays Golden, which had a very low percentage of multiple-eared plants. In the past, selection within this variety had been for a single-eared plant type.

Yield and resistance to lodging. The single-plant heritability for yield was estimated as 0.09. Using this figure the response to individual selection for yield is estimated as $k \times 2.1$ percent, where the response is expressed as a percentage of the mean yield and k is the selection intensity. The estimated response to selection may be compared with the response obtained from selection for yield among the thirty-six plants of the parent generation, which was $k \times 3.5$ percent.

The single-plant heritabilities for resistance to stemlodging and resistance to rootlodging were estimated respectively as 0.15 and 0.12. Using these figures the response to individual selection for stemlodging resistance is estimated as $k \times 13.8$ percent, and likewise for resistance to rootlodging $k \times 7.2$ percent, where the responses are expressed as percentage decrease in the amount of lodging. The response to selection depends on the selection intensity. When selecting directly for stem- or rootlodging resistance the selection intensity depends again on the percentage of non-lodged plants, which means that the selection intensity and thus the response to selection should be low.

Lodging normally has an adverse effect on yield because part of the yield is lost as a result of lodging. In the experiment care was taken to reduce the loss in yield resulting from lodging. Lodged plants were lifted off the ground so as to save the ears from decay. Still, stemlodging had an adverse effect on yield because the plants were sometimes broken before reaching maturity, and where this happened only small underdeveloped ears were harvested. This resulted in a positive phenotypic correlation between yield and resistance to stemlodging ($\hat{r} = 0.17$) and it probably also caused an upward bias in the genetic correlation between yield and resistance to stemlodging ($\hat{r} = 0.04$).

It was difficult to make a clear distinction between stemlodging and rootlodging. It often happened that the plants were leaning, showing the first symptoms of rootlodging, before they broke off as a result of the increased force working on the stem of the plant. Whether a plant was classified as rootlodging or stemlodging often depended on the stage the observation was made in. It is therefore not surprising that there was a fairly high genetic correlation between resistance to stem- and rootlodging ($\hat{r} = 0.61$). In the foregoing it was assumed on theoretical grounds that this correlation would be negative, but the underlying assumption was that it was possible to make a clear distinction

between both types of lodging (see par. 3.3., page 19).

A further point is that broken plants were recorded as stemlodging, and therefore could not at the same time be recorded as rootlodging. This means that a broken plant was classified as susceptible to stemlodging and as resistant to rootlodging, which explains the negative phenotypic correlation between resistance to stemlodging and rootlodging ($\hat{r} = -0.35$).

Characters correlated with resistance to stemlodging. Resistance to stemlodging was highly correlated with the dry weight of a 5-cm stalk section ($\hat{r} = 0.97$) and with the crushing strength of the stalk ($\hat{r} = 0.92$). Low correlations were found between resistance to stemlodging and the stalk characters: rind thickness ($\hat{r} = 0.35$) and square diameter ($\hat{r} = 0.08$). These results agree with the reports from literature, with an exception only for the results obtained for the rind thickness. ZUBER and GROGAN (1961) and THOMPSON (1963) reported that resistance to stemlodging was highly correlated with crushing strength as well as with rind thickness. THOMPSON (1970) reported a high correlation between resistance to stemlodging and the dry weight of a 5-cm stalk section. No correlation was found between the diameter of the stalk and resistance to stemlodging (ZUBER and GROGAN, 1961).

The single-plant heritabilities of the crushing strength ($\hat{h}^2 = 0.39$) and of the dry weight of a 5-cm stalk section ($\hat{h}^2 = 0.34$) should be large enough to make individual selection for these characters successful. Both the crushing strength and the dry weight of a 5-cm stalk section may be used to select indirectly for resistance to stemlodging. A choice between these characters would, for reason of convenience, lead to the dry weight of a 5-cm stalk section, because the determination of the crushing strength is rather laborious.

While there was no genetic correlation between yield and resistance to stemlodging ($\hat{r} = 0.04$), positive genetic correlations were found between yield and crushing strength ($\hat{r} = 0.60$), respectively dry weight of a 5-cm stalk section ($\hat{r} = 0.74$). These results agree with the findings of SINGH (1970). In par. 3.3., page 18, it was suggested that there might be a competition for development between the stalk and the ears. As shown by the positive correlation between the stalk characters and yield such a competition apparently does not exist in the unimproved population used in this study. The correlations with yield show that crushing strength and dry weight of a 5-cm stalk section are by no means identical to the character resistance to stemlodging, despite the high correlation between the stalk characters and resistance to stemlodging.

Characters correlated with resistance to rootlodging. Resistance to rootlodging was correlated with the root weight ($\hat{r} = 0.74$) and with the pulling strength ($\hat{r} = 0.63$). The single-plant heritability of the pulling strength ($\hat{h}^2 = 0.12$) was low in comparison to the heritability of the root weight ($\hat{h}^2 = 0.31$), so that the root weight should be the obvious character to use when selecting for rootlodging resistance.

The low heritability of the pulling strength was due to the heterogeneous condition of the soil. Under dry conditions the pulling strength may become

very high and difficult to determine. SNELL (1966) determined the pulling strength after a soaking rain or after irrigation. In the present study the pulling strength was determined under the wet conditions prevalent at the end of the wet season, with water sometimes standing in the field. Differences in soil conditions however still resulted in a low heritability.

There was a low correlation between resistance to rootlodging and the number of nodes with brace roots ($\hat{r} = 0.05$). The capacity to develop brace roots from nodes well above the ground is apparently not correlated with resistance to rootlodging.

Several authors used the pulling strength as a measure of resistance to rootlodging, they presented however no experimental data to substantiate their choice of the pulling strength (HOLBERT and KOEHLER, 1924; WILSON, 1930; SNELL, 1966). The root volume and the dry weight of the roots were both given as indicators for resistance to rootlodging (MUSICK et al., 1965; NORDEN, 1966). CRAIG (1968) used the ratio of pulling strength and ear height as a measurement of root strength. In the present study we found that the single-plant heritability of ear height ($\hat{h}^2 = 0.43$) was large in comparison to the single-plant heritability of the pulling strength ($\hat{h}^2 = 0.12$). This indicates that individual selection for root strength as practised by CRAIG should primarily result in a reduction in ear height. As the ear height was positively correlated with yield ($\hat{r} = 0.64$), a reduction in ear height should have an adverse effect on yield.

The characters root weight and pulling strength were genetically correlated with resistance to rootlodging ($\hat{r}$ was respectively 0.74 and 0.63) and with yield ($\hat{r}$ was respectively 0.80 and 0.89). However there was no genetic correlation between yield and resistance to rootlodging ($\hat{r} = 0.07$). These correlations may be explained by noting that plants which are resistant to rootlodging do not necessarily have a strong root system. Also small tiny plants with a reduced ear height and a low weight of straw may be resistant to rootlodging. Resistance to rootlodging therefore is not necessarily correlated with yield.

The characters root weight and pulling strength were not only correlated with both resistance to rootlodging and yield but also with resistance to stemlodging ($\hat{r}$ was respectively 0.65 and 1.05). Root weight, with its relatively high heritability, should be a valuable character for selection. Root weight was determined in this study rather inaccurately, because the root weight had to be determined after measuring the pulling strength. When we are only interested in the root weight, it may be determined more carefully, which possibly leads to even better results for the root weight.

5.4.3. *Discussion of the selection indices*

The possibilities for index selection were studied using twenty-seven different characters on which the selection could be based. One of the twenty-seven characters was the character yield. The characters resistance to stem- and rootlodging, however, were not taken into account for the following reason. Any lodged plant is normally excluded from selection, so that the selection index is only used in the selection among non-lodged plants. Stem- and rootlodging

resistance, as shown by the absence of stem- and rootlodging, are therefore irrelevant characters for the selection index. It may be argued that when using a selection index it is not correct to exclude the lodged plants from selection, as this introduces some kind of independent culling levels. However it is impractical to include lodged plants in the selection because it is often difficult, if not impossible, to obtain reliable single-plant measurements from lodged plants.

An estimation procedure was used to bring the total of twenty-seven characters down to only a few characters. The estimation procedure does not guarantee finding the same characters as the exhaustive method of investigating every subset, however it was assumed that the difference between the optimal solution and the actual solution should be small (see also par. 4.4., page 24). Within a large group of traits there should be several subgroups of correlated traits. Most of the information which may be obtained from such a subgroup of traits should be realized by choosing one major trait out of such a subgroup. A selection index based on only a few traits contains out of each subgroup of correlated traits usually only one major trait (see also par. 2.1., page 6). Which trait will be chosen out of such a subgroup of traits is decided somewhat arbitrarily through the estimation procedure.

The selection indices for the improvement of yield are presented in table 9. The first three characters in the selection indices, width of leaf eight, ear height, and days to shooting are characters indicating vigour and maturity. Other similar characters like weight of straw, root weight, and plant height were eliminated from the selection index, although these characters taken separately may give a better indication of the value of a plant than the characters which come as the fourth or fifth character in the selection indices.

The selection indices for the improvement of resistance to stemlodging are presented in table 10. The first two traits in the selection indices are the crushing strength of the stalk and the dry weight of a 5-cm stalk section. The two traits are highly correlated and both traits are expressions of the stalk strength. The stalk strength is apparently a very important factor in the resistance to stemlodging, so that both traits are represented in the selection index before consideration is given to other traits.

The selection indices for the improvement of resistance to rootlodging, table 11, contain as the first three characters ear height, root weight, and weight of straw, with ear height and weight of straw bearing a negative sign. The selection index based on these three characters is similar to the lodging index given by VAIDYA and coworkers (1962), except that they used the plant height instead of the ear height (see also par. 3.2.2., page 17).

Comparing the tables 9, 10 and 11 we notice that each table contains a different set of characters. A selection index for the simultaneous improvement of the three objectives: yield, resistance to stemlodging, and resistance to rootlodging, should be based on characters which are correlated to each of the three objectives. These characters are not necessarily also the best characters to be used in the separate improvement of each of the three objectives.

Table 12 and 13 present, each for a different set of relative economic weights,

selection indices for the simultaneous improvement of yield and resistance to stem- and rootlodging. Both tables give as the first three traits the characters root weight, crushing strength, and leaf angle. None of these characters is also represented in the selection indices for the improvement of yield (table 9). Apparently these three traits are of only secondary importance when selecting for only one objective, yield improvement. On the other hand, the characters which rank first in the selection indices for yield improvement, width of leaf eight, ear height and days to shooting, do not rank among the first characters in the selection indices for the three simultaneous objectives, because while these characters are correlated with yield they are only weakly correlated or even negatively correlated with resistance to stem- and rootlodging.

Several characters were positively correlated with yield but negatively correlated with resistance to stem- and rootlodging. Noteworthy among these is the ear height. The ear height is represented with a positive sign in the selection indices for yield improvement (table 9), while it is represented with a negative sign in the selection indices for the improvement of resistance to rootlodging (table 11). This clearly illustrates the danger of improving one character at a time. Characters such as ear height are not represented in the selection indices for the simultaneous improvement of yield and resistance to stem- and rootlodging (table 12 and 13). Characters which carry a positive sign in these indices were positively correlated with yield and with resistance to stem- and rootlodging, while characters with a negative sign were negatively correlated with both yield and resistance to stem- and rootlodging. The only exception is given by the hundred-seed weight in table 12, which had a low negative correlation with resistance to rootlodging, while it was positively correlated with yield and with resistance to stemlodging.

The crushing strength of the stalk was one of the most valuable characters in the selection indices for the three simultaneous objectives: yield, resistance to stemlodging, and resistance to rootlodging. In the foregoing we saw that the crushing strength was highly correlated to the dry weight of a 5-cm stalk section, while selection upon the latter character was more convenient. Selection indices based on the characters root weight, dry weight of a 5-cm stalk section, and leaf angle are presented at the bottom of the tables 12 and 13, using for each table the appropriate economic weights. As a result of the above correlation, the expected response to selection using these selection indices is only slightly inferior to the expected response when using selection indices which include the crushing strength instead of the dry weight of a 5-cm stalk section.

Selection indices for the three simultaneous objectives, yield, resistance to stemlodging, and resistance to rootlodging, were calculated for different sets of relative economic weights, as presented in table 12 and 13. Comparing these tables we notice that the influence of the relative economic weights is limited as long as the selection indices are based on only a few characters. The selection indices based on the three traits root weight, crushing strength, and leaf angle are almost identical in both tables, with a difference only in the mean value of the weighing factors which is of no consequence in the selection.

While estimates for the expected responses to index selection were given for yield and for resistance to stem- and rootlodging, it is possible to estimate the expected change occurring in any other character, using the formulae (38), (39) and (40), page 47.

Early selection on characters observable before flowering has the advantage that it then becomes possible to practise full parental control, thereby doubling the response to selection as compared with the response to selection after flowering. Selection indices based on characters observable before flowering are presented in table 14. A selection index based on length and width of leaf eight should be very efficient in improving yield. With selection on both the male and the female parent the response to index selection should be $k \times 8.0$ percent. Instead of such a selection index, one may use also single trait selection, selecting for leaf area, where the leaf area is measured as the product of length and width of leaf eight. Single trait selection for leaf area would be only slightly less efficient than index selection based on length and width of leaf eight.

Single trait selection for leaf area should be of special interest when one seeks to improve fodder production, because selection for leaf area should result in a correlated response in grain yield as well as in fodder production.

Using independent culling levels, selection before flowering on the leaf area may be combined with selection after flowering on other characters in the way as proposed by Young and Weiler (1961) (see also par. 2.1., page 7).

Apart from length and width of leaf eight there were two other characters which could be recorded before flowering, days to shooting and total number of leaves. The latter two characters should be less useful in selection because, while both characters are positively correlated with yield, they are negatively correlated with resistance to stem- and rootlodging (table 8).

While the selection before flowering offers a good opportunity for the selection for improved yields, there is little opportunity for early selection for stem- and rootlodging resistance, as none of the four characters observable before flowering is closely correlated to either stem- or rootlodging resistance.

The realized responses to index selection for yield for a number of selection indices are given in table 15 and 16. With the exception of the selection indices based on only one character, the realized responses to index selection were equal to or somewhat larger than the estimated expected responses to index selection. However the realized efficiency of index selection as compared to single-trait selection for yield was not as large as expected. The reason was that the realized response to single-trait selection for yield, which was $k \times 3.5$ percent, was much larger than the expected response, which was $k \times 2.1$ percent, where the response to selection is expressed as a percentage of the mean yield.

Individual plants may be selected on the basis of a single trait or on the basis of a selection index. Index selection will require more time, but it will be also more efficient than single-trait selection. The advantages to both methods may be combined to a certain extent by using indirect selection, that is single-trait selection for a character which is correlated to the character or characters which we seek to improve by selection. In the above we already saw that single-trait

selection for leaf area would be very efficient in improving yield. From table 12 and 13 we learn that single-trait selection for root weight should result in a correlated response in the three characters of economic importance, yield, resistance to stemlodging and resistance to rootlodging. When the selection is aimed at the simultaneous improvement of these three characters single-trait selection for root weight should certainly be an attractive alternative to index selection. Single-trait selection for crushing strength of the stalk or for dry weight of a 5-cm stalk section should result in a rapid improvement of the resistance to stemlodging, while it should also give a correlated response in yield.

6. GENERAL DISCUSSION

The selection methods used in plant breeding may be divided into two categories:
1. Mass selection or individual selection, that is the selection based upon the individual phenotype.
2. Selection methods based upon the mean progeny performance. The progenies may be either half or full sibs or they may be obtained by selfing. The progenies are usually tested in either single or replicated plots.

Index selection may be applied to individual selection as well as to selection methods based upon progeny means. However the literature on index selection is limited to index selection as applied to selection based upon progeny means (e.g. SMITH, 1936; ROBINSON et al., 1951; JOHNSON et al., 1955; MANNING, 1956, 1963; MILLER et al., 1958; BRIM et al., 1959).

With maize, as with many other crops, it is not difficult to obtain progenies of adequate size so as to allow for an extensive progeny testing programme. The value of each progeny may be estimated rather accurately from the mean progeny performance. A selection index should add only little to the accuracy with which the value of each progeny may be estimated, and the more extensively the progenies are tested the less should be the gain in selection efficiency obtained from a selection index (MILLER et al., 1958). Therefore, seeking to increase the response to selection it should be easier and more rewarding to increase the amount of testing rather than to use a selection index. This was already recognized by SMITH (1936) when the advocated index selection to be applied where the size of the progenies was limited (see also par. 2.3.2., page 15).

Mass selection without the use of a selection index was successful in improving the yield of open-pollinated varieties of maize (GARDNER, 1961; JOHNSON, 1963; LONNQUIST et al., 1966; LONNQUIST, 1967; ANON., 1968). However mass selection did not result in an improvement in yield in experiments reported by HALLAUER and SEARS (1969). In the experiments reported in the present study individual selection for yield, respectively among one hundred and twenty-one plants of Samaru Composite 2 and among thirty-six plants of Colombian Composite, resulted in an increase in yield of $k \times 2.0$ percent and $k \times 3.5$ percent, when k is the selection intensity.

WELLHAUSEN (1965) recommended to exploit the large amount of exotic germ plasm existing for maize as a source for future maize improvement programmes. The additive genetic variance available between the different varieties of maize should be enormous. This potential should be used by mixing varieties of diverse origin. Several generations of mixing should be followed by repeated cycles of mass selection so as to concentrate the additive genetic variance in one composite (WELLHAUSEN, 1965). EBERHART et al. (1967) presented a method to create composites with a diverse genetic background. They advocated the use of such composites, possessing a relatively large amount of additive genetic

variance, as a starting point whenever a new breeding programme is initiated. Mass selection should be the obvious method for the initial improvement of such composites (SPRAGUE, 1966).

Mass selection should have its place in the improvement programmes for other crops as well. Repeated cycles of mass selection may be applied as a selection procedure for any cross-pollinating crop. Crops with only a low amount of natural cross pollination can often be converted into fully cross-pollinating crops by using male sterility (SPRAGUE, 1966). Mass selection should be an appropriate method of selection at the initial stage of a crop improvement programme, either for completely new crops or for existing crops brought to a new environment. Mass selection may be used in an already existing crop improvement programme as a method to create a back-up population out of exotic materials, in the way proposed by WELLHAUSEN (1965).

The advantages of mass selection are:
1. Its relative simplicity.
2. It takes only one generation per cycle. Many generations may be realized within a limited span of time, thereby allowing for a rapid breaking up of linkage blocks and frequent recombinations.
3. It allows for the screening of large numbers of plants from which large numbers may be selected, thereby preventing a premature loss of genetic variability.

Several arguments may be given for the application of a selection index in individual selection:
1. The selection index makes an optimal use of the information available from a single individual. The phenotypic value of a single character will give just a very rough estimate for the genetic value of a plant, a much better estimate may be obtained by considering the phenotypic value of several traits at a time.
2. Index selection allows for the simultaneous improvement of several traits at a time. When the selection is aimed at the improvement of more than one trait index selection should be better than either tandem selection or selection using independent culling levels (HAZEL and LUSH, 1942; YOUNG, 1961).
3. A further advantage to index selection is realized when the selection index is based upon traits observable before flowering. In that case it becomes possible to select not only the seed parent but also the pollen parent, thereby doubling the response to selection. In the present study the characters days to shooting, total number of leaves, and length and width of leaf eight were recorded before flowering. The estimated response to individual selection for yield using a selection index based upon the length and the width of leaf eight was $k \times 8.0$ percent per cycle of selection.
4. The selection index may be used to select under conditions differing from the normal cropping environment. This point will be substantiated below.

The selection index is calculated using estimates for the population parameters obtained either from a sib relationship or from a parent-offspring relationship. A sib analysis as given in chapter 5 on the one hand supplies the data needed for the calculation of a selection index, and on the other hand offers a valuable insight into the population by giving estimates for the heritabili-

ties and the genetic and phenotypic correlations of the different characters of the plant. However the parent-offspring relationship offers several advantages when we are interested only in the calculation of a selection index:

1. The multiple regression of the value of the offspring on the characters of the parent plants gives a direct estimate for the selection index, which is independent of any quantitative genetic interpretation of the data.

2. The experimental procedure is rather simple. The individual characters have to be recorded only from the parent plants. The parent plants can be grown in any convenient pattern as long as the plants are grown under environmental conditions that are common to actual selection. Parent plants with incomplete records can be discarded from the experiment, because selection among the parents does not bias the selection index.

3. Using a parent-offspring relationship it is possible to obtain selection indices for the selection under conditions differing from the normal cropping environment. The parent-offspring relationship is then used to measure the relationship between the phenotypic value of the parents, as obtained in the modified selection environment, and the genetic value as obtained from the progeny means, when the progenies are measured under normal cropping conditions. This argument for a parent-offspring relationship was given above as the fourth argument for individual index selection. The crop production environment is not an optimal environment for individual selection, because the rather dense plant populations used in crop production result in a comparatively low single-plant heritability (ANON., 1969). In individual selection one should prefer to use low density plant populations, chosen such as to maximize the single-plant heritability. Moreover, to speed up a selection programme one should wish to select not only during the cropping season but also in the off-season, that is under conditions differing from the normal cropping environment. In tropical areas it should be possible in this way to select two or three times instead of only just once a year.

In the present experiment the response to individual selection could be improved by between thirty-five and seventy-one percent through the use of a selection index estimated from a parent-offspring relationship. Furthermore, for the populations used in this study it was shown that the response to individual index selection compared favourably to the response which could be expected from selection methods based upon progeny means.

The number of situations in which individual selection should be chosen as the appropriate method of selection is limited by the generally low realized heritability. The realized heritability of individual selection is increased through the use of a selection index, while in the foregoing still several more advantages were given for the use of a selection index. This implies that the number of situations in which individual selection should be the appropriate method of selection will increase as a result of using a selection index. Still, individual index selection should be less suited as a method to improve long established, high performing varieties, possessing only a limited amount of genetic variability.

SUMMARY

General considerations

A selection index may be applied to selection based either upon the performance of single plants or upon the performance of progenies. In the latter case however, index selection should only result in a modest gain in selection efficiency, when index selection is compared to single-trait selection for the desired character.

Index selection is a relatively efficient method of selection when it is applied in the selection of individual plants. Individual index selection, as we may call this type of selection, is presented in this study as a selection method for the initial stage of a population improvement programme. In general it may be used as a method of selection for cross-pollinating crops. Individual index selection combines the advantages of mass selection with these from index selection.

The advantages of mass selection are most obvious during the initial stage of a population improvement programme. Mass selection takes only one generation per cycle. A large number of generations can be grown in a relatively short period of time. When the population under selection is not yet at linkage equilibrium the successive generations will give a high frequency of recombinants implying a progressive breaking up of linkage blocks. With mass selection it is possible, even with limited facilities, to include a large number of plants in the selection, thereby preventing any premature loss of genetic variability.

There are several arguments for the application of a selection index in mass selection. The selection index makes an optimal use of the information available from a single phenotype. With index selection it is possible to select for the simultaneous improvement of several traits. When the selection index is based on traits which may be observed before flowering it is possible to select not only on the seed parent but also on the pollen parent, thereby doubling the response to selection. Furthermore, index selection may be used as a method to select under conditions differing from the normal environment of the crop. This means that it is possible to choose the selection conditions such as to maximize the single-plant heritability and this means then also that it is possible to select in an off-season crop.

Selection indices for individual selection in maize were calculated using estimates of the population parameters obtained either from a parent-offspring relationship or from a sib analysis. There are several advantages in using a parent-offspring relationship. Using a parent-offspring relationship the selection index can be estimated directly from the multiple regression of the value of the offspring on the characters of the parents, independent of any quantitative genetic interpretation of the data. The experimental procedure may be kept rather simple. It is possible to obtain selection indices for the selection under conditions differing from the normal environment of the crop. The latter may be realized by growing the parent generation in the selection environment, while the offspring is measured in the normal cropping environment.

Results

The parent-offspring relationship was studied on one hundred and twenty-one open-pollinated plants of Samaru Composite 2 and on thirty-six open-pollinated plants of Colombian Composite. Recorded from each plant were twelve different characters and the mean yield of its progeny. These records were used to construct several selection indices for the improvement of yield. The response to index selection was studied using Colombian Composite as the test population for the selection indices calculated for Samaru Composite 2, and vice versa. The response to individual selection could be improved by between thirty-five and seventy-one percent through the use of a selection index. An optimal response was obtained from selection indices including about four different traits. The response to selection obtained from a selection index was superior to the response to selection obtained from an 'estimated' index, that is an index in which the weighing factors for the different traits represented in the index are estimated according to some rule of thumb.

For the populations under study, composites of recent origin, it was shown that the response to individual index selection compared favourably with the response from selection methods based on progeny means.

A sib analysis was carried out using one hundred and forty-four half-sib progenies of Colombian Composite. Most of the progenies were lost as a result of the sudden outbreak of a disease, caused by *Helminthosporium maydis* race T, so that the study had to be limited to the results obtained from only thirty-six progenies, resistant to the disease.

The sib analysis was used to estimate the single-plant heritabilities and the genetic and phenotypic correlations with yield and with resistance to stem- and rootlodging for thirty different traits. It was found that the character leaf angle was correlated with yield, which indicates that at Mokwa, despite the rather low yield level of the crop, light is already a limiting factor in maize production. The stalk characters crushing strength and dry weight of a 5-cm stalk section were highly correlated with resistance to stemlodging. A low correlation was found between resistance to stemlodging and the rind thickness of the stalk. The root weight and the pulling strength of the roots were both correlated with resistance to rootlodging, while these two characters were also correlated with yield and with resistance to stemlodging.

The results of the sib analysis were used to construct selection indices for the improvement of yield, for the improvement of resistance to stemlodging, and for the improvement of resistance to rootlodging, while selection indices were also constructed for the simultaneous improvement of yield and resistance to stem- and rootlodging. A selection index for the three simultaneous objectives included first of all the character root weight, secondly it included either the crushing strength of the stalk or the dry weight of a 5-cm stalk section, and thirdly it included the leaf angle. When the selection is aimed at the simultaneous improvement of yield and resistance to stem- and rootlodging, single-trait selection for root weight should be an attractive alternative to individual index selection.

Out of the thirty different traits used in this study there were four traits which could be observed before flowering. These were: the days to shooting, the total number of leaves and the length and width of leaf number eight. Individual index selection before flowering should be efficient in improving yield, when using a selection index based on length and width of leaf eight. As an alternative to index selection one might practise also single trait selection for leaf area, measuring the leaf area as the product of length and width of leaf eight.

ACKNOWLEDGEMENTS

SAMENVATTING

MASSA-SELEKTIE IN MAÏS COMPOSITES MET BEHULP VAN SELEKTIE-INDICES

Algemeen

Een selektie-index kan worden toegepast in selektie gebaseerd of op de prestatie van individuele planten, of op de prestatie van nakomelingschappen. In het tweede geval echter kan van index-selektie, in vergelijking tot selektie rechtstreeks op de gewenste eigenschap, slechts een geringe verbetering van het rendement worden verwacht.

Index-selektie is een relatief doeltreffende selektiemethode wanneer zij wordt toegepast bij de selektie van individuele planten. Deze methode kunnen we aanduiden als individuele index-selektie. In dit proefschrift wordt individuele index-selektie beschouwd als een selektie-methode, te gebruiken tijdens de eerste fase in de verbetering van een populatie. De methode kan in het algemeen worden toegepast bij kruisbestuivende gewassen. Individuele index-selektie kombineert de voordelen van massa-selektie met die verkregen bij index-selektie.

De voordelen van massa-selektie zijn vooral duidelijk gedurende de eerste fase in de verbetering van een populatie. Massa-selektie verlangt slechts één generatie per cyclus. Een groot aantal generaties kan in relatief korte tijd worden verwezenlijkt. Wanneer de te verbeteren populatie nog niet in een koppelingsevenwicht verkeert zullen de opeenvolgende generaties vele rekombinaties opleveren, hetgeen een snel doorbreken van koppelingsgroepen inhoudt. Wanneer gebruik gemaakt wordt van massa-selektie is het mogelijk, ook bij aanwending van beperkte middelen, een groot aantal planten in de selektie te betrekken; een vroegtijdig verlies van genetische variabiliteit kan hierdoor worden voorkomen.

Verscheidene argumenten pleiten voor de toepassing van een selektie-index bij massa-selektie. Met behulp van een selektie-index is het mogelijk om de beschikbare informatie van een enkel fenotype optimaal te benutten. Eveneens is het mogelijk de selektie te richten op de gelijktijdige verbetering van meerdere eigenschappen. Wanneer de selektie-index gebaseerd is op eigenschappen welke kunnen worden waargenomen voor de bloei, is het mogelijk om niet alleen op de moederplant te selekteren maar ook op de vaderplant, waardoor het rendement van de selektie wordt verdubbeld. Index-selektie kan eveneens worden toegepast als een selektie-methode te gebruiken onder omstandigheden welke afwijken van de normale veldomstandigheden van het gewas. Dit betekent, dat het mogelijk is de omstandigheden waaronder wordt geselekteerd zodanig te kiezen, dat de invloed van het milieu op de fenotypische expressie van de individuele planten zo gering mogelijk wordt. Dit betekent dan eveneens dat het mogelijk is om te selekteren buiten het eigenlijke groeiseizoen.

Selektie-indices voor de individuele selektie in maïs werden berekend uitgaande van schattingen van de populatie parameters. Voor het maken van deze schattingen werd gebruik gemaakt hetzij van een ouder-nakomelingschap relatie, hetzij van een sib-analyse. Het gebruik van een ouder-nakomelingschap

relatie heeft verschillende voordelen. De selektie-index kan rechtstreeks worden geschat uit de multiple regressie van de waarde van de nakomelingschap op de eigenschappen van de ouderplanten. Deze schatting kan worden verricht onafhankelijk van enige kwantitatief genetische interpretatie van de gegevens. De proefopzet kan vrij eenvoudig blijven. Tevens is het mogelijk selektie-indices te verkrijgen welke kunnen worden gebruikt bij selektie onder omstandigheden welke afwijken van de normale veldomstandigheden van het gewas. Dit laatste kan worden verwezenlijkt door de ouderplanten te kweken onder de milieuomstandigheden welke worden gebruikt tijdens de selektie, terwijl de nakomelingschap gemeten wordt onder de normale veldomstandigheden van het gewas.

Resultaten

De ouder-nakomelingschap relatie werd bestudeerd van honderd-eenentwintig vrij bestoven planten van Samaru Composite 2 en van zesendertig vrij bestoven planten van Colombian Composite. Van iedere plant werden twaalf verschillende eigenschappen gemeten, terwijl van iedere plant eveneens de gemiddelde opbrengst van zijn nakomelingschap werd bepaald. Uit deze metingen werden verschillende selektie-indices berekend voor selektie gericht op opbrengstverbetering. Het rendement van index-selektie werd bestudeerd, waarbij gebruik gemaakt werd van Colombian Composite als toetspopulatie voor de selektie-indices berekend voor Samaru Composite 2 en vice versa. Door gebruik te maken van een selektie-index kon het rendement van individuele selektie worden verbeterd met vijfendertig tot eenenzeventig procent. Een optimaal resultaat werd verkregen wanneer een selektie-index werd toegepast, welke omstreeks vier verschillende eigenschappen bevatte. Index-selektie leverde een hoger rendement op dan selektie met behulp van een geschatte index. In zulk een geschatte index worden de waarden welke in de selektie moeten worden toegekend aan de verschillende eigenschappen van de plant geschat met behulp van een min of meer willekeurig gekozen vuistregel.

De populaties welke in deze studie werden gebruikt bestonden uit composites van recente oorsprong. Uitgaande van deze populaties werd aangetoond dat het rendement van individuele index-selektie gunstig afstak bij het rendement van selektie-methoden gebaseerd op het toetsen van de nakomelingschap.

Een sib-analyse werd uitgevoerd, waarbij gebruik gemaakt werd van honderdvierenveertig half-sib families van Colombian Composite. Als gevolg van het plotseling uitbreken van een ziekte, veroorzaakt door het T fysio van *Helminthosporium maydis*, ging het meeste materiaal verloren. Het onderzoek moest daarom worden beperkt tot de resultaten verkregen van slechts zesendertig families, welke resistent waren tegen de ziekte.

De sib-analyse werd gebruikt om de mate van overerfbaarheid te schatten van dertig verschillende individuele eigenschappen van de plant. Voor deze dertig eigenschappen werden eveneens de fenotypische en genetische korrelaties met opbrengst en met legering-resistentie geschat. Legering werd hierbij naar de oorzaak onderscheiden in stengel-legering, d.w.z. het omknakken of afbreken van het stengelgedeelte beneden de kolf, en wortel-legering, d.w.z. een onvol-

doende verankering van de wortels wat het legeren van de plant tot gevolg heeft. Tussen de opbrengst en de bladhoek, gemeten als de hoek tussen – van boven af geteld – het derde blad en de stengel, werd een korrelatie gevonden. Deze korrelatie wijst erop, dat in Mokwa de lichtintensiteit reeds een beperkende faktor vormt in de produktie van mais, ondanks het vrij lage opbrengstniveau. Twee eigenschappen van de stengel, de kracht benodigd om de stengel samen te drukken en het drooggewicht van een stengelgedeelte van 5 cm lang, waren hoog gekorreleerd met resistentie voor stengel-legering. De dikte van de verharde buitenlaag van de stengel was zwak gekorreleerd met resistentie voor stengellegering. Het gewicht van het wortelstelsel en de kracht, benodigd om de plant uit de grond te trekken, waren beide gekorreleerd met resistentie voor wortel-legering, terwijl deze beide eigenschappen ook gekorreleerd waren met de opbrengst en met resistentie voor stengel-legering.

De resultaten van de sib-analyse werden gebruikt bij het samenstellen van verschillende selektie-indices. Selektie-indices werden bepaald voor de selektie voor opbrengstverbetering, voor een verhoging van de resistentie voor stengel-legering en voor een verhoging van de resistentie voor wortel-legering, terwijl eveneens selektie-indices werden bepaald voor een gelijktijdige verbetering in opbrengst en in resistentie voor stengel- en wortel-legering. Een selektie-index, zoals genoemd in het laatste geval, bevatte in de eerste plaats het gewicht van het wortelstelsel, in de tweede plaats een van beide stengeleigenschappen: de kracht benodigd om de stengel samen te drukken, of het drooggewicht van een 5 cm lang stengelgedeelte en in de derde plaats de bladhoek. Selektie alleen op het gewicht van het wortelstelsel is, naar het zich laat aanzien, een aantrekkelijk alternatief voor individuele index-selektie wanneer de selektie gericht is op een gelijktijdige verbetering in opbrengst en in resistentie voor stengel- en wortel-legering.

Van de dertig verschillende eigenschappen welke bestudeerd werden, waren er vier welke voor de bloei konden worden waargenomen. Deze eigenschappen waren: het tijdstip waarop de pluim tevoorschijn komt, het totaal aantal bladeren en de lengte en breedte van het achtste blad. Individuele index-selektie vóór de bloei met behulp van een selektie-index welke gebaseerd is op de eigenschappen lengte en breedte van het achtste blad is, naar kan worden verwacht, een doeltreffende selektie-methode voor de verbetering van de opbrengst. In plaats van gebruik te maken van een dergelijke selektie-index is het ook mogelijk te selekteren op één enkele eigenschap, te weten de bladoppervlakte, waarbij de bladoppervlakte wordt gemeten als het produkt van de lengte en de breedte van het achtste blad.

De auteur, Frans de Wolff, werd in 1940 geboren te Leiden. Als student aan de Landbouwhogeschool, met als studierichting tropische landbouwplantenteelt, behaalde hij in 1966 het diploma van landbouwkundig ingenieur. Na zijn afstuderen werkte hij vier jaar in Mokwa, Nigeria, in de veredeling van mais. Op het ogenblik is hij opnieuw bezig met mais veredeling, nu in dienst van CIMMYT in Congo (Kinshasa).

REFERENCES

ABRAHAM, T. P., W. T. BUTANY, and R. L. M. GHOSH (1954). Discriminant function for varietal selection in rice. Indian J. Genet. Pl. Breed. 14: 51–53.

ALLISON, J. C. S., and D. J. WATSON (1966). The production and distribution of dry matter in maize after flowering. Ann. Bot. N.S. 30: 365–381.

ANONYMOUS (1968). CIMMYT Ann. Rep. 1967–'68, Mexico City.

ANONYMOUS (1969). CIMMYT Ann. Rep. 1968–'69, Mexico City.

AUTORENKOLLEKTIV (1967). Gleichzeitige Selektion nach mehreren Merkmalen und deren Anwending in der Pflanzen- und Tierzüchtung. FortschrBer. Landw. 5, no. 4, 72 p.

BHAT, B. K., and N. L. DHAWAN (1969). Effect of cytoplasm on quantitative characters of maize. Indian J. Genet. Pl. Breed. 29: 321–326.

BRIM, C. A., HERBERT W. JOHNSON, and C. CLARK COCKERHAM (1959). Multiple selection criteria in soybeans. Agron. J. 51: 42–46.

BYTH, D. E., B. E. CALDWELL, and C. R. WEBER (1969). Specific and non-specific index sélection in soybeans, *Glycine max* L. (Merrill). Crop Sci. 9: 702–705.

CALDWELL, B. E., and C. R. WEBER (1965). General, average, and specific selection indices for yield in F 4 and F 5 soybean populations. Crop Sci. 5: 223–226.

CAMPBELL, C. M. (1964). Influence of seed formation on accumulation of vegetative dry matter and stalk strength. Crop Sci. 4: 31–34.

CHAUDRI, MUHAMMAD YOUSAF (1964). Genetic variance for yield and its components in a synthetic population of corn (*Zea mays*). Diss. Abstr. 25: 1500–1501.

COCHRAN, W. G. (1951). Improvement by means of selection. Proc. second Berkeley Symp. Math. Statist. Probab. p. 449–470.

COCKERHAM, C. CLARK (1954). An extension of the concept of partitioning hereditary variance for analysis of covariances among relatives when epistasis is present. Genetics 39: 859–882.

COCKERHAM, C. CLARK (1956). Effects of linkage on the covariances between relatives. Genetics 41: 138–141.

COCKERHAM, C. CLARK (1963). Estimation of genetic variances. In: W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Publ. 982. Nat'l. Acad. Sci. – Nat'l. Res. Council, Washington, D.C. p. 53–93.

COMSTOCK, R. E., and H. F. ROBINSON (1948). The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4: 254–266.

COMSTOCK, R. E., and H. F. ROBINSON (1952a). Estimation of average dominance of genes. In: John W. Gowen (ed.) Heterosis. Iowa State College Press, Ames, Iowa. p. 494–516.

COMSTOCK, R. E., and H. F. ROBINSON (1952b). Genetic parameters, their estimation and significance. Proc. sixth int. Grassld Congr. 1: 284–291.

COMSTOCK, R. E., and R. H. MOLL (1963). Genotype-environment interactions. In: W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Publ. 982. Nat'l. Acad. Sci. – Nat'l. Res. Council, Washington, D.C. p. 164–194.

CRAIG, J. (1968). Selection for root strength in maize. Trop. Agric., Trin. 45: 343–345.

CRAIG, J. (1971). Occurrence of *Helminthosporium maydis* race T in West Africa. Pl. Dis. Reptr (submitted for publication).

CRANE, PAUL L., and W. E. NYQUIST (1967). Effects of different gene-cytoplasm systems on quantitative characters in reciprocal F 2 crosses of maize (*Zea mays* L.). Crop. Sci. 7: 376–378.

CRUMP, S. LEE (1946). The estimation of variance components in analysis of variance. Biometr. Bull. 2: 7–11.

CUNNINGHAM, C. C. (1916). The relation of ear characters of corn to yield. J. Am. Soc. Agron. 8: 188–196.

DAYNARD, T. B., J. W. TANNER, and D. J. HUME (1969). Contribution of stalk soluble carbohydrates to grain yield. Crop Sci. 9: 831–834.

DONALD, C. M. (1963). Competition among crop and pasture plants. Adv. Agron. **15**: 1–118.
DUDLEY, J. W., and R. H. MOLL (1969). Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci. **9**: 257–262.
DUNCAN, W. G., A. L. HATFIELD, and J. L. RAGLAND (1965). The growth and yield of corn. II. Daily growth of corn kernels. Agron. J. **57**: 221–223.
DURRELL, L. W. (1925). A preliminary study of fungous action as the cause of down corn. Phytopathology **15**: 146–154.
EBERHART, S. A. (1967). Recurrent selection methods. Sols afr. **12**: 129–139.
EBERHART, S. A. (1969). Factors effecting efficiencies of breeding methods. Paper presented at the third bienn. W. Afr. Sorghum, Maize, Millet Workshop Conf., Samaru, Nigeria, October 1969.
EBERHART, S. A., M. N. HARRISON, and F. OGADA (1967). A comprehensive breeding system. Züchter **37**: 168–174.
EISENHART, CHURCHILL (1947). The assumptions underlying the analysis of variance. Biometrics **3**: 1–21.
ELGIN JR., J. H., R. R. HILL JR., and K. E. ZEINDERS (1970). Comparison of four methods of multiple trait selection for five traits in alfalfa. Crop Sci. **10**: 190–193.
EIJNATTEN, C. L. M. VAN (1965). Towards the improvement of maize in Nigeria. Thesis, Wageningen.
FALCONER, D. S. (1960). Introduction to quantitative genetics. Oliver and Boyd. Edinburgh and London, 365 p.
FEDERER, WALTER T. (1955). Experimental Design. The Macmillan Company, New York. p. 319–336.
FISHER, R. A. (1918). The correlation between relatives on the supposition of Mendelian inheritance. Trans. R. Soc. Edinb. **52**, 399–433.
FLEMING, A. A., G. M. KOZELNICKY, and E. B. BROWNE (1960). Cytoplasmic effects on agronomic characters in a double-cross maize hybrid. Agron. J. **52**: 112–115.
FOCKE, R., W. FRANZKE, and A. WINKEL (1966). Trockensubstanz- Zucker- und Proteinbildung in befrüchtetem und nicht befrüchtetem Mais. Albrecht-Thaer-Arch. **10**: 585–600.
FOLEY, D. C. (1962). Stalk detoriation of plants susceptible to corn stalk rot. (Abstr.) Phytopathology **52**: 10.
FRANCIS, C. A., J. N. RUTGER, and A. F. E. PALMER (1969). A rapid method for plant leaf-area estimation in maize (*Zea mays* L.). Crop Sci. **9**: 537–539.
GARDNER, C. O. (1961). An evaluation of effects of mass selection and seed irradiation with thermal neutrons on yield of corn. Crop Sci. **1**: 241–245.
GARDNER, C. O. (1963). Estimates of genetic parameters in cross-fertilizing plants and their implications in plant breeding. In: W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Publ. 982. Nat'l. Acad. Sci. – Nat'l. Res. Council, Washington, D.C. p. 225–248.
GARWOOD, D. L., and R. J. LAMBERT (1968). Effect of different cytoplasms on oil, earheight, and plantheight in maize (*Zea mays* L.). Agron. Abstr. p. 7–8.
GARWOOD, D. L., EVELYN J. WEBER, R. J. LAMBERT, and D. E. ALEXANDER (1970). Effect of different cytoplasms on oil, fatty acids, plant height, and ear height in maize (*Zea mays* L.). Crop Sci. **10**: 39–41.
GENTER, C. F., G. D. JONES, and M. T. CARTER (1970). Dry matter accumulation and depletion in leaves, stems, and ears of maturing maize. Agron. J. **62**: 535–537.
GOODMAN, MAJOR M. (1965). Estimates of genetic variance in adapted and exotic populations of maize. Crop. Sci. **5**: 87–90.
HALLAUER, ARNEL R. (1968). Estimates of genetic variances in Iowa long ear synthetic, *Zea mays* L. Advg Frontiers Pl. Sci. **22**: 147–162.
HALLAUER, ARNEL R., and JAMES A. WRIGHT (1967). Genetic variances in the open-pollinated variety of maize, Iowa Ideal. Züchter **37**: 178–185.
HALLAUER, ARNEL R., and J. H. SEARS (1969). Mass selection for yield in two varieties of maize. Crop Sci. **9**: 47–50.
HANSON, W. D. and H. W. JOHNSON (1957). Methods of calculating and evaluating a general

selection index obtained by pooling information from two or more experiments. Genetics **42**: 421–432.

HARRIS, DEWEY L. (1963). The influence of errors of parameter estimation upon index selection. In: W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Publ. 982. Nat'l. Acad. Sci. – Nat'l. Res. Council, Washington, D.C. p. 491–500.

HARRIS, DEWEY, L. (1964). Expected and predicted progress from index selection involving estimates of population parameters. Biometrics **20**: 46–72.

HAYES, H. K. and I. J. JOHNSON (1939). The breeding of improved selfed lines of corn. J. Am. Soc. Agron. **31**: 710–724.

HAZEL, L. N. (1943). The genetic basis for constructing selection indexes. Genetics **28**: 476–490.

HAZEL, L. N., and J. L. LUSH (1942). The efficiency of three methods of selection. J. Hered. **33**: 393–399.

HENDERSON, C. R. (1963). Selection index and expected genetic advance. In: W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Publ. 982. Nat'l. Acad. Sci. – Nat'l. Res. Council, Washington, D.C. p. 141–163.

HOLBERT JR., R., and B. KOEHLER (1924). Anchorage and extent of corn root systems. J. agric. Res. **27**: 71–78.

HOYT, PAUL, and RICHARD BRADFIELD (1962). Effect of varying leaf area by partial defoliation and plant density on dry matter production in corn. Agron. J. **54**: 523–525.

HUNTER, R. B. and E. E. GAMBLE (1968). Effect of cytoplasmic source on the performance of double-cross hybrids in maize, *Zea mays* L. Crop Sci. **8**: 278–280.

JENKINS, M. T. (1929). Correlation studies with inbred and crossbred strains of maize. J. agric. Res. **39**: 677–721.

JOHNSON, E. C. (1963). Effects of mass selection for yield in a tropical corn variety. Agron. Abstr. p. 82.

JOHNSON, HERBERT W., H. F. ROBINSON, and R. E. COMSTOCK (1955). Genotypic and phenotypic correlations in soybeans and their implications in selection. Agron. J. **47**: 477–483.

JOHNSTON, RONALD R., K. E. McCLURE, L. J. JOHNSTON, E. W. KLOSTERMAN, and G. B. TRIPLETT (1966). Corn plant maturity. I. Changes in dry matter and protein distribution in corn plants. Agron. J. **58**: 151–153.

JORGENSON, LOUIS, and H. E. BREWBAKER (1927). A comparison of selfed lines of corn and first generation crosses between them. J. Am. Soc. Agron. **19**: 819–830.

KIESSELBACH, T. A. (1922). Ear-type selection and yield of dent corn. J. Am. Soc. Agron. **14**: 27–48.

LAIBLE, CHARLES ARTHUR (1964). Inheritance of ear number in four *Zea mays* genotypes. Diss. Abstr. **25**: 1506.

LAIBLE, CHARLES A., and V. A. DIRKS (1968). Genetic variance and selective value of ear number in corn (*Zea mays* L.). Crop Sci. **8**: 540–543.

LIEBHARDT, W. C., P. J. STANGEL, and T. J. MURDOCK (1968). A mechanism for premature parenchyma breakdown in corn (*Zea mays* L.) Agron. J. **60**: 496–499.

LINDSEY, M. F., J. H. LONNQUIST, and C. O. GARDNER (1962). Estimates of genetic variance in open-pollinated varieties of cornbelt corn. Crop Sci. **2**: 105–108.

LONNQUIST, J. H. (1964). A modification of the ear-to-row procedure for the improvement of maize populations. Crop Sci. **4**: 227–228.

LONNQUIST, J. H. (1967). Mass selection for prolificacy in maize. Züchter **37**: 185–188.

LONNQUIST, J. H., A. O. COTA, and C. O. GARDNER (1966). Effect of mass selection and thermal neutron irradiation on genetic variances in a variety of corn (*Zea mays* L.). Crop Sci. **6**: 330–332.

LOVE, H. H., and J. B. WENTZ (1917). Correlations between ear characters and yield in corn. J. Am. Soc. Agron. **9**: 315–322.

LUSH, J. L. (1940). Intra-sire correlations or regressions of offspring on dam as a method of estimating heritability of characteristics. From: Hazel (1943).

MANNING, H. L. (1956). Yield improvement from a selection index technique with cotton. Heredity **10**: 303–322.

MANNING, H. L. (1963). Realized yield improvement from twelve generations of progeny

selection in a variety of upland cotton. In W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Publ. 982. Nat'l. Acad. Sci. – Nat'l. Res. Council, Washington, D.C. p. 329–349.

McCALL, A. G., and CLARK WHEELER (1913). Ear characters not correlated with yield in corn. J. Am. Soc. Agron. 5: 117–118.

McROSTIE, G. P., and J. D. MacLACHLAN (1942). Hybrid corn studies, I. Scient. Agric. 22: 307–313.

MILLER, P. A., J. C. WILLIAMS JR., H. F. ROBINSON, and R. E. COMSTOCK (1958). Estimates of genotypic and environmental variances and covariances in upland cotton and their implications in selection. Agron. J. 50: 126–131.

MODE, C. J., and H. F. ROBINSON (1959). Pleiotropism and the genetic variance and covariance. Biometrics 15: 518–537.

MORTIMORE, C. G., and G. M. WARD (1964). Root and stalk rot of corn in southwestern Ontario, III. Sugar levels as a measure of plant vigor and resistance. Can. J. Pl. Sci. 44: 451–457.

MüHLING, H.-G. (1963). Zur Stoffbildung und Stoffspeicherung bei Mais. Z. Acker. Pflanz. 116: 129–153.

MURTY, G. S., and N. N. ROY (1957). Study of the Indian collection of maize varieties with special reference to relationship between yield and other characters. Indian J. Genet. Pl. Breed. 17: 73–86.

MURTY, G. S., and M. V. PAVATE (1962). Studies on quantitative inheritance in *Nicotiana tabacum* L. I. Varietal classification and selection by multivariate analysis. Indian J. Genet. Pl. Breed. 22: 68–77.

MUSICK, G. J., M. L. FAIRCHILD, V. L. FERGASON, and M. S. ZUBER (1965). A method of measuring root volume in corn (*Zea mays* L.). Crop. Sci. 5: 601–602.

NANDA, D. N. (1949). The standard errors of discriminant function coefficients in plant-breeding experiments. J. R. Stat. Soc. Ser. B 11: 283–290.

NILSSON-LEISSNER, GUNNAR (1927). Relation of selfed strains of corn to F 1 crosses between them. J. Am. Soc. Agron. 19: 440–454.

NORDEN, A. J. (1966). Response of corn (*Zea mays* L.) to population, bed height, and genotype on poorly drained sandy soil II. Top growth and root relationships. Agron. J. 58: 299–302.

PANSE, V. G., and S. A. KHARGOKAR (1949). A discriminant function for selection of yield in cotton. From: Murty and Pavate (1962).

PARODA, R. S., and A. B. JOSHI (1970). Correlations, path-coefficients and the implication of discriminant functions for selection in wheat (*Triticum aestivum*). Heredity 25: 383–392.

PENDLETON, J. W., D. B. EGLI, and D. B. PETERS (1967). Response of *Zea mays* L. to a 'light rich' field environment. Agron. J. 59: 395–397.

PENDLETON, J. W., G. E. SMITH, S. R. WINTER, and T. J. JOHNSTON (1968). Field investigations of the relationship of leafangle in corn (*Zea mays* L.) to grain yield and apparent photosynthesis. Agron. J. 60: 422–424.

PESEK, J., and R. J. BAKER (1969a). Comparison of tandem and index selection in the modified pedigree method of breeding self-pollinated species. Can. J. Pl. Sci. 49: 773–782.

PESEK, J., and R. J. BAKER (1969b). Desired improvement in relation to selection indices. Can. J. Pl. Sci. 49: 803–804.

PESEK, J., and R. J. BAKER (1970). An application of index selection to the improvement of self-pollinated species. Can. J. Pl. Sci. 50: 267–276.

RASMUSON, MARIANNE (1964). Combined selection for two bristle characters in *Drosophila*. Hereditas 51: 231–256.

RICHEY, FREDERICK D. (1922). The experimental basis for the present status of corn breeding. J. Am. Soc. Agron. 14: 1–17.

ROBINSON, H. F., R. E. COMSTOCK, and P. H. HARVEY (1949). Estimates of heritability and the degree of dominance in corn. Agron. J. 41: 353–359.

ROBINSON, H. F., R. E. COMSTOCK, and P. H. HARVEY (1951). Genotypic and phenotypic correlations in corn and their implications in selection. Agron. J. 43: 282–287.

RUEBENBAUER, T., and S. WEGRZYN (1963). Die Bedeutung einfacher taxonomischer Methoden für die Pflanzenselektion. Züchter **33**: 167–168.

SAYRE, J. D. (1948). Mineral accumulation in corn. Pl. Physiol. **23**: 267–281.

SAYRE, J. D., V. H. MORRIS, and F. D. RICHEY (1931). The effect of preventing fruiting and of reducing the leafarea on the accumulation of sugars in the corn stem. J. Am. Soc. Agron. **23**: 751–753.

SCHULZE, J. (1962). Ein Vergleich zwischen erwartetem und erreichtem genetischen Fortschritt bei Anwendung des Selektionsindex. Biom. Z. **4**: 58–65.

SEN, B. K., and ALAN ROBERTSON (1964). An experimental examination of methods for the simultaneous selection of two characters, using *Drosophila melanogaster*. Genetics **50**: 199–209.

SHARMA, B. R., and V. SWARUP (1964). Correlation studies and the use of selection indices in the F 2 population of an intervarietal cross of cabbage. Indian J. Hort. **21**: 213–220.

SHARMA, D., V. P. GUPTA, and B. SINGH (1968). Index scoring in relation to combining ability of germplasm complexes in maize. Pl. Breed. Abstr. **39**: 2275.

SIKKA, S. M., and K. B. L. JAIN (1958). Correlation studies and the application of discriminant function in *aestivum* wheats for varietal selection under rainfed conditions. Indian J. Genet. Pl. Breed. **18**: 178–186.

SIMLOTE, K. M. (1947). An application of discriminant function for selection in *durum* wheats. Indian J. agric. Sci. **17**: 269–280.

SINGH, G. (1966). Study of local maize varieties with reference to relationship between yield and other characters. Indian J. Agron. **11**: 109–112.

SINGH, M. (1962). Cytoplasmic effects on agronomic characters in maize. Diss. Abstr. **23**: 2670.

SINGH, M. (1965). Cytoplasmic effects on some agronomic characters in backcross maize hybrids. Indian J. Genet. Pl. Breed. **25**: 198–207.

SINGH, T. P. (1970). Association between certain stalk traits related to lodging and grain yield in maize (*Zea mays* L.). Euphytica **19**: 394–397.

SINGH, T. P., M. S. ZUBER, and G. F. KRAUSE (1969). Relationship of certain stalk characters with grain yield in corn (*Zea mays* L.). Crop Sci. **9**: 265–267.

SMITH, H. FAIRFIELD (1936). A discriminant function for plant selection. Ann. Eugen. **7**: 240–250.

SNEDECOR, GEORGE W. and WILLIAM G. COCHRAN (1967). Statistical methods. 6th. ed. Iowa State Univ. Press, Ames, Iowa p. 381–418.

SNELL, ROBERT S. (1966). Simple apparatus for measuring resistance to root lodging in sweet corn. Agron. J. **58**: 362.

SPRAGUE, G. F. (1952). Early testing and recurrent selection. In: J. W. Gowen (ed.) Heterosis. Iowa State College Press, Ames, Iowa. p. 400–417.

SPRAGUE, G. F. (1955). Corn breeding. In: George F. Sprague (ed.). Corn and corn improvement. Academic Press Inc. New York. p. 221–292.

SPRAGUE, G. F. (1966). Quantitative genetics in plant improvement. In: Kenneth J. Frey (ed.) Plant Breeding. Iowa State Univ. Press, Ames, Iowa. p. 315–347.

SPRAGUE, G. F., and W. T. FEDERER (1951). A comparison of variance components in corn yield trials: II. Error, year x variety, location x variety, and variety components. Agron. J. **43**: 535–541.

STRUBE, H. G. (1967). Merkmalskorrelationen bei Hybrid Mais und ihre Bedeutung für die Selektion. Diss. Landw. Hochsch. Hohenheim. 61 p.

STUBER, C. W., R. H. MOLL, and W. D. HANSON (1966). Genetic variances and interrelationships of six traits in a hybrid population of *Zea mays* L. Crop Sci. **6**: 455–458.

SWARUP, V., and D. S. CHAUGALE (1962). Studies on genetic variability in Sorghum, II. Correlation of some important quantitative characters contributing towards yield and application of some selection indices for varietal selection. Indian J. Genet. Pl. Breed. **22**: 37–44.

TANG, W.-T. (1963). (Studies on a selection index for hybrid progenies of soyabean). Pl. Breed. Abstr. **33**: 5305.

THOMPSON, B. W. (1965). The climate of Africa. Oxford Univ. Press. Nairobi, London, New York.

THOMPSON, D. L. (1963). Stalk strength of corn as measured by crushing strength and rind thickness. Crop. Sci. 3: 323–329.

THOMPSON, D. L. (1964). Comparative strength of corn stalk internodes. Crop Sci. 4: 384–386.

THOMPSON, D. L. (1970). Specific gravity of corn stem sections. Crop Sci. 10: 15–17.

TORREGROZA, M., and D. D. HARPSTEAD (1967). Effects of mass selection for ears per plant in maize. Agron. Abstr. p. 20.

VAIDYA, S. M., et al. (1962). A new lodging index for the use of maize breeders. Curr. Sci. 32: 28–29.

VAN REEN, ROBERT, and W. RALPH SINGLETON (1952). Sucrose content in the stalks of maize inbreds. Agron. J. 44: 610–614.

WALLACE, A. T., G. K. MIDDLETON, R. E. COMSTOCK, and H. F. ROBINSON (1954). Genotypic variances and covariances of six quantitative characters in oats. Agron. J. 46: 484–488.

WEILING, F. (1964). Ueber Bedeutung und Handhabung der multiplen Regressionsanalyse bei der Untersuchung von Zusammenhängen im biologischen Bereich. Biom. Z. 6: 24–36.

WELLHAUSEN, E. J. (1965). Exotic germ plasm for improvement of cornbelt maize. Proc. 20th ann. Hybrid Corn Ind. Conf. p. 31–45.

WILLIAMS, J. C., L. H. PENNY, and G. F. SPRAGUE (1965). Full-sib and half-sib estimates of genetic variance in an open-pollinated variety of corn, Zea mays L. Crop Sci. 5: 125–129.

WILLIAMS, J. S. (1962). Some statistical properties of a genetic selection index. Biometrika 49: 325–337.

WILSON, H. K. (1930). Plant characters as indices in relation to the ability of corn strains to withstand lodging. J. Am. Soc. Agron. 22: 453–458.

YOUNG, S. S. Y. (1961). A further examination of the relative efficiency of three methods of selection for genetic gains under less restricted conditions. Genet. Res. 2: 106–121.

YOUNG, S. S. Y., and H. WEILER (1961). Selection for two correlated traits by independent culling levels. J. Genet. 57: 329–338.

ZUBER, M. S., and C. O. GROGAN (1961). A new technique for measuring stalk strength in corn. Crop Sci. 1: 378–380.

ZUBER, M. S., and P. J. LOESCH JR. (1966). Effects of years and locations on stalk strength in corn (Zea mays L.). Agron. J. 58: 173–175.