GENETIC VARIABILITY AND RESPONSES TO SELECTION FOR THE SPOTTED STEM BORER, *Chilo partellus* (Swinhoe) RESISTANCE IN A MAIZE (*Zea mays* L.) POPULATION

BY

CHARLES J. M. MUTINDA.

A THESIS SUBMITTED IN FULL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

DEPARTMENT OF CROP SCIENCE.
UNIVERSITY OF NAIROBI.

1996

Declaration

This thesis is my original work and has not been presented for any other degree in any other University.

Signature________________ Date 18/7/96

CHARLES JOHN MASAKU MUTINDA

This thesis has been submitted for examination with my approval as the principal University supervisor

Signature________________ Date 18/7/96

DR. P.O. AYIECHO

Department of Crop science

And with my aproval as the resident supervisor in the African Regional Post graduate Programme in Insect Science (ARPPIS)

Signature________________ Date 20/9/97

DR. S.O. Ajala

International Centre of Insect Physiology and Ecology (ICIPE)

Dedication

This thesis is dedicated to my parents. Their love and counselling profoundly inspired me.

Acknowledgements

I acknowledge with appreciation and sincere gratitude the contributions of many people to this piece of work. Particularly, Dr. S.O. Ajala whose relentless effort shaped my interest and knowledge in plant breeding. His critisms, patience and understanding contributed immensely to the final form of this report. No doubt it was learning and working at the master's foot until he left the thesis in my hands.

Dr. P.O. Ayiecho, my principal university supervisor visited most of the research fields and critically evaluated my experimental plots. Indeed it is an honour to have had him on the supervisory committee. His guidance in the writing of the thesis is highly appreciated.

Dr. A. Odulaja served on the committee as a biometrician . His statistical knowledge further helped shape the thesis. The thesis would not have been complete without the contribution of Professor K.N. Saxena whose expertise in host plant resistance helped in the final format of the manuscript.

The international Centre of Insect Physiology and Ecology (ICIPE) provided the funding and facilities for the research work whilst the Director, KARI granted the study leave. My appreciation for the support.

Nicholas Odongo of KARI-Muguga helped in formating, printing and proof reading of the manuscript.

My parents, brothers and sisters accepted my long stay away from home with patient endurance.

Finally and nonetheless the least, the piece of work would not have been a success without the very understanding and patience of my dear wife, Cyndy and sons John and Kelvin whose support and encouragement were an inspiration.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF APPENDICES

ABSTRACT

The major objectives of this study were to determine genetic variability for parameters of resistance to C. Partellus and other desired agronomic traits, construct and test appropriate selection procedures, and estimate heritabilities, predict both direct and correlated responses to selection. The study involved a white grained parental population named ICZ3 from which 163 S_2 lines and 150 S_2 testcrosses were obtained and evaluated according to the study objectives so far stated.

Genetic variability and predicted responses to S_2 and S_2 testcross selection methods were studied in the ICZ3 population. Evaluation of progress after one cycle of selection for grain yield, parameters of resistance to *Chilo partellus* and agronomic traits were investigated.

The results of determining the genetic variability for each of the three parameters of resistance (leaf feeding, dead heart and stem tunnelling) and grain yield in each progeny type revealed high levels of variability for effective selection to be practised. Using a 9 - point rating scale for leaf feeding, populations derived from S_2 and testcross progenies showed a difference of 5.00-6.33 and 5.00- 6.17, 3.14%-3.29% and 2.56%-3.14% for dead heart, 27.97%-28.52% and 19.46%-23.92% for stem tunnelling and 5.65-11.10 and 7.85-8.60 t/ha for grain yield for S_2 and testcross progenies, respectively. After one cycle of selection the S_2 and testcross progenies exhibited a reduction in leaf damage rating of 0.01-0.11 and 0.05-0.08 per cycle corresponding to a decrease of 0.40%-4.38% and 1.99%-3.19% per cycle relative to the source population (C_0) respectively. Stem tunnel length decreased by 0.15%- 1.81 % per cycle in S_2 progenies and 0.13%-1.76% per cycle in the test cross hybrids corresponding to 1.15% - 13.92% and 1.00% - 13.54% per cycle relative to C_0. Grain yield increased by 5.29% to 24.23% per cycle and plant height by 4% per cycle of selection.

Genetic variances and heritability estimates were moderate to high for the S_2 progenies with the heritability estimates being higher for the agronomic traits compared to the resistance parameters.

Predicted direct response for grain yield, parameters of resistance and rank summation index were generally higher in the S_2 selections as opposed to the test crosses. Generally more gain/cycle of selection was achieved through single trait selections than by index selection.

Predicted correlated response in grain yield assuming selection was done for the parameters of resistance were smaller than predicted direct responses to selection for grain yield.

In all cases, there was poor correspondence between predicted and observed gains to selection.

A breeding procedure involving recurrent selection for parameters of resistance (leaf feeding, dead heart and stem tunnelling) and selection indices should aid in combining C. Partellus resistance with desirable agronomic traits.

CHAPTER 1

1.0 INTRODUCTION

Maize (Zea mays L.) is the third most important cereal crop in the world after wheat (Triticum aestivum L.) and rice (Oryza sativa L.) (FAO, 1991). In Kenya, it is the single most important food crop; being the only cereal crop that is grown in every part of the country - from areas of low agricultural potential to those endowed with high agricultural potential. Apart from being the staple food crop, it is also important in the production of livestock feeds. But despite its significance as a major cereal crop its yields are low due to a number of factors which include, amongst a host of other problems, environmental hazards caused by insufficient rainfall, poor soil conditions and presence of obnoxious weeds such as Striga spp. Other factors include low levels of inputs due to limited availability of resources for the majority of the small scale farmers, diseases and insect pests.

The most important maize disease in Kenya is maize streak (Theuri et al, 1988) which is caused by maize streak virus (MSV) and transmitted by leaf hoppers of the genus Cicadulina. As for the insect pests, stem borers constitute the most important field insect pests of maize in Africa. The most important species are the pink stalk borer, (Sesamia calamistis Hmps), the African sugar cane borer,(Eldana saccharina Walker), the maize stalk borer, (Busseola fusca Fuller) and the spotted stalk borer, (Chilo partellus Swinhoe) (Bosque-Perez et al, 1987). In the Kenyan lowlands, C. partellus is the most important (Walker, 1967; Warui and Kuria, 1983; Overholt, 1991). Losses in maize yield due to

Chilo *spp* stem borer damage range from 18% in Kenya (Walker, 1967; Warui and Kuria 1983) to 44% in Pakistan (Mohyuddin and Attique 1978).

The attack of *C. partellus* on the plants begins with the laying of its eggs on the leaves. The eggs hatch into neonate first instar larvae which move into the leaf whorls where they feed and develop on the bases of the leaves, causing lesions. The larvae then develop to the late third or early fourth instar, bore into the stem, feeding on the tissues and making tunnels. As a result of the larvae feeding within the leaf whorl or stem, the meristematic tissues are cut through and the central leaves dry up to produce the "dead heart" symptom and the plant dies. The three damage parameters, namely, leaf feeding, dead heart and stem tunnelling, lead to grain yield loss. A number of studies have been reported which give information on the resistance levels of some genotypes that are resistant to *C. partellus* that can be used in the management of the pest (Omolo, 1983; Ampofo and Saxena, 1984; Ampofo et al, 1986a and b; ICIPE, 1991; Ajala and Saxena, 1994). Furthermore it is known that genotype by damage parameter interaction exists such that a genotype may be highly resistant to leaf feeding but less to the stem tunnelling and vice versa (Ampofo et al, 1986b). Therefore commensurate improvement in each of the damage parameters is necessary to achieve an overall improvement in resistance levels.

Inheritance studies on parameters of maize resistance to the spotted stem borer have shown resistance to be quantitative (polygenic) and preponderately additive (Pathak and Othieno, 1990; Ajala, 1992a). Recurrent selection, a breeding procedure involving the identification and recombination of superior genotypes in a population to form a new but improved population from which further selection can be practiced, is a method of increasing frequency of favourable alleles for quantitatively inherited traits. Appropriate recurrent selection schemes that utilize more of additive gene action e.g. S_1, S_2 or their test crosses selection procedures can therefore be used to effectively improve on levels of resistance to *C. partellus* attack.

This study was undertaken with the main objective of simultaneously improving on the level of resistance to the *C. partellus* attack, grain yield and desirable agronomic traits using appropriate selection parameters or aggregate traits in identified progeny from a maize population, ICZ3.

Specific objectives for the study were to :

(a) determine the genetic variability for parameters of resistance to *C. partellus* and other desired agronomic traits.

(b) construct and test appropriate selection indices that combine *C. partellus* resistance with desirable agronomic traits.

(c) estimate heritabilities, predict both direct and correlated responses to selection.

CHAPTER 2

2.0 LITERATURE REVIEW

2.1 Insect pest-host plant resistance.

Host plant resistance is an important component of integrated pest management schemes in crop production (Kumar et al, 1993). However, the ease of insect control by the use of insecticides has often superseded the study of host plant resistance to insects. Painter (1951) defined resistance of plants to insects as the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect. Resistance in plants therefore represents the ability of a certain variety to produce a larger crop of good quality than ordinary varieties at the same level of insect population.

The mechanisms of plant resistance to insects have been well documented by Painter (1951). He outlined and described three main components of resistance: preference or non-preference (otherwise called antixenosis), antibiosis and tolerance.

Preference and/or non-preference refers to the ability of host plant to attract or discourage the feeding, colonization or oviposition of an insect pest. This may be attributable to morphological, physiological or biochemical factors in the host plant. Wiseman (1987) reported that resistance of maize to the corn earworm (CEW), *Heliothis zea* (Boddie), was associated with the structure of the silk. He noted that the preferred oviposition site for the females was the fresh silks. When large quantities of succulent silks were present the larva could complete its life cycle in the silk channel without inflicting damage for the developing channels as opposed to loose insufficient silks. Size, shape and colour of plants have also been observed to contribute immensely to the degree of non-preference shown by insect pests. For instance, the boll weevil (Anthonomus grandis) has a marked preference for cotton plants with green foliage to those with red ones (Isley, 1928). In maize the adult moths of the corn earworm (CEW) showed a general preference for taller plants to shorter ones. Whilst stem hardiness contributed to reduction in insect infestation (Wiseman, 1987).

Preference or non-preference type of resistance is sometimes due to biochemical compounds which attract or repel the insects. Visser and Minks (1982) reported a potent factor in carrot which influences the attractiveness of the carrot fly (Psila rosae) for ovipositional stimulant as trans-methyliso-eugenol. Whilst in cucumber, cucurbitacin is responsible for resistance to the two spotted spider mite (Tetranychus urticae). Thus various behavioural stimuli would contribute to non-preference types of pest resistance.

Antibiosis includes all adverse effects exerted by the plant on the insect's biology such as survival, development and reproduction. Brazzel and Martin (1956) studied the number of eggs laid by the pink bollworm on Gossypium thurberi in comparison with the number laid on the susceptible cotton species Gossypium hirsutum. When the two kinds of plants were confined together in the same cage, 79 percent of the bolls of the resistant variety were without eggs compared to 53 percent when the same variety was alone in the cage. Such could be attributed to the presence of chemical senses in host selection. Antibiosis type of resistance may be due to insufficient supply of nutritional requirements. Mize and

Wilde (1986) reported antibiosis resistance in sorghum breeding lines which adversely affected development rate and adult size of chinch bugs (Blissus leucopterus leucopterus Say). In maize, Davis and Williams (1986) observed significant reduction in the survival, growth and development rates of the south west corn borer (SWCB). These adverse effects on the insect biology indicate that antibiosis is a mechanism operating within the resistant plants.

Tolerance is the ability of the plant to withstand infestation and support insect populations that would severely damage those that are susceptible. It can be conditioned by increased vigour of the plant, ability to repair damaged tissues and or the ability to metabolize toxic substances produced by the pest into non-toxic compounds. Olonju Dixon et al (1990) noted that crosses between resistant and susceptible lines of sorghum had increased levels of tolerance to the green bug biotype. E. More recently, Ajala et al (1993) reported mid-parent heterosis associated with leaf feeding and stem tunnelling damage parameters for Chilo partellus in some maize crosses. Ability to replace or repair of damaged tissues was observed by Coon (1946) in soybean varieties resistant to the Japanese beetle.

Normally resistant cultivars do possess combinations and/or varying levels of resistance mechanisms. Thus, a cultivar that is non-preferred does not require the same level of antibiosis or tolerance that a more preferred cultivar must possess. Therefore different cultivars may possess the same level of resistance with different mechanisms of resistance and levels of resistance components (Wiseman, 1985).

2.2 Inheritance of pest resistance.

Resistance to insect pests in plants is either qualitative (particulate) in which the genetic control is under the influence of a few genes, or quantitative, that is conferred by several genes each with smaller individual effects. Therefore development of an efficient resistance breeding programme requires a thorough understanding of the inheritance pattern of the traits under consideration (Penny and Dicke, 1956).

Most expressions of the qualitative type of inheritance follows a gene-for-gene relationship, that is, for each gene conferring the specific resistance in the host there is also a specific and "matching" gene in the pest, which when present gives it the ability to overcome the resistance (Kim, 1992). This gene in the pest is known as virulence gene. In a plant with race-specific expression, this major gene controlled resistance is often called "vertical" resistance. Such type of resistance is easy to incorporate into susceptible lines or cultivars through conventional backcrossing programmes: for instance, resistance of barley to greenbug (Schizaphis graminum Rondani) (Merkle et al, 1987), improved rice to blast (Pyricularia oryzae), potato to late blight and cereal rusts and leaf blights (Kim, 1992).

Because of its simplicity and race-specificity, however, vertical resistance often breaks down with time as the virulent gene spreads in the pest population. Velnsammy et al (1987) reported the occurrence of a new biotype of the brown plant hopper (Nilaparvata lugens Stal) in rice fields. He observed that reduced genetic variability of a short-statured, high yielding cultivar coupled with continuous monocropping of the rice, use of high levels of nitrogenous fertilizers and insecticides induced brown hopper resurgence due to a biotype which had overcome the resistance. Obanni et al (1989) observed that despite this shortcoming, however, vertical resistance had been used to control Hessian fly (Mayetiola destructor Say) in durum wheat for more than 30 years through sequential release of cultivars with single genes for resistance to the emerging biotypes. Multiline cultivars may also be utilized. The approach was explored in breeding crown rust resistant cultivars (Browning and Frey, 1969). However, the use of such a technique is yet to be explored for the control of insect pests.

Quantitatively inherited insect pest resistance is not wide spread in literature. However, a few cases have been reported. Scott et al (1964) showed that in corn leaf feeding resistance to the European corn borer (ECB), Ostrinia nubilalis (Hubner), is polygenically controlled. Estimates obtained from analysis of F_3 and selfed backcrossed progenies indicated that most of the genetic variance observed was additive. Earlier reports had suggested qualitative inheritance (Penny and Dicke, 1956; 1957). These authors reported that resistance of leaf feeding to the pest was conditioned by 1 to 2 or 3 or more genetic factors depending on the source of resistance.

Other cases of quantitative inheritance have been reported in other crops: in common bean (Phaseolus vulgaris) resistance to the leafhopper (Empoasca kraemeri Ross and Moore) Kornegay and Temple (1986) is quantitative. In sorghum non-preference resistance to shootfly (Antherigona soccata Rondani) is also quantitatively inherited and mainly governed by additive genes (Rao et al, 1974).

Quantitatively inherited resistance is called horizontal, general or nonspecific resistance (Maxwell and Jennings, 1980). Unlike the vertical resistance which offers protection against a particular biotype of an insect pest, horizontal resistance protects the crop against all the known biotypes of a given pest. Kim (1992) argues that it is more difficult for a pest to overcome a number of minor genes, rather than a single major gene since polygenes by their number and complexity would offer a far greater challenge to the pest attempting to overcome them. Thus, rather than aiming at eliminating the pest with a dominant gene, which has the side-effect of challenging it into evolving a new biotype in order to survive, polygenic resistance attempts to defuse the situation by allowing a small number of the pest to survive at levels that do not cause economic damage.

There are relatively few reports of comprehensive studies on the inheritance of the resistance to stem borers. The information available is either contradictory or inconclusive (Ortega et al, 1980). Whereas resistance to the European corn borer and south western corn borer is quantitatively inherited (Brindley and Dicke, 1963; Scott et al, 1964; 1967; Onukogu et al, 1978; Williams et al 1989), that of the first brood generation is quite independent of the second brood (Brindley et al, 1975; Gallun et al, 1975; Williams and Davis, 1983). Most genes that condition resistance to leaf feeding by first generation corn borers do not have an important role in controlling the resistance to sheath collar feeding by second generation broods.

Studies reporting inheritance of resistance to the spotted stem borer, Chilo partellus, are also very few and inconclusive. A recent review by Guthrie (1989) indicated resistance to be multigenic with both additive and non-additive genes being involved. Recent studies at the International Centre of Insect Physiology and Ecology (ICIPE) on resistance to this pest, however showed that the resistance is quantitative with a preponderance of additive gene action (Pathak and Othieno, 1990; Ajala, 1992a). It was observed that resistance to parameters of resistance namely, leaf feeding, stem tunnelling and dead hearts were generally additive with some non-additive gene control for the stem tunnelling.

Since gene action conditioning resistance to stem borers in maize is predominantly additive (Ortega, et al, 1980) and that polygenic resistance is more durable for sustainable crop production, then recurrent selection schemes would be appropriate in accumulating desirable genes for resistance (Kim, 1992).

2.3. Recurrent Selection Schemes

Quantitative traits, such as grain yield and resistance to insects which are conditioned by large number of genes whose effects can not be individually classified, are improved through recurrent selection schemes (Hull, 1945), Change in gene and genotypic frequencies being the consequence of such traits. These result in changes in means and variances during selection (Hallauer and Miranda, 1988). Thus, selection within a population is aimed at improving the population *per se* and this is accomplished by increasing the frequency of favourable alleles within the population.

Generally recurrent selection involves the selection of plants with superior phenotypes in the breeding population and intermating the selected individuals to form a new but improved population which serves as source material from which further selections can be made. Population improvement schemes can be categorized as Intra-population selection methods and inter-population or reciprocal selection methods. The first is aimed at the improvement of the population <u>per se</u> whereas the last two are for the improvement of the interpopulation cross or the hybrids of inbred lines to be extracted from two reciprocally selected populations. Inter-population improvement was stimulated by the expression of heterosis (Hallauer <u>et al</u>, 1988).

There are two types of selection procedures under recurrent selection, namely, Mass selection and family selection. The major difference between the two types being that in family selection some type of progeny testing is carried out such that plant genotypes are evaluated on the basis of the average performance of their progeny whilst in mass selection, individual plants selected are also the ones recombined to form another cycle of improvement. In family selection, however, the recombined plants for the proceeding cycle of selection are the parents of the best progenies after evaluation. Thus, in family selection, the selection unit is different from the recombination unit unlike the situation in mass (phenotypic) selection.

Types of family selection methods include selfed family selection, full-sib family selection, half-sib family selection, and combined family selection procedures. In selfed family selection method, S_1 or S_2 progenies are evaluated to determine superior genotypes and the remnant seed of the selected progenies are recombined to produce a new base population for further improvement. Full-sib family selection, unlike the selfed family procedure, involves evaluation of crosses in which each of the progenies have the two parents in common. Progenies are produced by crossing two S_0 plants from the same population. Remnant seed of the selected progenies or their selfed progenies are recombined. In the half-sib family selection the progenies to be evaluated have only one of the two parents in common. Another form of half-sib family selection is test-cross selection. The procedure is used either to evaluate combining ability of inbred lines to be used in hybrid combinations or to evaluate the breeding values of plants for population improvement. In both cases, there is need for a tester in order to identify superior genotypes to meet the objective of selection. A combination of two or more selection methods in the same programme is also feasible.

Often the choice of the best tester is obscure. For inbred evaluation, a desirable tester was defined by Matzinger (1953) as one that combines the greatest simplicity in use with the maximum information on performance to be expected from tested lines when used in other combinations or grown in other environments. Rawlings and Thomson (1962) defined a good tester as one that classifies correctly relative performance of lines and descriminates efficiently among lines under test. For improvement of breeding populations, Allison and Curnow (1966) noted that a good tester must maximize the expected mean yield of the population produced from random mating of selected genotypes. It was recognized, however that no single tester can completely fulfill all of the criteria in the above definitions. It was therefore concluded that the choice of a tester should be determined to a considerable extent by the expected use for a particular group of lines. If these are destined as replacements for lines in existing hybrid combinations, the tester chosen will certainly differ from that selected if the lines are to be screened for average performance to be tested in new combinations. Matzinger (1953) opined that for inbred lines to be used as replacement for an existing line in a certain combination, specific combining ability is of prime importance and the most appropriate tester would be the opposite single cross parent of the double cross or its component inbred lines and that ranking of lines with respect to general combining ability can be accomplished most economically through use of a tester having a broad genetic base. Hallauer and Miranda (1981) concluded from an extensive review of literature that the choice of a tester on the basis of its performance depends largely on chance. They favoured the use of the parental variety as tester in intra-population improvement schemes because only such a case would ensure that high frequency of recessive allele in the tester is associated with high frequency of recessive allele in the material being tested.

Several intra-population recurrent selection methods have been explored for the improvement of breeding populations. However, methods which are effective for improving one population may not be effective for another (Lonnquist, 1968; Burton et al, 1971). Also, different selection methods have shown differences in effectiveness when utilized in the improvement of the same population. Penny et al, (1967) reported on three cycles of S_1 recurrent selection for resistance to first brood European corn borer (Ostrinia nubilalis, Hubner). Progress from selection was measured from the original (C_o) and third cycle (C_3) of selection on five populations. Based on a rating of 1 (resistant) to 9 (susceptible), the procedure improved the mean rating for the five populations from 5.5 in C_o to 2.5 in C_3 (Frey, 1981). More recently, Widstrom (1992) observed significant reduction in damage to leaf feeding by Fall Armyworm on maize after five cycles of S_1 recurrent selection.

Family selection methods have also been employed in improving grain yield and agronomic traits of several maize populations. Burton et al (1971) observed increase of 4.1% per cycle whilst Lonnquist (1968) reported an increase of 15% after four cycles of S_1 test-cross selection. Hoard and Crosbie (1985) observed that five cycles of S_1 recurrent selection for improved cold tolerance in two maize populations, BS13 (SCT) and BSSS2 (SCT), resulted in significant genetic gains; 2.1% and 0.04g per cycle for percent emergence and seedling dry weight respectively. It was therefore concluded that S_1 recurrent selection could effectively increase and/or change allelic frequencies at different loci (Hoard and Crosbie, 1985; Walters et al, 1991). This however, requires the existence of genetic variability in the population under improvement. Cyclical selection procedures are imposed on populations in order to increase the frequency of favourable alleles for the selected traits (Hallauer, 1981).

2.4 Genetic variability and heritability.

Quantitative characterization of variability in plant populations is a prerequisite for designing an effective breeding programme. The choice of the breeding method to be used in the improvement of a particular trait depends on the mean and magnitude of genetic variation present in the population. Observable differences among individuals in a population can be quantified as phenotypic variance which includes both genetic (hereditary) variance and environmental variance plus the interaction between these two components (Falconer, 1960). For purposes of describing the various types of gene action, genetic variation can be partitioned into two broad-based coomponents, the additive and non-additive variances. The former is due to average effects of genes and is also termed variance of breeding value. It reflects the degree to which progenies are likely to resemble their parents. The larger the additive variance the more the phenotype approximates the genotype and the more the progress expected from selection. Furthermore, additive genetic variance can be used in obtaining reliable estimates of heritability and progress from selection. The non-additive genetic component, on the other hand, consists of the dominance and epistatic variances; dominance variance being occasioned by the occurrence of interaction of average effects of alleles at the same locus whereas epistatic variance is due to interaction of additive and/or dominance effects of two or more loci.

In both evolution and in plant breeding, populations are constantly being sifted for superior types. In this continual sifting, the primary force is selection, in which individuals with certain characteristics are favoured in reproduction.

Allard (1960) stipulated that in selection two attributes are important to the understanding of breeding principles, namely, that selection can act effectively only on heritable differences and that selection does not create variability but acts only on that which is already in existence. It is in connection with the second attribute that inbreeding assumes importance in plant improvement for it causes an increase in homozygosity. Such effect is deemed to affect all loci, so that quantitatively inherited characters as well as those determined by major genes are subject to its influence. The effect of sufficiently long and intense inbreeding is therefore the fixation of genetic characters, i.e, separation of the population into genetically distinct groups each uniform within itself. Thus, inbreeding which is the mating of closely related parents, uncovers genetic variability concealed in heterozygotes for selection to act upon. The converse, outbreeding, is those matings involving individuals not so closely related.

Pathak and Othieno (1990) studied the types and magnitude of gene action for resistance to both leaf feeding and stem tunnelling in maize to C. partellus. Estimates of additive variance for parameters of resistance were considerately larger than those of dominance variance. Ajala (1990) in a separate study also observed the presence of substantial amount of additive genetic variance. Resistance to both leaf feeding and stem tunnelling was predominantly additive, non-additive variance being important for stem tunnelling.

Widstrom et al (1992) used S_1 recurrent selection to improve resistance in maize synthetics to leaf feeding by larvae of the European Corn Borer (Ostrinia nubilalis Hubner).

Analyses of variance of S_1 progenies indicated the presence of significant genetic variation for resistance to the larval feeding by the pest within each cycle. He observed genetic variance of 0.08 ± 0.018 in C_0 which increased to 0.36 ± 0.049 in C_3. This was attributed probably to genetic recombination in later cycles, thus, generating additional genetic variance. In sorghum, Olunju Dixon et al (1990) reported significant general combining ability (GCA), specific combining ability (SCA), maternal and specific reciprocal effects among inbred lines for resistance to Greenbug Biotype E. General combining ability was more significant in determining both antibiosis and tolerance. The significant maternal and specific reciprocal differences found among parents and crosses suggested that the variation observed was not only due to direct genetic effects but also highly influenced by maternal and cytoplasmic inheritance or their interactions.

In maize, Obilana et al (1979) estimated the genetic variability for grain yield and agronomic traits in a variety cross (inter-population) (BS10 and BS11) and showed that additive variance was of greatest importance (accounting for 75% or more of the genetic variability). He reported genetic variances of 167 ± 39 (Ear length), 399 ± 95 (ear diameter), 226 ± 51 (Kernel depth) and 248 ± 59 (days to silk), 218 ± 47 (Ear height), 1410 ± 384 (tiller length) for grain yield and agronomic traits respectively. Ajala (1992b) evaluated S_2 lines from three maize populations (TZSR-Y1, DMR-LSRY and EV 8443 SR) for emergence index (EI), a measure of seedling index, days to 50% silking, number of standing plants at harvest and grain yield. Means and ranges, from an analysis of variance, for each of the four traits in each population revealed significant levels of variability for effective selection to be practised. There was a difference of about two days for EI, 13 to 20 days for 50% S, 7 to 8 stands and 3.4 to 4.6 t/ha for yield.

Progress in breeding for economic characters that are quantitative in inheritance and therefore subject to environmental variability is determined by the nature and magnitude of the genetic variability. Such characters present difficulties in selection programmes since heritable variations are often masked by non-heritable variation. Hence the need to partition overall variability into heritable and non-heritable components with the aid of genetic parameters such as genotypic and phenotypic coefficients of variation. Ariyo (1989) studied variation in fifteen characters of Okra (*Abelmoschus esculentus* (L.) Moench). The wide range of variability exhibited by all lines for most of the characters measured was a reflection of their diverse eco-geographical backgrounds suggesting that the traits in the study were influenced more by environment than by their genetic constitution.

Adeyemo (1986) studied the genetic variability in an open-pollinated maize variety, TZSR-Y1 using full-sib (FS), half-sib (HS), S_1 and S_1 testcross (TCH) selection methods. Grain yield ranged from 3.4 to 9.2 t/ha for the FS, 2.9 to 7.5 t/ha for HS, 1.75 to 8.0 t/ha for S_1 and 3.2 to 8.8 t/ha for TCH. Genetic variances were equally large, suggesting that there was sufficient genetic variability for selection to occur. Partitioning of this variability so observed showed that the additive genetic variance was the most important component for both grain yield and agronomic traits. Studies elsewhere have unravelled somaclonal variation. In grasses (Lolium temulentum, Lolium perene and Lolium multiflorum) Mutinda (1989) showed that somaclones derived from tissue culture could generate genetic variability for the improvement of such grasses.

Hallauer and Miranda (1981) reviewed the literature on the types of gene action that condition quantitative traits in maize and concluded that genetic variability of the quantitatively inherited traits such as grain yield and disease resistance is due largely to additive genetic effects. Although non-additive variance, i.e, dominance and epistasis, may exist, they are less important. Presence of significant amount of additive variance in maize populations would therefore indicate that progress would occur from intra-population selection programmes.

Differences that occur among individuals of a species in the expression of a particular trait, whether due to their genetic make up or the environmental effects, can be described in terms of the heritability concept. The concept and its estimates can also be useful in the selection of superior individuals from a germplasm pool and in the utilisation of the selected individuals to generate superior varieties. Generally, heritability is the proportion of the observed variability that is due to genetic causes expressed as a fraction of total phenotypic variation.

In biometrical terms, there are two types of heritability: broad and narrow sense heritability. In the broad sense heritability (BSH), the total genetic variation consists of both additive and non-additive genetic values expressed as a fraction of the total phenotypic variation.

Whilst in the narrow sense, heritability is estimated as the proportion of the total variability attributable to additive or due to the average effect of genes, that is, the ratio of the breeding value to the phenotypic variation (Falconer, 1960). Narrow sense heritability (NSH), therefore, determines the degree of resemblance between relatives and expresses its predictive advantage i.e the reliability of the phenotypic value as a measure of the breeding value. Since genes and not genotypes are transmitted from parent to the offspring, estimates of heritability in the narrow sense would be preffered to those in the broad sense for predictive purposes, particularly in selection programmes (Falconer, 1960). In those situations where the former can not be obtained, however, broad sense estimates provide useful approximations. The various basic methods for the computation of heritability estimates can be grouped into three: regression of offspring on parent (bo-p), which involves the regression of the mean value of a character in the progeny upon the value for the same character in the parent, variance components and usually obtained from analysis of variance (AOV) and recurrent selection experiments (Obilana and Fakorede, 1981).

Differences between heritability estimates obtained by different methods have been reported in the literature. Firstly, it should be pointed out that broad sense heritability estimates are generally larger than narrow sense heritability estimates. Therefore, any methods that do not separate non-additive from additive effects will usually bias H values upwards. In cases where the non-additive effect is relatively unimportant as in highly inbredlines, broad sense heritability may be very close to or even the same as narrow sense heritability.

Even when the same population is sampled, different methods of computation may give different estimates of heritability. Generally, regression of offsprings on parents tends to give lower values relative to variance component approach. Robinson, et al (1949) obtained heritability of 20.1% for yield in maize using variance component method while values of 15.5% and 9.5% were obtained for regression of offspring on male and female parents, respectively. Frey and Horner (1955) reported heritability estimates of 59% and 39% while using component of variance and regression methods respectively for yield in barley (*Hordeum vulgare* L.).

Generally, most of the traits of economic value such as grain yield and related traits in cereals have variable heritability values. For example, Robinson, et al (1949) obtained low heritability estimates for yield and ear traits but high values for plant and ear heights. Ajala (1992) reported broad heritability estimates (%) of 15.4, 10.92 and 5.25 for leaf feeding, stem tunnelling and tolerance resistant parameters for *C. partellus* in maize lines, respectively. These estimates were generally low, probably, due to large genotype by environment interaction and the levels of genetic diversity involved. However, narrow sense heritability estimates for leaf feeding was quite high (66.66%). It would therefore appear that heritability estimates are a property of not only the trait, genetic constitution of the population and the environmental conditions to which the individuals in the population are subjected, but also the method of computation.

2.5 Predicted and correlated responses to selection.

Usually recurrent selection procedures involve long generation intervals and require a lot of effort and resources. It is therefore necessary to predict progress from selection for the purposes of determining the extent to which a population is suitable for breeding work and comparison of different selection methods. Moll and Stubber (1974) and Hallauer and Miranda (1988) have demonstrated that estimation of expected progress from selection generally utilizes the regression approach. Thus with assumption that X is the selection unit for the identification of superior genotypes and W represents the improved population and that a linear relationship exists between X and W, then for each unit change in X, a response of bwx is expected in W.

Reports in literature show different findings in correspondence between observed and predicted responses to selection. Widstrom et al (1992) using S_1 selection for resistance to leaf feeding by Fall Armyworm on maize observed varied responses to selection from cycle to cycle. Response to selection was on average about two thirds as large as that predicted from estimated parameters. In maize, Moll and Robinson (1966) observed poor agreement between predicted and actual grain yield in C121 x Nc7 population, Jarvis and Indian chief varieties. Eckebil et al (1977) while working on three random-mating Sorghums NP3R, NP5R and NP7BR predicted genetic advances in grain yield of 16.6, 28.8 and 15.2 % respectively, which was in agreement with the actual yields obtained. Elsewhere, Silva and Lonnquist (1968) and more recently Schipper and Frey (1991) reported good correspondence between the predicted and actual responses to selection. The discrepancies so observed could be attributed to the presence of non-additive variation such as dominance and epistasis in the estimation of genetic variance (Widstrom et al, 1992). Another contributory factor for the differencies between the expected and realized responses to selection may be the inadequacy of the data to account for all the variation due to interaction of genotypes with the environment (G X E). It would, therefore, suggest that evaluations involving a large number of environments should show close agreement between predicted and actual response to selection. Also, agronomic selection and mated pairs of the same phenotype occuring more often than would by chance, technically referred to as assortative mating, in the recombination nurseries may contribute to poor agreement between predicted and realized gains.

Whereas several authors have advocated for S_1 family selection in preference to other forms of family selection (Bradshaw, 1983), the formula of the predicted response to S_1 family selection as proposed by Empig et al (1972) involves some non-additive (dominance) variance. Hence estimates of the predicted response to S_1 family selection from the genetic variance among S_1 family means as it is commonly done are deemed biased (Eckebil et al, 1977; Bradshaw, 1983). Perhaps this also, may be one of the causes of the discrepancies often observed between predicted and observed responses to S_1 family selection.

Bradshaw, 1983, therefore, proposed the use of covariance between S_1 and half-sib or S_1 and full-sib families in the prediction of response to selection in order to partition the genetic variance into its components. Bradshaw's proposal is yet to be validated from empirical results.

In breeding programmes, responses to selection are either direct or indirect (correlated responses) (Falconer, 1960; Fakorede and Mock, 1982). Such correlated changes are either genetic or environmental in origin. For instance, a positive environmental correlation would be expected between plant and ear heights. This is also true of the traits that are taken from the same or closely related individuals (Hallauer and Miranda, 1988). The genetic mechanisms that condition correlated responses are either pleiotropic or linkage disequilibrium. The former occurs when a gene influences the expressions of two or more traits, the latter being the phenomenon by which combinations are held together with tendency of being transmitted together. Predicted correlated responses are, therefore, of interest to plant breeders because they provide information on how the improvement of one trait influences other traits. Such information is useful in selecting for yield and other agronomic traits alongside the main effort of breeding for insect resistance, (Gardner, 1978).

Many experiments designed to evaluate various selection methods have concentrated on single traits. Correlated changes in other traits, however, have been studied in several selection programs. Moll and Robinson (1966) reported observed and expected responses to recurrent selection for grain yield in maize. They found good agreement between observed and expected correlated responses for number of ears per plant. Grain yield of a maize population increased at the rate of 6.3% per cycle through indirect selection for number of ears per plant (Lonnquist, 1967). Other studies of recurrent selection in maize (Harris et al, 1972; Russel et al, 1973; Horner et al, 1976 and Darrah et al, 1978) also demonstrated consistent positive associations between grain yield and number of ears per plant. Elsewhere, three cycles of recurrent selection for stalk rot resistance resulted in correlated responses for 11 other traits (Jinahyon and Russel, 1969). In this study, grain yield showed a positive correlated response with improved stalk-rot resistance.

Negative correlated responses to selection have also been observed. For example, Nyhus et al (1989) studied S_1 progenies derived from BSAA and BSBB maize populations for resistance to both first generation European Corn Borer (ECB) and Diplodia stalk rot (DSR). In their study, improvement in resistance to ECB and DSR was associated with considerable reductions in yield.

One way of simultaneously improving a number of quantitatively inherited traits in any breeding programme is through use of selection indices. Several workers (Smith, 1936; Hazel, 1943; Williams, 1962) have developed appropriate selection indices while Elston (1963) further improved on these by proposing weight free indices. More recently, Mulamba and Mock (1978) developed a parameter free index, the Rank Summation Index (RSI) to improve density tolerance in maize (Zea mays L). In their study three rank summation indices were developed to evaluate progress from selection in a maize population, Eto Blanco. Each index was based on several traits and was calculated by ranking family means for each trait included in the index and summing the rankings for the traits for each family. The first RSI-1 in Mulamba and Mock's (1978) study was constructed from rankings of family means for leaf orientation rating, leaf area per plant and pollen-shed-to-silking interval, all of which were measured at 50,000 plants/ha. RSI-2 and RSI-3 included the three parameters and grain yield at 50,000 and 80,000 plants per hactare respectively. The experiment involved 250 full-sib families grown in only one experiment. The three RSI's appeared to be nearly equal in effectiveness because 19 of the top 25 full-sib families selected by RSI-2 were also selected by RSI-1 and the 25 families selected by RSI-3 included 21 selected by RSI-1. It seems, therefore, that the three indices were highly correlated.

The use of selection indices for the improvement of quantitatively inherited traits is, therefore, important to plant breeders for they aid in the simultaneous selection of several desirable traits.

CHAPTER 3

3.0 MATERIALS AND METHODS

3.1 Maize genotype (parental population)

ICZ3 (IC-90-WI), a white grained early to medium maturity population whose development was initiated in 1990 was used for this study. To develop it crosses were made between MP704, a highly resistant maize inbred to *Chilo partellus* from Mississippi, U.S.A. and selections from MMV400 (Mount Makuru Variety 400 from Zambia), PR 7832, Katumani composite, V-37, and a few others (ICIPE, 1990). Seeds from selfed materials of the multiple cross were subsequently separated along colour lines and recombined by random mating to form two experimental varieties (EVS); EV-90-WI and EV-90-YI, white and yellow genotypes respectively. Three generations of random mating within each genotype culminated in the formation of two populations, IC90-WI and IC90-YI respectively. For purposes of availability of the genotypes to other users, they were later renamed ICZ3 and ICZ4; both being germplasm bases for further selection and improvement (Ajala, 1992; Ajala and Saxena, 1994). For this study ICZ3 was used mainly due to its colour which is white and thus more preferable to the farmers.

3.2 Progeny type development.

In the long rains (LR) of 1992, a total of 163 S_1 lines were obtained by selfing individual plants at random within ICZ3 maize population. The S_1 progenies were planted out in single-row plots of 1.5 m in the short rains (SR) of 1992 and selfed to generate S_2 progenies. Some seeds of the S_2 progenies were planted so as to make test-crosses to the parental population (serving as tester) during the off season (Dec

1992-March 1993) to obtain test-crosses. A total of 150 S_2 test-cross (S_2TCH) hybrids were obtained in this way.

3.3 Evaluations

3.3.1 **Determining genetic variability.**

The S_2 and S_2test-cross progenies from ICZ3 were evaluated for damage parameters (leaf feeding, dead hearts and stem tunnelling) caused by Chilo partellus and agronomic traits including grain yield in three locations during the long rains (LR) of 1993. The experimental locations were Mbita Point Field Station (MPFS) of the International Centre for Insect Physiology and Ecology (ICIPE), Ungoye (another field site of the ICIPE) and Matuga, in the Coast province of Kenya. Mbita Point Field Station has a bimodal rainfall distribution with two distinct peaks. The early season (long rains) starts from late March and ends in late September or early October; the late season (short rains) starts from late September or early October to December. It is situated on the shores of lake Victoria in Western Kenya (Latitude 0° 25'-0 ° 30' south, Longitude 34° 15' east and altitude. 1240 m). Ungoye is 35 km from Mbita Point Field Station with similar rainfall distribution pattern , and also situated along the lake region (latitude 0° 0'- 0° 1' south, longitude 34 ° 30' east. The third site, Matuga is in the coastal region of Kenya (latitude 4° - 5° south, longitude 39° east) and has a bimodal rainfall distribution similar to the afforementioned sites.

At each site a total of 144 S_2 lines and 140 S_2test-cross progenies were planted in two replicate experiments. The genotypes were grown in a randomized complete block design with single row plots. Each row was 5.0 m long but separated into two 2.25 m halves with a space of 0.5 m in the middle. Spacing was 0.75 m between rows and 0.25 m between hills. Each hill was planted with two plants but later thinned to one three weeks after germination to give a maximum of 10 plants/2.25 m row and a density of approximately 53,333 plants/ha. Cultural practices included ploughing and harrowing, weed control by hand weeding, twice or thrice as necessary during the season. In all plantings a minimum of 50kg/ha of DAP (fertilizer) was applied in each location. Each plant in one half of the row was artificially infested with a batch of C. partellus egg masses reared on artificial diet and containing about 40 eggs at the black-head stage at three weeks after emergence (3WAE).

3.3.2 **Data collection**

Data for the three resistance parameters namely, leaf feeding lesions, dead heart and stem tunnnelling were taken for each plant in both the infested and the uninfested control. The data on both leaf feeding lesions and dead hearts were obtained at 4 weeks after infestation (4WAI). Leaf feeding was scored for each plant on a scale of 1 = resistant (no visible damage) to 9 = susceptible (severe damage). A general description of the visual leaf feeding scoring scale is given in the following summary (Guthrie et al 1960):-

Score 1. No visible leaf damage or small amount of short-hole type of damage on a few leaves.

Score 2. Small amount of short-hole type lesions on a few leaves.

Score 3. Short-hole damage common on several leaves.

Score 4. Several leaves with short-hole and elongated lesions.
Score 5. Several leaves with elongated lesions.
Score 6. Several leaves with elongated lesions (about 0.4cm)
Score 7. Long lesions common on about one-half of the leaves
Score 8. Long lesions common on about two-thirds of the leaves
Score 9. Most of the leaves with long lesions.

Data on dead hearts were obtained as absolute counts of plants showing the symptom in a plot expressed (In percentage) as a proportion of the number of plants per plot. Stem tunnelling was estimated at harvest by splitting each plant longitudinally to measure the stem length tunnnelled and this was expressed as a proportion of the plant height. Data were taken for six plants in a row of ten plants per plot.

Days from the date of planting to the dates when 1st plant and 50% of the plants in a plot showed tassel emergence, pollen shedding and silk extrusion were recorded.

The heights from the soil surface to the nodes bearing the flag leaf and the top ear were obtained for six random plants in a plot and their means were expressed as plant and ear heights respectively. At harvest, the number of standing plants per plot was recorded. All the ears from each plot were weighed separately to obtain the field weight (FWT) and grain weight (GWT) was estimated as 80% shelling percentage. Ear length (EL) was estimated as the length of five shelled ears in each plot. Some of the grain was put in a moisture meter to determine the moisture content expressed as a percentage (M%). Grain yield per plot was adjusted to 13% moisture content and converted to tonnes per hactare.

Yield reduction was calculated as the difference between the yield of uninfested control and the infested.

3.3.3 **Selection indices:**

Two rank summation indices (RSI) were constructed to determine the ranking of each line within the population for suitable response. The first index (RSI-1) was obtained by ranking the means of each leaf feeding (LF), dead hearts (DH) and stem tunnelling (ST) for each line, summing the ranking of the line to obtain its aggregate performance when compared with other lines within the same population. A second RSI (RSI-2) was obtained using the three traits and grain yield. Rank summation index (Mulamba and Mock, 1978) was summed as follows:

RSI = Ri's

Where R is the rank of the mean of each of the desired traits.

RSI-1 = Aggregate performance of a genotype using the rankings of leaf feeding, dead heart and stem tunnelling.

RSI-2 = Aggregate performance of a genotype based on ranked means of leaf feeding, deadheart, stem tunnelling and grain yield.

The Smith-Hazel index, I= $b_i x_i$ where i= is the rank of the genotype, x = the phenotypic value for each of the resistance parameters and the grain yield was used as an appropriate selection index. The index coefficient (b) was obtained by solving the equation $b_i = ((x_{ij})^{-1} (g_{ij}) (a_i))$, where x_{ij} and g_{ij} are variance-covariance matrices of the phenotypic and genotypic values respectively for the traits. Two indices were constructed. One based on leaf feeding, dead heart and stem tunnelling and another on the three parameters of resistance and grain yield. Economic weights (a_i) were determined for the calculation of the index coefficients for leaf feeding, dead hearts, stem tunnelling and grain yield (Smith, H.F. (1936) ; Hazel, L.N. (1943)).

Based on this evaluation the best 10% of the genotypes, based on the single trait selections (leaf feeding, dead heart, stem tunnelling and grain yield) in addition to the two rank summation and Smith-Hazel index selections, from each progeny type selection i.e S_2 and S_2 test-cross hybrid (TCH) families were recombined in the short rains (SR) of 1993 to form improved versions of the populaton i.e the C_1 populations. As a result, 35 of improved populations (C_1) i.e 16 selections for single traits (leaf feeding, stem tunnelling, dead heart and grain yield) from each of the progeny types (S_2 and S_2 test cross hybrids) based on their performance in each of the sites (MPFS and UFS), 8 selected for rank summation indices (RSI-1 and RSI-2) from the two progeny types for the two sites, Another 8 selected for Smith-Hazel indices (B_1 and B_2), 1 selected for yield from the test crosses evaluated at Matuga in Mombasa. And 2 more selected for yield performance combined for two sites MPFS and UFS (Table 1). Together with the original population (ICZ3) C_1 populations were evaluated in four replicate experiments at MPFS, Ungoye and Muguga (medium altitude, medium agricultural potential with a bimodal rainfall distribution) for selection gains in the LR 1994. The experimental design was as for the evaluation of the progeny types in the LR of 1993. In addition, remnant seeds of S_2 and S_2 testcross progenies were evaluated for entomological observations related to mechanisms of resistance such as leaf feeding lessions, development and establishment of C. partellus larvae at MPFS and Ungoye. In this case the two halves of each row were infested with 30 first instar larvae at three weeks after emergence. Four weeks after infestation data on both leaf feeding and dead heart were recorded from the whole row while that of stem tunnelling was only taken from one half. The larvae recovered were counted and categorized into various instars by measuring the head capsule width using a calibrated microscope. At harvest stem tunnelling, number of larvae recovered, their instars and grain yield were recorded for the remaining half.

.Table 1: List of 35 C_1 populations selected from S_2 and $_2S$ testcross families derived from ICZ3 maize population and evaluated at MPFS, UFS and Matuga (MGA).

Progeny type	S_2	S_2TCH
Name-	S_2mpfs lf- 9 *	S_2tchmpfs lf- 13
Number	S_2mpfs st- 10	S_2tchmpfs st- 14
	S_2mpfs dh- 11	S_2tchmpfs dh- 15
	S_2mpfs yld- 12	S_2tchmpfs yld- 16
	S_2mpfs rsi-1- 21	S_2tchmpfs rsi-1- 23
	S_2mpfs rsi-2- 22	S_2tchmpfs rsi-2- 24
	S_2mpfs b1- 29	S_2tchmpfs b1- 31
	S_2mpfs b2- 30	S_2tchmpfs b2- 32
	S_2com yld- 33	S_2tchcom yld- 34
	S_2ufs lf- 1	S_2tchufs lf- 5
	S_2ufs st- 2	S_2tchufs st- 6
	S_2ufs dh- 3	S_2tchufs dh- 7
	S_2ufs yld- 4	S_2tchufs yld- 8
	S_2ufs rsi-1- 17	S_2tchufs rsi-1- 19
	S_2ufs rsi-2- 18	S_2tchufs rsi-2- 20
	S_2ufs b1- 25	S_2tchufs bi- 27
	S_2ufs b2- 26	S_2tchufs b2- 28
		S_2tchmga yld- 35

---

* lf, st, dh and yld = leaf feeding, stem tunnelling dead heart and yield, respectively. The number represents the randomization assigned to each genotype

Com = selections based on combined yield data from MPFS and UFS.

3.4 Statistical analyses

Data obtained on each type of progeny (e.g S_1, S_2 and S_2TCH) were subjected to both analyses of variance (ANOVA) and covariance (ANCOVA). Care was taken to ensure that data was taken from competitive plants in each plot. The two forms are given in Tables 2 and 3 below.

Table 2. Analysis of variance

Source	Df	MS	EMS
Env. (E)	e-1		
Reps/E	e(r-1)		
Genotype (G)	g-1	M_3	$\sigma^2e + r\sigma^2ge + re\sigma^2g$
G X E	(g-1)(e-1)	M_2	$\sigma^2e + r\sigma^2ge$
Error	e(g-1)(r-1)	M_1	σ^2e

Where

r = No of reps/site

g = No of genotypes under test

e = No of sites (environments)

Table 3. Analysis of covariance

Source	Df	MCP	EMCP
Env. (E)	e-1		
Reps/E	e(r-1)		
Genotype (G)	g-1	M_{3xy}	$\sigma^2exy + r\sigma^2gexy + re\sigma^2gxy$
G X E	(g-1) (e-1)	M_{2xy}	$\sigma^2exy + r\sigma^2gexy$
Error	e(g-1)(r-1)	M_{1xy}	σ^2exy

Where

r, g and e are as defined above

x = independent variable or covariate

y = dependent variable

The model used for the combined analysis of variance across locations was:

$Y_{ijk} = u + e_k + b\ (e)_{jk} + g_i + (ge)_{ik} + e_{ijk}$.

Where,

Y_{ijk} = the observation made in the j^{th} replication of the k^{th} environment on the i^{th} genotype.

u = overall experiment mean.

e_k = effect of the k^{th} evironment, $b(e)_{jk}$ is the effect of the j^{th} replication within the k^{th} environment.

g_i = effect of the i^{th} genotype.

$(ge)_{ik}$ = effect of the interaction of the i^{th} genotype with the k^{th} environment.

e_{ijk} = random error.

Data from Matuga site was not included in the combined analysis since the S_2 and S_2TCH progenies were only evaluated under natural infestation unlike those at Mbita and Ungoye field sites. As a result the analysis of variance carried out was for selection of a sub population for the site alone. Likewise, the Muguga site experiment was not included in the analysis for the same reason.

Expectation of mean squares (EMS) and the expectation of mean cross products (EMCS) from ANOVA and ANCOVA respectively (Tables 1 and 2) were used to obtain the following components

Genetic variance ($\sigma^2 g$) = $m_3 - m_2/re$

Genotype x environment interaction variance ($\sigma^2 ge$) = $m_2 - m_1/r$

Environmental variance ($\sigma^2 e$) = m_1

Genotypic correlation: $r_{g\ (x.y)} = cov\ xy\ /\ \sqrt{}\ (\sigma^2 x\ X\ \sigma^2 y)$

Genotypic component of covariance (σ_{xy}) = $cov_{\ xy} = (M_{3xy} - M_{2xy})/re$

Standard errors (s.e.) for each of the variances ($\sigma^2 i$) except phenotypic variance were calculated as follows:

s.e ($\sigma^2 i$) = $(2/c^2\ \Sigma(msi^2/dfi+2))^{1/2}$. While that for phenotypic variance was computed as:

s.e ($\sigma^2 ph$) = $((1)/(re)(2(msg)^2/(dfi+2))^{1/2}$.

Where $\sigma^2 i$, msi^2, c and dfi are the components of variance, mean squares, coefficients of the component in the EMS for trait i, and degrees of freedom, respectively. Msg is the mean square for genotype.

Estimate of phenotypic variance ($\sigma^2 ph$) was obtained as:

$\sigma^2 ph = \sigma^2/re + \sigma^2 ge/e + \sigma^2 g$.

Broad sense heritability (h^2) estimates were calculated as:

$h^2 = \sigma^2 g/\sigma^2 g + \sigma^2 ge/e + \sigma^2/re$

With s.e calculated as proportions of s.e $\sigma^2 g$ to $\sigma^2 ph$.

Note: The genetic expectations for S_2 and S_2 test cross hybrids (S_2TCH) selection are predominantly additive.

S_2TCH ($\sigma^2 g$) = $1/8\ \sigma^2 A = 8\ \sigma^2 g$

Whilst the S_2 ($\sigma^2 g$) = $3/2\ \sigma^2 A + 3/16\ \sigma^2 D$

Therefore, it is expected that the heritability estimates for each of the S_2TCH and S_2 families were in the narrow sense.

Correlation coefficients (phenotypic) were determined between all possible pairs of traits, while stepwise multiple regression was further obtained using yield or yield reduction as the dependent variable and all other traits as independent variables. These include: Leaf feeding, stem tunnelling and dead hearts.

Least significant difference (lsd) was used to compare specific means for significant differences for various traits for the original population and improved versions.

Predicted responses to selection was estimated as:-

$\Delta G = ck\sigma ph^2$

where, k = standardized selection differential (k=1.76 for selection
intensity of 10%), c = parental control (c = 1 for S_2 families and c = 2 for TCH), σp = phenotypic standard deviation and h^2 = heritability estimate.

RSI values were subjected as for a trait, to both analyses of variances and covariance and information obtained were used to estimate variances, genotypic correlations and heritability. Predicted response to aggregate trait created by RSI was then calculated using the formula above. The formula of Mock and Eberhart (1972) for calculating gains from aggregate selection was used as follows:

$H = \Sigma a_i \Delta g_i$.

Where a_i is the economic weight for the ith trait and g_i, that was calculated using the formula of Pesek and Baker (1969a), which is the predicted response to that trait due to index selection. Economic weights were -1, -1, -1 and 1 for LF, DH, ST and yield respectively.

Correlated responses due to single and aggregate trait selection were calculated as:-

$CR_{y.x} = k_x h_x h_y rg_{(x.y)}\ \sigma P_y$ (Falconer,1960)

where k_x = selection intensity for trait X.

h_x and h_y = square root of heritability estimates for traits X and Y, respectively.

$rg_{(x.y)}$ = genetic correlation between traits X and Y.

σP_y = phenotypic standard deviation of trait y.

A Chi-square test (X^2) was performed to check whether both observed direct and correlated responses to selection conform to expected responses.

$X^2 = (0_i - E_i \mid - 0.5)^2 / E_i$ (Gomez and Gomez, 1984)

O_i = observed response for the i^{th} trait

E_i = expected response for the i^{th} trait

Gains from aggregate trait selection obtained by use of indices were also predicted. The predicted gains from both single and aggregate traits were compared with their respective observed responses.

CHAPTER 4

4.0 RESULTS

Combined analysis of variance for all entries (Tables 4 to 7) revealed highly significant differences ($p < 0.01$) for environment (E) only for leaf feeding, plant height, ear height, stand count and moisture % at harvest for the S_2 progenies whilst for the testcrosses all traits were highly significant ($P < 0.01$) except for grain yield and ear number. Highly significant differences among replications ($P < 0.01$) were observed for all traits except grain yield, ear length ($P < 0.05$), dead heart, stem tunnelling and grain moisture content at harvest for the S_2 progenies. In case of the testcrosses, there was no significant replicate differences for leaf feeding and plant height. Genotype mean squares (MS) were highly significant ($P < 0.01$) for plant height, ear height, stand count, ear number, ear weight, ear length, moisture % at harvest, grain weight and significant ($P < 0.05$) for leaf feeding for S_2 families. No significant genotype differences were observed for grain yield in the S_2 progenies. Only ear height showed significant ($P < 0.05$) differences among the genotypes for the testcross hybrids. Genotype by Environment (G X E) interactions were not significant for any of the traits of the S_2 lines but were highly significant ($P < 0.01$) for stand count of the testcross hybrids.

Means and ranges (Table 8) for each of the three parameters of resistance (leaf feeding, dead heart and stem tunnelling) and grain yield in each progeny type revealed highly significant levels of variability for effective selection to be practised. There was a difference of about

5.00 - 6.33 and 5.00 - 6.17 for leaf feeding, 3.14% - 3.29% and 2.56% - 3.14% for dead heart, 27.97% - 28.52% and 19.46% - 23.92% for stem tunnelling and 6.70 - 11.10 t/ha for grain yield for S_2 and testcross progenies, respectively. The standard error of the mean (S.e) for all the traits in each progeny were small (Table 8). Other mature plant traits such as stand count, plant height, ear height, days to 50 % tasselling,

Table 4: Mean squares and standard errors(s.e) from an analysis of variance for grain yield, and parameters of resistance of S_2 families across two enviroments (Mbita and Ungoye).

		Mean squares			
Source of variation	Df	Grain yield	Dead heart	Leaf feeding	Stem tunnelling
Env.(E)	1	6.95	4.09	119.33**	10792.94
Reps /(E)	2	14.82	1.79	10.34**	205.18
Genotype (G)	132	3.10	0.46	0.87*	24.81
G X E	132	2.32	0.44	0.76	20.35
Error	264	2.54	0.45	0.64	21.47
Mean		2.47 t/ha	0.24 %	3.37	10.14 %
S.e.		0.07	0.03	0.04	0.28

*, ** significant at $P < 0.05$ and 0.01, respectively

Table 5: Mean squares and standard errors (S.e.) from an analysis of variance for agronomic traits of S_2 families across two environments (Mbita and Ungoye)

		Mean squares							
Source of variation	Df	Plant height	Ear height	Stand count	Ear number	Ear weight	Ear length	Moisture %	Grain weight
Env (E)	1	58968.42**	20671.40**	44.00**	0.42	0.05	203.46	2445.43**	0.001
Reps /(E)	2	2840.04**	1387.17**	8.98	49.86**	0.59**	906.98*	30.94	0.34**
Genotype (G)	132	965.44**	350.06**	6.91**	11.58**	0.15**	377.84**	55.77**	0.10**
G X E	132	491.03	156.34	4.04	6.60	0.08	255.08	34.19	0.05
Error	264	444.54	144.17	3.63	5.82	0.07	240.01	34.54	0.05
Mean		107.10 cm	58.44 cm	8.50	6.00	0.50 kg	62.62 cm	14.05 %	0.41 kg
S.e		1.15	0.67	0.09	0.11	0.01	0.72	0.29	0.01

*, ** significant at $P < 0.05$ and 0.01, respectively.

Table 6: Mean squares and standard errors (S.e) from an analysis of variance for grain yield and parameters of resistance of testcross hybrids across two environments (Mbita and Ungoye).

		Mean squares			
Source of variation	Df	Grain yield	Dead heart	Leaf feeding	Stem tunnelling
Env. (E)	1	0.57	3.85**	115.54**	12104.27**
Reps/(E)	2	51.93**	5.79**	2.68	179.90**
Genotype (G)	141	4.17	0.30	0.86	14.46
G X E	141	3.80	0.28	0.81	12.66
Error	282	3.51	0.27	0.95	10.86
Mean		4.20 t/ha	0.17 %	3.37	9.99%
S.e		0.08	0.02	0.04	0.26

** significant at $P < 0.01$.

Table 7: Mean squares and Standard errors (S.e) from an analysis of variance for agronomic traits of test cross hybrids across two environments (Mbita and Ungoye)

		Mean squares							
Source of variation	Df	Plant height	Ear height	Stand count	Ear number	Ear weight	Ear length	Moisture %	Grain weight
Env (E)	1	181842.55**	69003.28**	98.06**	2.68	1.77**	4218.85**	1675.70**	1.20**
Reps /(E)	2	381.96	2958.21**	75.89**	45.97**	2.16**	1078.91**	329.17**	1.32**
Genotype (G)	141	7256.16	234.38*	3.36	5.98	0.19	167.84	6.90	0.12
G X E	141	6000.04	177.05	2.73**	3.67	0.14	139.66	5.70	0.09
Error	282	5151.24	176.26	2.49	5.32	0.17	124.64	4.20	0.11
Mean		151.43 cm	84.05 cm	9.00	8.50	1.21 kg	76.55 cm	12.77 %	0.96kg
S.e		3.69	0.75	0.07	0.09	0.02	0.51	0.18	0.01

*, ** significant at $P < 0.05$ and 0.01, respectively.

Silking and pollen shed exhibited great variability (Table 8). Generally, the S_2 progenies were less yielding and shorter with delayed maturity than their contemporary testcross hybrids (Table 8).

Estimates of pertinent components of variance obtained for each of the two types of progeny are presented in Tables 9 and 10. In most cases, genetic (σ^2g), environmental (σ^2e) and phenotypic (σ^2ph) variances exceeded twice their standard errors except the genetic variances for stem tunnelling, plant height and moisture % at harvest of the testcross hybrids. On average, estimates of genotype x environment variances (σ^2ge) were either negative or smaller than their respective standard errors (S.e) in all cases, except for plant height in the testcross hybrids and leaf feeding, ear weight in the S2 progenies. Also, most of the genetic variances were larger for the S_2 progeny types than for the testcross hybrids corresponding to high heritability estimates in the former than the latter. Heritability estimates for parameters of resistance, grain yield, mature plant traits and selection indices in most cases were moderate for the S_2 families thus suggesting that simultaneous improvement of these traits in the desired direction should be possible, and especially so with the use of selection indices to effectively combine the traits (Table 11). However, for the testcross hybrids the heritability estimates were low for the majority of the traits except for ear placement (0.78).

Table 8: Means and standard errors (s.e) of means and ranges for yield, parameters of resistance and desirable agronomic traits of S_2 and test crosshybrids (S_2TCH) derived from ICZ3 maize population and evaluated at Mbita point field station (MPFS) and Ungoye (Ufs).

		Mbita Point Field Station		Ungoye Field Site	
Traits		S_2	S_2TCH	S_2	S_2TCH
Grain yield (t/ha)	(i)	2.35 ± 0.09	5.82 ± 0.10	2.58 ± 0.10	5.76 ± 0.13
	(ii)	1.05 - 6.70	2 35 - 10.20	0.00 - 11.10	2.40 - 11.00
Leaf feeding	(i)	3.84 ± 0.06	3.82 ± 0.07	2.89 ± 0.05	2.92 ± 0.04
	(ii)	2.17 - 7.17	1.33 - 7.50	0.00 - 6.33	1.00 - 6.50
Dead heart (%)	(i)	0.32 ± 0.05	0.25 ± 0.04	0.16 ± 0.03	0.08 ± 0.02
	(ii)	0.00 - 3.29	0.00 - 3.14	0.00 - 3.14	0.00 - 2.56
Stem tunnelLing	(i)	14.68 ± 0.27	14.61 ± 0.22	5.59 ± 0.31	5.37 ± 0.27
	(ii)	0.00 - 27.97	2.07 - 25.99	0.00 - 28.52	0.00 - 19.46
plant height (Cm)	(i)	96.63 ± 1.30	133.59 ± 1.06	117.48 ± 1.61	169.27 ± 0.72
	(ii)	36.60 - 154.00	52.50 - 174.00	50.46 - 180.00	60.57 - 215.00
ear height (cm)	(i)	52.17 ± 0.76	73.07 ± 0.77	64.71 ± 0.93	95.03 ± 0.90
	(ii)	22.00 - 87.50	3.15 - 125.00	0.00 - 96.60	50.52 - 133.00
stand count	(i)	9.00 ± 0.11	9.00 ± 0.07	8.00 ± 0.15	9.00 ± 0.90
	(ii)	3.00 - 10.00	3.00 - 10.00	2.00 - 11.00	4.00 - 12.00
ear number	(i)	6.00 ± 0.14	8.00 ± 0.10	6.00 ± 0.15	9.00 ± 0.16
	(ii)	3.00 - 11.00	2.00 - 13.00	2.00 - 11.00	4 00 - 16.00
ear weight (Kg)	(i)	0.51 ± 0.02	1.15 ± 0.02	0.49 ± 0.02	1.26 ± 0.03
	(ii)	0.05 - 1.60	0.07 - 2.30	0.00 - 1.60	0.80 - 2.40
ear length (cm)	(i)	61.69 ± 0.76	73.87 ± 0.75	63.54 ± 1.19	79.23 ± 0.66
	(ii)	20.00 - 91.00	30.00 - 100.00	22.00 - 97.00	35.50 - 113.00
moisture (%)	(i)	16.16 ± 0.38	9.49 ± 0.25	11.93 ± 0.38	16.05 ± 0.20
	(ii)	14.00 - 27.70	16.00 - 33.10	13.00 - 21.30	16.00 - 27.00
grain weight (Kg)	(i)	0.41 ± 0.01	0.92 ± 0.02	0.41 ± 0.02	1.00 ± 0.02
	(ii)	0.00 - 1.28	0.56 - 1.84	0.05 - 1.85	0.64 - 1.92
Days to 50% tasselling	(i)	58.00 ± 0.23	54.00 ± 0.13		
	(ii)	49.00 - 78.00	47.00 - 67.00		
days to 50% silking	(i)	63.00 ± 0.37	59.00 ± 0.18		
	(ii)	51.00 - 81.00	51.00 - 72.00		
days to 50% pollen shed	(i)	60.00 ± 0.38	57.00 ± 0.13		
	(ii)	52.00 - 74.00	50.00 - 67.00		

(i) = Mean ± S.e
(ii) = Range

Table 9: Estimates of genetic (σ^2g), genotype X environment (σ^2ge), environmental (σ^2e) and phenotypic variances (σ^2ph) for test cross hybrid families developed from the maize variety (ICZ3).

Traits	σ^2g	σ^2ge	σ^2e	σ^2ph
Grain yield (t/ha)	0.10 ± 0.12	0.15 ± 0.22	3.51 ± 0.29	1.05 ± 0.25
Dead heart (%)	0.01 ± 0.01	0.01 ± 0.02	0.27 ± 0.02	0.09 ± 0.02
Leaf feeding	0.01 ± 0.02	-0.07 ± 0.05	0.95 ± 0.08	0.21 ± 0.05
Stem tunnelling (%)	0.45 ± 0.43	0.90 ± 0.74	10.86 ± 0.82	3.62 ± 0.86
Plant height (cm)	314.03 ± 214.53	424.40 ± 354.79	5151.24 ± 430.77	1814.04 ± 304.60
Ear height (cm)	14.33 ± 8.68	0.40 ± 10.47	15.80 ± 14.79	18.48 ± 13.86
Stand count	0.16 ± 0.13	0.12 ± 0.14	2.49 ± 0.21	0.84 ± 0.20
Ear number	0.58 ± 0.21	-0.83 ± 0.38	27.34 ± 0.45	6.84 ± 0.35
Ear weight (kg)	0.01 ± 0.01	-0.02 ± 0.01	34.64 ± 0.01	8.66 ± 0.01
Ear length (cm)	7.05 ± 4.96	7.51 ± 8.26	124.64 ± 10.46	41.97 ± 9.92
Moisture %	0.30 ± 0.20	0.75 ± 0.34	4.20 ± 0.35	1.73 ± 0.41
Grain weight (kg)	0.01 ± 0.00	-0.01 ± 0.01	34.12 ± 0.01	8.53 ± 0.01
Rsi-1	40.61 ± 16.54	-38.62 ± 40.27	3956.47 ± 332.02	1010.42 ± 229.15
Rsi-2	6.55 ± 2.12	-4.90 ± 5.24	5071.93 ± 425.63	1272.08 ± 300.68

Rsi-1 = Aggregate performance of a genotype based on ranked means of the three parameters of resistance.

Rsi-2 = Aggregate performance of a genotype based on ranked means of the three parameters of resistance and grain yield.

Table 10: Estimates of genetic (σ^2g), genotype x environment (σ^2ge),environmental (σ^2e) and phenotypic variances for S_2 families developed from the maize variety (ICZ3)

Traits	σ^2g	σ^2ge	σ^2e	σ^2ph
Grain yield (t/ha)	0.20 ± 0.11	-0.11 ± 0.14	2.51 ± 0.22	0.78 ± 0.18
Dead heart (%)	0.01 ± 0.01	-0.01 ± 0.02	0.45 ± 0.04	0.11 ± 0.03
Leaf feeding	0.03 ± 0.03	0.06 ± 0.04	0.64 ± 0.06	0.11 ± 0.05
Stem tunnelling (%)	1.12 ± 0.99	-0.56 ± 1.24	21.47 ± 1.86	6.21 ± 1.47
Plant height (cm)	118.60 ± 33.33	23.25 ± 29.99	444.54 ± 38.55	241.37 ± 1.84
Ear height (cm)	48.43 ± 11.80	6.09 ± 9.55	144.17 ± 12.50	162.62 ± 1.11
Stand count	0.72 ± 0.25	0.21 ± 0.25	3.63 ± 0.31	1.74 ± 0.16
Ear number	1.25 ± 0.41	0.39 ± 0.40	5.82 ± 0.50	2.91 ± 0.20
Ear weight (kg)	0.02 ± 0.01	0.01 ± 0.00	0.07 ± 0.01	0.05 ± 0.01
Moisture %	5.40 ± 2.01	0.18 ± 2.09	34.54 ± 2.99	13.95 ± 3.30
Grain weight (kg)	0.01 ± 0.01	0.00 ± 0.00	0.05 ± 0.00	0.02 ± 0.01
Ear length (cm)	30.69 ± 14.03	7.54 ± 15.58	240.01 ± 20.81	94.46 ± 22.34
Rsi-1	18.05 ± 15.40	-17.98 ± 30.80	3604.90 ± 309.12	910.29 ± 218.87
Rs1-2	405.30 ± 223.71	-790.6 ± 447.43	5173.87 ± 443.66	1303.47 ± 361.54

Rsi-1 = Aggregate performance of a genotype based on ranked means of parameters of resistance.

Rsi-2 = Aggregate performance of a genotype based on ranked means of parameters of resistance and grain yield.

Table 11: Heritability estimates (broad) for grain yield, parameters of resistance and desirable agronomic traits of the two progeny types developed from ICZ3

Traits	Test cross hybrids	S_2 families
Grain yield (t/ha)	0.10 ± 0.11	0.26 ± 0.14
Dead heart (%)	0.11 ± 0.11	0.09 ± 0.09
Leaf feeding	0.05 ± 0.09	0.27 ± 0.27
Stem tunnelling (%)	0.12 ± 0.11	0.18 ± 0.16
Plant height (cm)	0.17 ± 0.12	0.49 ± 0.14
Ear height (cm)	0.78 ± 0.47	0.30 ± 0.07
Stand count	0.19 ± 0.15	0.41 ± 0.14
Ear number	0.08 ± 0.03	0.43 ± 0.14
Ear weight (kg)	0.01 ± 0.00	0.40 ± 0.20
Ear length (cm)	0.17 ± 0.15	0.32 ± 0.15
Moisture %	0.17 ± 0.12	0.39 ± 0.14
Grain weight (kg)	0.01 ± 0.00	0.50 ± 0.50
Rsi-1	0.04 ± 0.02	0.02 ± 0.16
Rsi-2	0.01 ± 0.002	0.31 ± 0.17

Rsi-1 = Aggregate performance of a genotype based on ranked means of parameters of resistance.

Rsi-2 = Aggregate performance of a genotype based on ranked means of parameters of resistance and grain yield.

Phenotypic correlations among parameters of resistance, grain yield and the selection indices (Tables 12 and 13) were in all cases low except that of leaf feeding and dead heart for the S_2 progenies (-0.97) combined for the two locations (Mbita Point Field Station and Ungoye Field Site). Corresponding genotypic correlations were much higher and to an extent exceeding unity, especially, for the testcrosses.

Correlations of parameters of resistance to C. partellus (leaf feeding and stem tunnelling) with mature plant characteristics, including grain yield (Table 14), were generally negative with a few exceptions. Whilst those of dead heart showed highly significant correlations with stand count, ear length, ear number and moisture % at harvest for the two progeny types. Rank summation index (RSI-1) involving the three parameters of resistance namely, leaf feeding, dead heart and stem tunnelling also showed highly significant ($P < 0.01$) correlations with the four agronomic traits as opposed to those involving RSI-2 which were generally negative apart from a few cases. The possible contribution of each of the damage parameters to grain yield was examined using stepwise multiple regressions. Results obtained (Table 15) indicated that in the testcrosses, stem tunnelling accounted for at least 45 % of the total variation in grain yield reduction (R^2

= 0.45) whilst in the S_2 progenies leaf feeding accounted for 20% of the variation in yield reduction. In the two progey types, stem tunnelling seemed to have the most contribution towards grain yield determination (R^2 being 0.36 for S_2 lines and 0.45 for the testcrosses).

Pedicted direct responses to grain yield, parameters of resistance i.e leaf feeding, dead heart and stem tunnelling due to index selection were much lower than when each of the traits was selected directly (Tables 16 and 17). There was higher response in the S_2 selections than in the test crosses for the four traits (grain yield, leaf feeding, dead heart and stem tunnelling) including rank summation indices (RSI-1 and RSI-2).

Table 12: Genotypic (r_g) correlations (lower diagonal) and phenotypic (r_p) correlations (upper diagonal) amongst grain yield, parameters of resistance to Chilo partellus, agronomic traits and rank summation indices for test cross hybrids derived from ICZ3 population.

	Grain yield (t/ha)	Dead heart (%)	Leaf feeding	Stem tunnelling (%)	RSI-1	RSI-2
Grain yield (t/ha)		-0.15	-0.08	-0.02	-0.002	-0.002
Dead heart (%)	-1.05		-0.18	-0.04	-0.04	-0.01
Leaf feeding	-1.01	-0.20		-0.10	0.003	0.01
Stem tunnelling (%)	-1.00	-1.03	0.13		-0.001	-0.002
RSI-1	-0.04	0.29	-0.001	-0.01		-0.001
RSI-2	-1.12	-1.10	-1.11	-1.21	-0.19	

Rsi-1 = Aggregate performance of a genotype based on ranked means of parameters of resistance

Rsi-2 = aggregate performance of a genotype based on ranked means of parameters of resistance and grain yield

Table 13: Genetic (r_g) correlations (lower diagonal) and phenotypic (r_p) correlations (upper diagonal) among grain yield, parameters of resistance to _Chilo partellus_ and rank summation indices for S_2 progenies derived from ICZ3 population.

	Grain yield (t/ha)	Dead heart (%)	Leaf feeding	Stem tunelling (%)	RSI-1	RSI-2
Grain yield (t/ha)		-0.01	-0.05	-0.02	-0.001	0.001
Dead heart (%)	-1.03		-0.97**	0.03	0.03	0.01
Leaf feeding	-0.49	-0.58		0.05	-0.01	-0.01
Stem tunnelling (%)	-1.20	0.20	0.01		-0.002	0.002
RSI-1	-0.14	0.28	-0.003	-0.01		0.002
RSI-2	-1.01	-1.02	-0.08	0.53	0.05	

** significant at $P < 0.01$.

Rsi-1 = Aggregate performance of a genotype based on ranked means of parameters of resistance.

Rsi-2 = Aggregate performance of a genotype based on ranked means of parameters of resistance and grain yield.

Table 14: Simple linear correlations of *Chilo partellus* resistance parameters including resistance index (RSI) on mature plant traits and grain yield from testcross hybrids and S_2 progenie combined for Mbita point and Ungoye locations of western Kenya.

Trait	Progeny type	Leaf feeding	Dead heart (%)	Stem tunnelling (%)	RSI-1	RSI-2
Plant ht (cm)						
	(i)	0.11	-0.07	0.29**	-0.13	0.00
	(ii)	0.05	-0.03	0.22**	-0.13	-0.02
Stand count	(i)	-0.09	0.19*	-0.11	0.31**	-0.04
	(ii)	-0.08	0.30**	-0.08	0.48**	0.08
Ear length (cm)	(i)	-0.07	0.40**	-0.09	0.95**	-0.13
	(ii)	-0.14	0.32**	-0.15	0.99**	0.21**
Ear number	(i)	0.01	0.26**	0.09	0.34**	-0.14
	(ii)	-0.10	0.25**	-0.03	0.45**	0.12
Moisture (%)	(i)	-0.09	0.27**	-0.14	0.49**	-0.14
	(ii)	0.04	0.24**	-0.14	0.61**	-0.02
Grain yield (t/ha)	(i)	-0.03	-0.04	-0.05	-0.01	-0.08
	(ii)	-0.01	-0.03	-0.04	-0.02	0.04

*, ** significant at $P < 0.05$ and 0.01, respectively. (i) = Test crosses (ii) = S_2 progenies

Table 15: Unstandardized partial regression coefficients (b-values), coefficients of determination (R^2) and R^2 change (ΔR^2) from stepwise multiple regression of grain yield on parameters of resistance (leaf feeding, dead heart and stem tunnelling) in each of the progeny types.

Family type	Trait	b-value	R^2	ΔR^2
Testcrosses	Leaf feeding	-0.01	0.01	0.01
	Dead heart (%)	1.40	0.01	0.00
	Stem tunnelling (%)	-0.14	0.45	0.44
S_2 lines	Leaf feeding	0.002	0.20	0.20
	Dead heart (%)	-0.09	0.27	0.07
	Stem tunnelling (%)	0.02	0.36	0.09

Table 16: Predicted direct response (ΔG)/cycle and observed Gain/cycle to single trait selection for grain yield, parameters of resistance (leaf feeding, dead heart and Stem tunnelling) and rank summation index (RSI).

Family types		grain yield (t/ha)	leaf feeding	dead heart (%)	stem tunnelling (%)	RSI-1	RSI-2
S_2	expected	0.40	-0.16	-0.05	-0.79	1.06	10.75
families	observed	0.55	-0.08	-2.19	-0.72	0.79	0.11
		(23.21)	(-2.09)	(-67.18)	(-4.92)	(33.33)@	(4.64)@
Test	expected	0.32	-0.08	-0.12	-0.22	4.48	1.26
crosses	observed	0.46	0.03	-0.81	-0.54	0.34	0.27
		(7.90)	(0.78)	(-31.40)	(-3.69)	(5.84)@	(4.64)@

( ) Gain expressed as % of the overall means of their respective family means.

@ Gain expressed as % of the overall means of the yield in the respectiv families.

Table 17: Predicted direct response (ΔG/cycle) and observed gain/cycle to aggregate trait selections for grain yield, parameters of resistance (leaf feeding, dead heart and stem tunnelling) for S_2 families and test crosses derived from ICZ3 population.

Progeny types	aggregate trait		grain yield (t/ha)	leaf feeding	dead heart (%)	stem tunnelling (%)	aiΔgi
S_2 families	B_1	expected	0.10	-0.08	-0.04	-0.63	3.55
		observed	-0.27	-0.27	-2.27	1.09	-1.45
			(-11.39)	(-7.05)	(-69.48)	(7.45)	(-20.03)@
	B_2	expected	0.10	-0.08	-0.03	-0.55	4.64
		observed	-0.15	-0.44	-3.13	-0.15	-3.87
			(-6.33)	(-11.49)	(-96.01)	(-0.99)	(-64.18)@
Test crosses	B_1	expected	0.12	-0.09	-0.06	-0.08	4.20
		observed	-0.10	-0.02	-1.25	0.43	-1.78
			(-1.63)	(-0.01)	(-48.45)	(2.90)	(-25.39)@
	B_2	expected	0.13	-0.05	-0.06	-0.09	4.78
		observed	-0.07	-0.49	-2.17	-3.03	-5.76
			(-0.01)	(-12.66)	(-83.91)	(-20.71)	(-85.71)@

( ) Gain /cycle expressed as % of the verall mean of their family means.

@ Gain /cycle expressed as % of the overall mean of the yield in the respective families.

B_1 = Smith-Hazel index constructed using parameters of resistance

B_2 = Smith-Hazel index constructed using parameters of resistance and grain yield.

$a_i\Delta g_i$ = Aggregate gain.

In all cases, predicted direct and observed responses to both single and aggregate trait selections showed poor correspondence as confirmed by Chi-square X^2 test (Table 18).

Predicted correlated responses in grain yield when selection was done for parameters of resistance and the rank summation indices are presented in Table 19. When these gains were expressed as a proportion of the means of their respective families in the two progeny types, they were lower than those expected from direct selection for grain yield per se. Comparatively, higher correlated gains were observed for the S_2 families for all traits than for the test crosses. Aggregate selection with the Smith-Hazel index (B_1) where only the parameters of resistance were included in the index gave more progress than when the same traits were included in the rank summation index (RSI-1) in the two selection methods (Tables 16 and 17). However, when grain yield was included in the two indices as a trait, rank summation index (RSI-2) consistently gave more gains than the Smith-Hazel index. There was a gain of -11.05% - 8.16% compared to -6.33 - -0.01% (Tables 17 and 19) for RSI-2 and Smith-Hazel index (B_2), respectively. Highly significant ($P < 0.01$) Chi-square values (Table 20) were obtained suggesting poor agreement between predicted and observed correlated responses to selection for all the characters studied.

Table 18: Chi-square test X^2 for homogeneity of ratio for predicted and observed responses to selection for single and aggregate traits in ICZ3 population.

	S_2 families				Testcross hybrids			
Trait	observed	expected	X^2	df	observed	expected	X^2	df
Grain Yield (t/ha)	0.55	0.40	0.31	1	0.46	0.32	0.41	1
Leaf feeding	-0.08	-0.16	-1.10	1	0.03	-0.08	-1.90	1
Dead heart (%)	-2.19	-0.05	-139.39	1	-0.81	-0.12	-11.80	1
Stem tunnelling (%)	-0.72	-0.79	-0.23	1	-0.54	-0.22	-3.06	1
RSI-1	0.79	1.06	2.30	1	0.34	4.48	4.81	1
RSI-2	0.11	10.75	11.54	1	0.27	1.26	1.76	1
Total	-1.54	13.21	-126.57**	6	-0.25	5.64	-9.78**	6
B_1	-1.45	3.55	8.52	1	-1.78	4.20	10.0	1
B_2	-3.87	4.64	17.50	1	-5.76	4.78	25.50	1
Total	-5.32	8.19	26.02**	2	-7.54	8.98	35.50**	2

df = P-1, where p = number of classes.

**, significant at $P < 0.01$

B_1 = Smith-Hazel index constructed using parameters of resistance

B_2 = Smith-Hazel index constructed using parameters of resistance and grain yield.

Rsi-1 = Aggregate performance of a genotype based on ranked means of parameters of resistance.

Rsi-2 = Aggregate performance of a genotype based on ranked means of parameters of resistance and grain yield.

Table 19: Predicted correlated responses (per cycle) in grain yield (t/ha) when selection was done for parameters of resistance including rank summation index (RSI) in ICZ3 population.

Selection criteria	S_2 families	Testcross hybrids
Leaf feeding	-0.05	-0.02
	(-2.04)	(-0.84)
Dead heart (%)	-0.23	-0.20
	(-9.39)	(-3.45)
Stem tunnelling (%)	-0.32	-0.25
	(-13.06)	(-4.32)
RSI-1	-0.001	-0.002
	(-0.04)	(-0.03)
RSI-2	0.20	-0.64
	(8.16)	(-11.05)

( ) .correlated responses expressed as % of the overall mean yield of the respective progeny types.

Rsi-1 = Aggregate performance of a genotype based on ranked means of parameters of resistance.

Rsi-2 = Aggregate performance of a genotype based on ranked means of parameters of resistance and grain yield.

Table 20: Chi-square test X^2 for homogeneity of ratio for both predicted and observed correlated responses to selection for grain yield when selection was done for parameters of resistance and rank summation index (RSI) in ICZ3 population.

Progeny types	Traits	observed	expected	X^2	Df
S_2 families	Leaf feding	1.17	-0.05	-29.77	1
	Dead heart (%)	0.37	-0.23	-1.57	1
	Stem tunnelling (%)	0.75	-0.32	-3.53	1
	RSI-1	0.79	-0.001	-623.68	1
	Rsi-2	0.19	0.20	0.001	1
	total	3.27	-0.399	-658.55**	5
Test crosses	Leaf feeding	0.28	-0.02	-1.33	1
	Dead heart (%)	0.43	-0.20	-1.98	1
	Stem tunnelling (%)	0.66	-0.25	-1.25	1
	RSI-1	0.34	-0.002	-58.48	1
	RSI-2	0.27	-0.64	-1.29	1
	Total	1.98	-1.11	-64.33**	5

df = P - 1, where P = number of classes.

**, significant at $P < 0.01$.

Rsi-1 = Aggregate performance of a genotype based on ranked means of parameters of resistance.

Rsi-2 = Aggregate performance of a genotype based on ranked means of parameters of resistance and grain yield

The means of the source of the source population (C_0) and progenies of first selection (C_1) cycle opresented in Table 21 suggest that selection lead to some improvement in the parameters of resistance, grain yield and related agronomic traits. However,the selection gains were not significantly different from the values observed in the original population. Ther was yield improvement of 24.23% for S_2 lines and 5.29% for testcrosses. Plant height, stand count, ear number, ear weight, ear length and grain weight were on the increasing trend with selection in the two progeny types. Moisture % and ear height seemed to decrease with selection in the two cases. Generally, the improvements were higher in the S_2 progenies than in S_2 testcross progenies. When the means of each of the individual C_1 populations derived from ICZ3 for grain yield, leaf feeding, dead heart and stem tunnelling were computed (Table 22), significant differences ($P < 0.05$) were observed for grain yield where 60.79 % improvement over the source population was observed. The C_1 populations recombined from S $_2$ and testcross progenies exhibited a reduction in rating for leaf damage, on a scale of 1-9, of 0.01-0.11 and 0.05-0.08 per cycle corresponding to a decrease of 0.40% - 4.38% and 1.99% - 3.19 % per cycle relative to the source population (C_0), respectively. Stem tunnel length decreased by 0.15% - 1.81% per cycle in S_2 progenies and 0.13% - 1.76% per cycle in testcross hybrids corresponding to

1.15% - 13.92% and 1.00% - 13.54% per cycle relative to C_0. Dead heart damage was reduced by 1.87% per cycle corresponding to 74.8 % per cycle compared to C_0. Selection for resistance to leaf feeding, dead heart and stem tunnelling by larvae of C. partellus was feasible after one cycle of family selection suggesting that more progress is possible with more cycles of selection.

Table 21: Mean grain yield, parameters of resistance and agronomic traits after one cycle (C_1) of selection in the open-pollinated maize variety (ICZ3).

Traits	C_0	C_1 populations		LSD
		S_2 families	testcrosses	(0.05)
Grain yield (t/ha)	2.27	2.82 (24.23)	2.39 (5.29)	NS
Leaf feeding	2.51	2.59 (0.03)	2.51 (0.00)	NS
Dead heart (%)	2.50	4.69 (87.6)	3.13 (25.2)	NS
Stem tunnelling (%	13.00	13.72 (5.54)	13.54 (4.15)	NS
Plant height (cm)	122.63	127.03 (3.59)	22.93 (0.24)	NS
Ear height (cm)	65.85	62.54 (-5.03)	59.61 (-9.48)	NS
Stand count	13.00	13.49 (3.77)	12.93 (-0.52)	NS
Ear number	10.25	11.78 (14.93)	10.36 (1.07)	NS
Ear weight (kg)	1.00	1.12 (12.00)	1.16 (16.00)	NS
Ear length (cm)	69.63	75.27 (8.10)	75.00 (7.71)	NS
Moisture %	17.65	17.10 (-3.10)	17.02 (-3.57)	NS
Grain weight (kg)	0.80	0.97 (21.25)	0.97 (15.00)	NS

\+ values in parentheses represent observed gains expressed as % of the source population (C_0);

NS No significant difference among means within a row.

Table 22: Mean yield, parameters of resistance and agronomic traits after one cycle of selection in the open-pollinated maize population (ICZ3).

	Traits			
Selections	yield (t/ha)	Dead heart (%)	Leaf feeding	Stem tunnelling (%)
S_2ufs lf	3.65** (60.79)	1.88 (-24.80)	2.68 (6.77)	13.64 (4.92)
S_2ufs st	3.01 (32.60)	1.88 (-24.80)	2.82 (12.35)	12.85 (-1.15)
S_2ufs dh	2.40 (6.17)	1.25 (-50.00)	2.94 (17.13)	13.35 (2.69)
S_2ufs yld	2.18 (-3.96)	1.25 (-50.00)	2.51 (0.00)	14.11 (8.54)
S_2tchufs lf	2.47 (8.81)	0.63 (-74.80)	2.58 (2.79)	13.82 (6.31)
S_2tchufs st	2.58 (13.66)	1.88 (-24.80)	2.64 (5.18)	14.33 (10.23)
S_2tchufs dh	2.71 (19.38)	2.13 (-14.80)	2.94 (17.13)	14.65 (12.69)
S_2tchufs yld	2.26 (0.44)	1.25 (-50.00)	2.70 (7.57)	13.30 (2.31)
S_2mpfs lf	3.22 (41.85)	3.75 (50.00)	2.50 (-0.40)	14.39 (10.69)
S_2mpfs st	3.13 (37.89)	1.88 (-24.80)	2.60 (3.59)	14.58 (12.15)
S_2mpfs dh	2.86 (25.99)	1.88 (-24.80)	2.78 (10.76)	13.17 (1.31)
S_2mpfs yld	2.90 (27.75)	0.63 (-74.80)	2.40 (-4.38)	14.17 (9.00)
S_2tchmpfs lf	2.62 (15.42)	1.88 (-24.80)	2.43 (-3.19)	12.80 (1.54)
S_2tchmpfs st	3.27 (44.05)	2.50 (0.00)	2.84 (13.15)	12.74 (-2.00)
S_2tchmpfs dh	2.69 (18.50)	2.13 (-14.80)	3.18** (26.69)	13.20 (1.54)
S_2tchmpfs yld	2.52 (11.01)	6.88 (175.20)	2.69 (7.17)	11.24 (-13.54)
S_2ufs rsi-1	2.55 (12.33)	5.00 (100.00)	2.75) (9.56)	12.32 (-5.23)
S_2ufs rsi-2	2.28 (0.44)	2.50 (0.00)	2.79 (11.16)	12.57 (-3.31)
S_2tchufs rsi-1	2.55 (12.33)	3.13 (32.52)	2.69 (7.17)	11.46 (-11.85)
S_2tchufs rsi-2	2.44 (7.49)	4.38 (75.20)	2.76 (9.96)	13.76 (5.85)
S_2mpfs rsi-1	3.57** (57.27)	0.63 (-74.80)	2.65 (5.58)	11.19 (-13.92)
S_2mpfs rsi-2	2.48 (9.25)	4.38 (75.20)	2.99 (19.22)	13.14 (1.08)
S_2tchmpfs rsi-1	2.66 (17.18)	2.50 (0.00)	2.93 (16.13)	15.12 (16.31)
S_2tchmpfs rsi-2	2.64 (16.30)	0.63 (-74.80)	2.59 (3.19)	11.93 (-8.23)
S_2ufs b1	1.73 (-23.79)	3.13 (32.52)	2.59 (3.19)	12.04 (-7.38)
S_2ufs b2	2.09 (-7.93)	5.63 (125.20)	2.90 (15.54)	13.42 (3.23)
S_2tchufs b1	2.29 (0.88)	5.00 (100.00)	2.58 (2.79)	12.28 (-5.54)
S_2tchufs b2	2.15 (-5.29)	5.63 (25.20)	3.00 (19.52)	12.87 (-1.00)
S_2mpfs b1	2.27 (0.88)	6.25 (150.00)	2.97 (18.33)	11.54 (-11.23)
S_2mpfs b2	2.45 (7.93)	3.75 (50.00)	3.09 (23.11)	11.33 (-12.85)
S_2tchmpfs b1	2.06 (-9.25)	2.50 (0.00)	2.46 (-1.99)	13.39 (3.00)
S_2tchmpfs b2	2.25 (-0.88)	3.75 (50.00)	2.99 (19.12)	16.16 (24.31)
S_2com yld	3.39** (49.34)	3.75 (50.00)	2.49 (-0.80)	12.28 (-5.54)
S_2tchcom yld	3.55** (56.39)	2.50 (0.00)	2.63 (4.78)	12.14 (-6.62)
S_2tchmga	2.60 (14.54)	1.25 (-50.00)	2.72 (8.37)	15.45 (18.85)
C_0	2.27	2.50	2.51	13.00
Lsd (0.05)	1.03	4.77	0.59	3.88

+, Values in parentheses represent observed gains expressed as % of the source population.

*, Significant at $P < 0.05$

Means of grain yield, number of larvae and pupae at four weeks after infestation (4 WAI) and at harvest plus various instal stadia is presented in Table 23: sub populations 13, 1, 14 and 10 produced more grain yield than the rest. The four were of single trait selections. 1 and 10 selected for leaf feeding and stem tunnel length while 13 and 14 were for leaf feeding and stem tunnelling but from the test crosses. At 4WAI, the average number of larvae recovered for all the C_1 populations was from 3 - 10 (Table 23) of the initial thirty (30) first instar larvae used for artificial infestation. Consequently, there was no pupae recovered suggesting that the survival and development rate of these larvae were severely affected by the sub-populations. The most resistant of the sub-poulations was a single selection for stem tunnelling from S_2 progenies (2) whilst the least resistant was a single selection for leaf feeding from S_2 progenies (9). Most of the larvae recovered were in their fourth, fifth and sixth stadia with the majority in the first two larval stages. Higher numbers were present in sub-populations 21 (a rank summation index selection), 28 (a Smith-Hazel selection) and 1 (a single trait selection for leaf feeding). At the fifth stage the larvae were still lowest in sub-population 2 and highest in sub-population 9 with means 0f 2.00 and 7.00, for the two recombined populations, respectively. For the sixth stage mean ranges of the larvae were 0.00 - 1.00, with the same sub-population 2 having the least number and 22 (a Smith-Hazel selection) with the highest number of larvae recorded. It would therefore appear that the cycle one (C_1) populations were highly resistant to C. partellus larvae damage with sngle trait selected sub-populations being better in terms of resistance than the aggregate selected ones.

At harvest, larval recovery was minimal; ranging from 0 - 1 for all the sub-populations. Only five of the C_1 populations i.e 2 (1), 13 (1), 27 (1), 30 (1) and 7 (1) (see Table 23), the first two (2 and 13) being single selections of leaf feeding, 27 and 30 were selections of the Smith-Hazel index while sub-population 7 was a single selection for dead heart were significant (Lsd 0.05). No pupae were recovered at harvest from any of the cycle one populations. This was attributed to the long duration of about three months before the crop had matured. Hence majority of the larvae had suffered arrested development culminating in death or delayed pupation. A close look at the larval stages at harvest revealed that C_1 sub-population 2 had the highest number of the fourth instar which was 1 compared to 0 for each of 30 and 27, respectively. The rest of the larval stages, namely, fifth and sixth were recorded in 27 and 30 (Table 23). Incidentally, more males were recovered from sub-population 27 than 30. These materials therefore were resistant enough to adversely affect the biology of the larvae leading to delayed or arrested growth as shown in this study where larvae never even pupated.

Table 23: Means of grain yield, number of larvae, number of pupae and various instal stadia from C_1 populations derived from ICZ3 maize population

		Traits									
Selec-tions	yield (t/ha)	Nl1	Np1	4th instar	5th instar	6th instar	Nl2	Np2	4th instar	5th instar	6th instar
S_2mpfs yld	3.04 (62.57)	8.00	0.00	1.00	6.00*	1.00*	1.00*	0.00	0.00	0.00	0.00
S_2ufs lf	2.86 (52.94)	7.00	0.00	2.00*	4.00	1.00*	0.00	0.00	0.00	0.00	0.00
S_2tchmpfs st	2.82 (50.80)	6.00	0.00	1.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchmpfs rsi-2	2.70 (44.39)	7.00	0.00	1.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2ufs dh	2.68 (43.32)	5.00	0.00	1.00	3.00	0.00	0.00	0.00	0 00	0.00	0.00
S_2tchufs st	2.67 (42.78)	6.00	0.00	1.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchufs lf	2.66 (42.25)	5.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2mpfs st	2.64 (41.18)	8.00	0.00	1.00	5.00	1.00*	0.00	0.00	0.00	0.00	0.00
S_2mpfs b2	2.58 (39.97)	5.00	0.00	1.00	6.00*	1.00*	1.00*	0.00	0.00	0.00	1.00*
S_2tchufs b1	2.51 (34.32)	5.00	0.00	1.00	4.00	0.00	1.00*	0.00	0.00	1.00*	0.00
S_2mpfs ri-2	2.40 (28.34)	4.00	0.00	1.00	3.00	1.00*	0.00	0.00	0.00	0.00	0.00
S_2tchmpfs yld	2.38 (27.27)	6.00	0.00	1.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2ufs rsi-2	2.38 (27.27)	7.00	0.00	0.00	6.00*	1.00*	0.00	0.00	0.00	0.00	0.00
S_2tchcom yld	2.36 (26.20)	6.00	0.00	2.00*	4.00	1.00*	0.00	0.00	0.00	0.00	0.00
S_2tchmpfs rsi-1	2.36 (26.20)	4.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2com yld	2.34 (25.13)	4.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2mpfs b1	2.24 (19.79)	7.00	0.00	1.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchufs yld	2.14 (14.44)	7.00	0.00	1.00	6.00*	0.00	0.00	0.00	0.00	0.00	0.00
S_2mpfs rsi-1	2.06 (10.16)	9.00*	0.00	2.00*	5.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchmpfs dh	2.05 (9.63)	8.00	0.00	1.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2ufs b2	2.02 (8.02)	6.00	0.00	1.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2ufs rsi-1	2.00 (6.95)	6.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchufs dh	1.98 (5.88)	5.00	0.00	1.00	4.00	0.00	1.00*	0.00	0.00	0.00	1.00*
S_2tchmpfs b1	1.91 (2.14)	7.00	0.00	1.00	4.00	1.00*	0.00	0.00	0.00	0.00	0.00
S_2tchufs b2	1.89 (1.07)	4.00	0.00	2.00*	3.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2mpfs dh	1.74 (-6.95)	4.00	0.00	1.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchmpfs b2	1.74 (-6.95)	9.00*	0.00	2.00*	6.00*	0.00	0.00	0.00	0.00	0.00	0.00
S_2ufs st	1.73 (-7.49)	3.00	0.00	1.00	2.00	0.00	1.00*	0.00	1.00*	0.00	0.00
S_2tchufs rsi-1	1.72 (-8.02)	6.00	0.00	1.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchmga	1.71 (-8.56)	7.00	0.00	1.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2tchufs rsi-2	1.70 (-9.09)	7.00	0.00	1.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00
S_2ufs b1	1.69 (-9.63)	5.00	0.00	1.00	4.00	1.00*	0.00	0.00	0.00	0.00	0.00
S_2mpfs lf	1.54 (-17.65)	10.00*	0.00	1.00	7.00*	0.00	0.00	0.00	0.00	0.00	0.00
S_2ufs yld	1.48 (-20.86)	5.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00
C_0	1.87	4.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00
Lsd (0.05)	1.13	5.00	0.00	1.00	3.00	1.00	1.00	0.00	1.00	1.00	1.00

+, Values in parentheses represent observed gain expressed as % of the source population (C_0)
*, Significant at $P < 0.05$
Nl1, Np1 = number of larvae and pupae at 4 weeks after infestation, respectively.
Nl2, Np2 = Number of larvae and pupae at harvest at harvest, respectively.

CHAPTER 5

5.0 DISCUSSION

G 1984 - 1983 enetic variability is a pre-requisite for effective selection in any maize improvement programme. Means and ranges for parameters of resistance, grain yield and desirable agronomic traits used in this study were large in the two progeny types suggesting genetic variability in the maize variety ICZ3. This was confirmed by significant differences among genotypes in the S_2 progeny type for leaf feeding and yield components (stand count, ear number, ear weight ear length and grain weight). This suggested that there was opportunity for improvement of the various traits investigated. Also, although there were no significant differences between genotypes for dead heart and stem tunnelling in both progeny types, selection was carried out in order to exploit hidden variability due to unbroken linkages during the recombination phase. Generally, the S_2 families consistently showed larger ranges for most of the traits than the test crosses. Similarly, genetic (σ^2g) and phenotypic (σ^2p) variances were also large and higher among the S_2 families. These results compare well with those reported by Mulamba and Mock (1978), Obilana et al (1979), Opeke (1983) and Adeyemo

(1986) and more recently, Ajala (1992b) who worked on different maize populations and observed genetic variability for grain yield, desirable agronomic traits and seedling emergence.

Estimates of genotype X environment (g x e) interactions were large in some cases implying that the traits were influenced to some extent by the environment. However, negative values obtained in other instances does not indicate that the traits were insensitive to changes in the environment, rather, such cases do arise from computational method due to mean square from g x e being smaller than the error mean square. This could have been due to differential rankings of the genotypes as a result of poor weather conditions. More so during the time of artificial infestation of the C. Partellus larvae leading to poor establishment. Rather than the analysis model being not sensitive enough to etect all the error variance (Kang, 1990).

Heritability estimates reported here, though in the broad sense, are reliable for predicting progress from seletion (Obilana et al, 1981) since the genetic variances for each trait in each progeny type were moderate to high except in some instances where low estimates for parameters of resistance and agronomic traits occurred. It, therefore, seems that selection would be effective and in the desired direction. Heritability values for selection indices were also of sufficient magnitude to suggest that aggregate improvement of the population for C. partellus resistance using parameters of resistance would be feassible and progress from such selections would equally be high.

For improvement of pest resistance and grain yield as an aggregate of resistance parameters (leaf feeding, dead heart and stem tunnelling) together with yield, it was of interest, in this study, to find whether the traits were correlated. In general, phenotypic correlation coefficients were lower than genotypic correlations, indicating that the genotype primarily determined the phenotypic correlations (Robinson et al, 1951). Genotypic correlations among resistance traits were on the whole high, except for those between leaf feeding and stem tunnelling. Genotypic correlations among these traits and grain yield were indicative of the possibility of simultaneously improving the population by index selection in the two progeny types.

Correlations between the resistance parameters and the selection indices with mature plant characteristics including grain yield were generally very low, except for a few agronomic traits, implying that damage levels could not be used as measure of expected yield for the materials studied. Such findings are in agreement with that of Ajala et al (1993).

Since grain yield is of paramount importance to the breeder, possible contribution of each of the damage parameters examined using stepwise multiple regressions indicated that in both the testcrosses and S_2 lines, stem tunnelling was more important in yield reduction than any of the other damage parameters. In S_2 progenies leaf feeding seemed to contribute less towards yield reduction. Mohyuddin and Attique (1978) and Pathak and Othieno (1990) attributed yield reduction in maize to be caused more by dead heart. Results obtained in this study do not seem to concur with the observations of these researchers. Further investigations may be needed in this area since leaf feeding damage reduces the photosynthetic tissue required for the processes leading to grain filling whilst stem tunnelling damages the vascular tissues required for translocation of nutrients from the soil. It is also worth noting that yield in maize is measured on a plot basis which in the event of loss of one or a few plants through dead heart damage, there is the tendency to compensate by the other plants in way of utilising more of the available resources such as sunlight and soil nutrients such compensation has been very effective in tillering or branching plant species. However, correlation is a bivariate relationship that measures the association between a pair of variables independent of other variables, therefore there is the possibility of multicollinearity and/or spurious correlation, both of which are limitations to the use of correlations. Multicolinearity being a situation whereby the variables considered are highly inter-correlated.

Expected responses to grain yield and parameters of resistance due to index selection were much lower than when each of the traits was selected directly 1984 - 1983. In all cases, single trait selections would result in almost twice the progress expected from index selection. Opeke (1983) noted that relative to single trait selection, index selection usually gives lower progress from selection because superiority of a trait is negated by mediocrity of other traits included in the index.

Populations and their crosses may be improved by increasing the frequencies of genes that have more desirable dominance, additive and epistatic effects (Genter, 1973). However, populations, like inbred lines, may have high combining ability if they contain major genes for desirable dominant and additive effects, but they may be low in yield if they also contain homozygous deleterious recessive genes of sufficient effect to suppress or depress yield. Observed S_2 selections showed more gain/cycle in grain yield (23.21 %) as compared to 7.90 % of the testcrosses suggesting that there was effective selection for genes that contribute to yield and perhaps effective selection against genes that depress yield when homozygous. The higher predicted gains to selection in the S_2 families were as expected on the basis of high variances for most of the characters. Similar results by Genter (1973), Eckebil et al (1977) and Adeyemo (1986) show that S_1 or S_2 family selection may be superior to the testcross selection method. Matzinger, 1953 opined that broad gene based testers are more efficient than narrow gene based testers for the evaluation of general combining ability in inbred lines of maize. The importance of performance level or gene frequency of the tester as a criterion for choice of testers, however, has never been clearly established (Rawlings and Thomson, 1962). As Hull(1945) pointed out that theoretically the most efficient tester would be one that is homozygous recessive at all loci and that homozygosity for dominant alleles at any locus should be avoided; in the present study the original population was used as the tester for regeneration of the test crosses. Perhaps the posible explanation for the low variances and in effect the low predicted gains to selection would be due to the presence of homozygosity for dominant alleles at certain loci of the tester population and hence not being able to discriminate amongst genotypes effectively for selection purposes. Also, researchers have attributed the inferiority of testcross selection method compared to S_1 family selection to the fact that an extra season is required for the testcross method hence more resources in terms of labour, land e.t.c. required unlike in the S_1 method.

Smith-Hazel index gave more progress than the rank summation indices (RSIs) of Mulamba and Mock (1978) in the two progeny types. However, progress from RSIs (4.64% - 33.33%) was much more realistic than for the Smith-Hazel index which was (20.03% - 85.71%). Probably, the best index would depend on ease of handling in addition to giving appreciable progress to selection. Studies suggesting approaches aimed at reducing limitations associated with selection index construction have been reported (Elston, 1963, Pesek and Baker, 1969b, 1970) but the problems in assigning appropriate economic importance (weights) to each trait and those associated with extensive computation still exist. RSIs, therefore have the advantage of not only giving appreciable progress for aggregate gain but also the ease with which they can be handled.

Generally, predicted gains to selection showed poor correspondence with the observed gains. On average the observed gains exceeded the predicted gains for all traits in both the progeny types for single and aggregate traits. Although the results for the rank summation indices (RSI-1 and RSI-2) the predicted gains were higher than what was realized.

Reports in literature have shown different findings. Widstrom et al (1992),while working on leaf feeding damage by fall army worm in maize obtained results which concurred with the results in the present study. Also, Moll and Robinson (1966) showed similar findings. However, the results of the present study differed with those of Eckebil et al (1977), Silva and Lonnquist (1968) and Schipper and Frey (1991). The discrepancies observed could be attributed to the presence of non-additive variation which often biases the estimation of genetic variance or the effects of geenotype x environmental interaction. A lot of concern has been shown over the adequacy of some of the prediction formulae more so with the S_1 family selection method where the estimated response to selection is from the genetic variance among the S_1 family means (Eckebil et al, 1977 and Bradshaw, 1983). Further investigation is, therefore, required in order to improve on prediction equations.

Correlated responses among traits are important considerations in breeding programmes where more than one trait is usually improved simultaneously. Results obtained in this study suggest that selection for any of the parameters of resistance and RSI would lead to the improvement of grain yield, but in most cases, such gain would be lower than that expected from direct selection for grain yield *per se.* However, selection for some traits would result in better correlated responses in some traits than in others. For instance, selecting for increased plant height would invariably lead to increased ear height but not necessarily increased grain yield. In all cases, predicted correlated responses for single and aggregate trait selections did not agree with the observed correlated responses. Probably due to the same reasons which cause discrepancies between expected and observed direct response to single and aggregate traits.

Evaluation of progress after one cycle of selection for leaf feeding and stem tunnelling in both progeny types revealed a reduction of 0.11 in leaf rating corresponding to a decrease of 4 % per cycle. Stem tunnelling was improved by 2 % corresponding to actual gain of 14 % per cycle. The response obtained in this study suggests that recurrent selection for simultaneous reduction in foliar damage and stem tunnel length due to C. partellus attack is feasible. More cycles of selection would therefore be required to significantly shift the gene frequencies. Widstrom et al (1992) noted that S_1 progeny selection reduced leaf feeding damage by larvae of the fall arny worm by 0.31 per cycle after five cycles of selection.

It was of interest to determine the effect of selection for reduction in both leaf feeding and stem tunnelling on plant height. Increase in plant height is an undesirable character commonly associated with yield in tropical maize germplasm (Miranda Filho, 1985). Results obtained in this study showed a similar trend. Grain yield increased by 5.29 to 24.23 per cycle relative to the source population with the plant height increasing by 4 %. Excessively tall plants can lead to stalk lodging especially in windy weather (Ajala, 1990). The association or correlated response to selection for a trait on other unselected traits occur either due to linkage or pleiotropy (Fakorede, 1982). The increase in plant height and grain yield associated with selection for parameters of resistance, as observed in this study, may probably be due more to pleiotropy than linkage because recombination phase in the selection procedure could have broken up existing gene combinations while creating new ones.

Reduction in ear height with selection for reduced folliar damage, dead heart and stem tunnelling was observed. Acosta and Crane (1972), Jinahyon and Russell (1969) observed positive correlated response for grain yield with selection for reduced ear height as well as with improved stalk-rot resistance in maize. The reduction in ear placement with reduced stem tunnelling dead heart and leaf feeding could have been due to correlated responses that are obligate rather than facultative. Facultative correlated responses is a situation where certain traits are affected in one selection programme and different traits in another. According to Lerner (1958) such responses occur because of differences in combinations of alleles in one population relative to the other. For example, combinations of alleles with a net "plus" effect on character Y may be linked with plus acting alleles for character X in one population and with "minus" alleles in another. In such a case, selection to improve the mean performance of X in the two populations will invariably be accompanied by correlated responses of Y in the opposite direction. Obligate correlated responses are associated with decreased fitness. In this study, obligate correlated responses could have been the cause of decreased ear height in ICZ3 maize population. And such may be due to linkages that were not broken during the recombination phase.

There are several kinds of adverse effects expressed by the antibiosis mechanism of resistance. Wilson et al (1984) showed that for Corn Ear Worm (CEW) larvae feeding on silks incorporated into a pinto bean diet, those feeding on susceptible silks took half as long as those on silks from resistant material to gain equal weight. Ampofo et al (1986b) observed that of the total number of first instar larvae released on a plant, 8.7 % larval recovery was obtained in a resistant cultivar (MP704) compared to 23.4 % in susceptible cultivars. With reference to the larval development, the percentage of the recovered insects which had reached pupal stages ranged from nil in MP701 and MP704 to 44.7 in the susceptible materials. Similar observations were made by Kumar (1993) who reported significant loss of weight in larvae artificially infested on resistant maize cultivar (MP704) compared to the susceptible (inbred A). Inbred A was a very susceptible line to *C. partellus* attack and one of the lines used in the development of maize hybrids in Kenya. Of the larvae recovered from inbred A, most of them were in the fourth instar and a few had advanced to fifth instar. However, in cultivar MP704, the percentage of larvae in the fourth instar was signifcantly ($P < 0.01$) lower than that of the susceptible inbred A. Results in this study indicate a low percentage of larval recovery after 28 days of infestation which ranges from 10 to 33.33 % of the initial first instar larvae used for artificial infestation. These observations suggest that C_1 populations were highly resistant to C. partellus larvae damage. This, however, was anticipated since the population (ICZ3) from which the sub-populations were developed was moderately resistant to the pest. The type of mechanism of resistance as observed in this study was antibiosis. And the most antibiotic of the C_1 populations being sub-population 2 which was developed as a single selection for stem tunnelling from S_2 progenies. On this C_1 population, a significantly (LSD, 0.05 $P < 0.05$) greater percentage of larvae remained in the fourth instar, suggesting slower growth than in the other sub-populations.

The ultimate objective of this study was to simultaneously improve the level of resistance to C. partellus attack, grain yield and desirable agronomic traits using appropriate selection parameters or aggregate traits in ICZ3 maize population. Reduction in foliar rating damage by 0.11 per cycle and stem tunnel length by 2 % per cycle, increased grain yield by 5.29 to 24.23 % per cycle, plant height by 4 %

per cycle together with positive correlated responses in yield components attest to significant additive genetic variation and success of the recurrent selection process. More cycles of selection would further concentrate resistance genes in this population thus making ita good germplasm source for resistance to *C. partellus* larvae damage

6.0 CONCLUSIONS AND RECOMMENDATIONS.

The two recurrent selection methods (S_2 and S_2 TCH) employed in the present study to determine the genetic variation in ICZ3 maize population for parameters of resistance, grain yield and related agronomic traits showed that S_2 family selection method revealed higher genetic variation than the S_2 testcross method. The differences in the responses to selection observed in the two progeny types indicated that different types of genes had increased in importance. Means and ranges obtained for various traits indicated that the tester used for S_2 testcross selection was effective in increasing the frequencies of genes with dominant effects that improved yield of crosses and also those of deleterious genes that suppress yield when homozygous as shown by the slow response to selection in the testcrosses. A low yielding tester developed from ICZ3 population rather than the population itself would have eliminated the problem of depressed yield by homozygous alleles.

The present study showed that rank summation indices (RSIs) were better in predicting progress to selection than the Smith-Hazel indices (b_1 and b_2). This could be attributed to the problem of assigning economic weight to each of the traits included in the construction of the Smith-Hazel indices. For construction of these indices , parameters of resistance were each assigned a negative economic weight of 1. In assigning these values it was assumed that the contributions of the parameters of resistance towards yield reduction were equal. However, the results obtained in this study showed that their contributions were different in the two progeny types. Also, yield per se may not be a satisfactory measure of economic value in maize, since such characters as lodging, ear height, husk cover and plant height have a bearing on the final yield expression. Hence the economic weight of 1 assigned to yield in the construction of the Smith-Hazel index (b_2) may not be appropriate. There is, therefore, need to investigate how much each of the three damage parameters used in the present study contributes towards the genetic worth of the genotypes.

The best 10% of the genotypes from each progeny trype (S_2 and S_2TCH) were selected for recombination. Results obtained after one cycle of selection for grain yield and parameters of resistance including related agronomic traits showed that some imrovement was made. However, dramatic increases in levels of resistance were not expected for the population was known *a priori* to have moderate to high levels of resistance to C. Partellus attack. The situation would have been different if the best 20 % of the genotypes were selected. This would probably avoid loss of genotypes with desirable recessive alleles through reduced selection pressure. And this might have led to higher correlated gains to selection as well.

Results obtained in this study showed that the cycle one (C_1) selections were highly resistant to C. Partellus larvae damage and the mechanism of resistance was antibiosis. However, breeding for tolerance rather than resistance per se may be a better option since high yielding varieties with the ability to withstand high levels of infestation could be obtained. It is, therefore, recommended that the C_1 populations be assessed for tolerance. That way, rather than completely eliminating the insect, tolerant varieties so obtained could co-exist with the insect. It is also recommended that some infussion of new materials be done in future related research studies in order to increase the level of variability of the ICZ3 population. That way, together with more cycles of selection, would further concentrate resistance genes in this population. The results showed no significant genotypic differences for majority of the parameters of resistance.

The C_1 populations developed in this study, therefore, could be recommended for the early and medium maturity agroecological zones as well as the coastal and lake regions in Kenya and elsewhere in the tropics where C. Partellus is a serious crop pest.

7.0 REFERENCES

Acosta, A.E. ,and Crane, P.L. 1972. Further selection for lower ear height in maize. Crop Sci. 12:165-167.

Adeyemo, M.O. 1986. Genetic variability and predicted responses to selection in a Nigerian maize (Zea mays L.) population. Phd. thesis, department of Crop Sci. Univ. of Ife, Ile-Ife, Nigeria. 124pp.

Ajala, S.O. 1990. Combining ability for maturity and agronomic traits in some tropical maize (Zea mays *L.*) populations Trop. Agri. (Trinidad) 69 (1):29-34.

Ajala, S.O. 1992a. Inheritance of resistance in maize to the spotted stem borer Chilo partellus (swinhoe). Maydica. 37:363-369.

Ajala, S.O. 1992b. Selecting maize (Zea mays L.) Lines for developing varieties better adapted to small farm environments. J. Genetics and Breeding. 46:215-220.

Ajala, S.O., Mutinda, C.M., Chiliswa, P. 1993. Heterotic effects and association of Chilo partellus (Swinhoe) resistance parameters with mature plant traits in some maize populations. African Crop Sci. jour. 1:9-13.

Ajala, S. O. and Saxena, K. N. 1994. Registration of ICZ3 and ICZ4 Maize Germplasms with resistance to spotted Stem Borer *Chilo partellus* (Swinhoe). Crop Sci. 34: 317-318.

Allard, R.W. 1960. Principles of plant breeding. John Wiley and sons, inc. , New York. 485pp.

Allison, J.C.S. and Curnow, R.N. 1966. The choice of tester parent for the breeding of synthetic varieties of maize (Zea mays l.). Crop Sci. 6:541-544.

Ampofo, J.K.O and Saxena, K.N. 1984. Evaluation of germplasm from other centres (USA). ICIPE Annual Report. 1984: 10-11.

Ampofo, J.K.O., Dabrowski, Z.T and Omolo, E. 1986a. Registration of ICZ1-CM (GP 145) and ICZ2-CM (GP 146 M Maize Germplasm lines. Crop Sci. 26:650.

Ampofo, J.K.O. , Saxena, K.N. , Kibuka J.G. , Nyangiri, E.O. 1986b. Evaluation of some maize cultivars for resistance to the stem borer Chilo partellus (swinhoe) in western Kenya. Maydica. 31:379-389.

Ariyo, O.J. 1989. Variation and heritability of fifteen characters in Okra (Abelmoschus esculentus (L.) Moench). Trop. Agric. (Trinidad) 67 (3):213-216.

Bradshaw, J.E. 1983. Estimating the predicted response to S1 family selection. Heredity 51:415-418.

Bosque-perez, N.A., Mareck, J.H. Dabrowski, Z.T. ,Everett, L. ,Kim, S.K. and Efron, Y. 1987. Screening and breeding maize for resistance to Sesamia calamistis and Eldana saccharina. p163-169 Proceedings of the international symposium on methodologies for developing host plant resistance to maize insects. In Toward Insect Resist ant Maize for The Third World.

Brazzel, J.R. and Martin, D. F. 1956. Texas Agr. Expt. Sta. Bull. 843, 20pp.

Brindley, T.A. and Dicke, F.F. 1963. Significant developments in European Corn Borer in North America. Ann. Rev. Entomol. 8:155-176.

Brindley, T.A. , Sparks, A.N., Showers, W.B., Guthurie, W.D. 1975. Recent research advances on the European Corn Borer in North America. Ann. Rev. Entomol. 20: 221-239.

Browning, J.A. and Frey, K.J. 1969. Multiline cultivars as a means of disease control. Phytopath. 7:355-382.

Burton, J.W. , Penny, L.H., Hallauer, A.R and Eberhart, S.A. 1971. Evaluation of synthetic populations developed from a maize variety (BSK) by two methods of recurrent selection. Crop Sci. 11:361-367.

Coon, B.F. 1946. Resistance of soybean varieties to japanese beetle attack. Jour. Econ. Entom. 39:510-513.

Darrah, L.L. , Eberhart S.A. and Penny, L.H. 1978. Six years of maize selection in 'Kitale synthetic II' , 'Ecuador

573' and 'Kitale composite A' using methods of the comprehensive breeding system. Euphytica 27:191-204.

Davis, F.M. and Williams, W.P. 1986. Survival, growth and development of South Western Corn Borer (Lepidoptera: Pyrallidae) on resistant and susceptible maize hybrids. J. Econ. Entomol. 79: 847-851.

Eckebil, J.P. , Ross, W.M. , Gardner, C.O. and Maranville, J.W. 1977. Heritability estimates, genetic correlations and predicted gains from S_1 progeny tests in three grain sorghum random- mating populations. Crop Sci. 17:373-377.

Elston, R.C. 1963. A weight free index for the purpose of ranking or selection with respect to several traits at a time. Biometrics 19:85-97.

Empig, L.T. , Gardner, C.O.and Compton, W.A. 1972. Theoretical gains for different population improvement procedures. Nebraska Agric. Expt. Stn. Mp 26 revised.

Fakorede, M.A.B. and Mock, J.J.1982. Correlated responses to recurrent selection foor grain yield in maize. Agriculture and Home Econ. Expt. Stn. Iowa state Univ. of Sci. and Tech. Research Bull. 596:179-204.

Falconer, D.S. 1960. Introduction to quantitative genetics. Ronald press company, New York, 365 pp.

FAO. 1991. Production year book vol 44: 283pp.

Frey, K.J. 1981. Plant breeding II. Iowa state Univ. Press, Ames, 497pp.

Frey, K.J. and Horner, T. 1955. Comparisons of actual and predicted gains in barley selections. Agron. J. 47:186-188.

Gallun, R.L., Starks, K.J. ,Guthrie, W.D. 1975. Plant resistance to insects attacking cereals. Ann Rev. Entomol. 20:337-357.

Gardener, C.O. 1978. Population improvement in maize p207-208 in Walden, D.B (ed) Maize breeding and genetics John Wiley and sons inc; New York.

Genter, C.F. 1973. Comparison of S_1 and testcross evaluation after two cycles of recurrent selection in maize. Crop Sci. 13:524-527.

Gomez, K.A. and Gomez, A.A. 1984. Statistical procedures for agricultural research, 2nd edition. John Wiley and sons, New York. 680pp.

Guthrie, W.D. , Dicke, F.F. and Neiswander, C.R. 1960.Leaf and sheath feeding resistance to the European Corn Borer in eight inbred lines of dent corn. Ohion Agric. Exp. Stn. Res. Bull. 860, 38pp.

Guthrie, W.D. 1989. Breeding for insect resistance in maize. Plant breeding reviews 6:209-243.

Hallauer, A.R. 1981. Selection and breeding methods p3-55 in Frey K.J. (eds) Plant breeding II. Iowa state univ. Press ; Ames, Iowa. 468pp.

Hallauer, A.R. and FO Miranda, J.B. 1988. Quantitative genetics in maize breeding 2nd edition.Iowa state Univ. Press, Ames. 468pp.

Hallauer, A.R. , Russell, W.A. and Lamkey, K.R. 1988. Corn breeding p463-564. In G.F. Spraque and J.W. Dudley (eds) corn and corn improvement. ASA, CSSA, and SSSA, Madison, W1.

Harris, R.E. , Gardner, C.O. and Compton, W.A. 1972. Effects of mass selection and irradiation in corn measured by random S_1 lines and their testcrosses. Crop Sci. 12:594-598.

Hazel, L.N. 1943. The genetic basis of constructing selection indices. Genetics 28:476-490.

Hoard, K.G. and Crosbie, T.M. 1985. S1 line recurrent selection for cold tolerance in Two maize populations. Crop Sci. 25:1041-1045.

Horner, E.S. , Lutrick, M.C. , Chapman W.H. and Martin, F.G. 1976. Effect of recurrent selection for combining ability with single cross tester in maize. Crop Sci. 16:5-8.

Hull, F.H. 1945. Recurrent selection for specific combining ability in corn. Journal Amer. soc. Agron. 37:134-145.

ICIPE 1990. Improvement and development of maize for resistance to stem borers. 18th Annual Report: 26-28.

ICIPE 1991. Integrated pest management of crop borers for resource poor farmers in Africa: Achievements and Highlights (1980-1990). ICIPE Science Press, Nairobi, Kenya.

Isley, D. 1928. The relation of leaf colour and leaf size to bollweevil infestation. J. Econ. Entomol. 21:553-559.

Jinahyon, S. and Russell, W.A. 1969. Effects of recurrent selection for stalk rot resistance on other agronomic characters in an open-pollinated variety of maize. Iowa state J. Sci. 43:239-251.

Kang, M.S. 1990. Genotype by environment interaction and plant breeding. Louisiana state university, Baton Rouge, Louisiana, 392pp.

Kim, S.K. 1992. Host plant resistance: polygenes vs major gene.IITA research briefs no5:20-21.

Kornegay, J.L. and Temple, S.R. 1986. Inheritance and combining ability of leaf hopper defense mechanisms in common bean. Crop Sci. 26:1153-1158.

Kumar, H. , Enock, M.O. , Nyangiri E.O. and Asino, G. O. 1993. Colonization responses and damage by Chilo partellus (Lepidoptera:Pyrallidae) to four variably resistant cultivars of maize. J. Econ. Entomol. 86:739-746.

Lerner, I.M. 1958. The genetic basis of selection. John Wiley and Sons, inc. , New York.

Lonnquist, J.H. 1967. Mass selection for prolificacy in maize. Zuchter 37:185-188.

Lonnquist, J.H. 1968. Further evidence on test cross versus Line performance in maize. Crop Sci. 8:50-53.

Matzinger, D.F. 1953. Comparison of three types of testers for the evaluation of inbred lines of corn. Agron. J. 45:493-495.

Maxwell, F.G. and Jennings, P.R. 1980 (eds). Breeding plants resistant to insects. John Wiley and sons.

Merkle, O.J. , Webster, J.A. and Morgan, G.H.1987. Inheritance of a Greenbug resistance in Barley. Crop Sci. 27:241-243.

Miranda Filho J.B., 1985. Breeding methodologies for tropical maize. In: Breeding strategies for maize production in the tropics. pp. 177-206, Florence and Bergano, Italy. FAO of United Nations. Instituto Agronomico per L'oltremare, Firence, 1985.

Mize, T.W. and Wilde, G. 1986. New grain sorghum sources of Antibiosis to the Chinch bug (Heteroptera: Lygaeidae) J. Econ. Entomol. 79:176-180.

Mohyuddin, A.I. and Attique, M.R. 1978. An assessment of loss caused by Chilo partellus to maize in Pakistan. PANS 24:111-113.

Mock, J.J. and Eberhart, S.A. 1972. Cold tolerance in adapted maize populations. Crop Sci. 12:466-469.

Moll, R.H. and Stuber, C.W. 1974. Quantitative genetics. Emperical results relevant to plant breeding. Adv. Agro 26:279-313.

Moll, R.H. and Robinson, H.F. 1966. Observed and expected response in four selection experiments in maize. Crop Sci. 6:319-324.

Mulamba, N.N. and Mock, J.J. 1978. Improvement of yield potential of Eto Blanco maize (Zea mays L) population by breeding for plant traits. Egypt. J. Gen. cytol. 7: 40-51.

Mutinda, C.J.M. 1989. The genetic stability of somaclonal regenerants of forage grasses. Msc. thesis University of Wales, Aberystwyth, U.K. 103pp.

Nyhus, K.A. , Russell, W.A.and Guthrie, W.D. 1989. Changes in Agronomic traits associated with recurrent selection in two maize synthetics. Crop Sci. 29:269-275.

Obanni, M. , Ohm, H.W. , Forster, J.E. and Patterson, F.L. 1989. Genetics of resistance of P1 422297 Durum wheatto the Hessian fly. Crop Sci. 29:249-252.

Obilana, A.T. , Hallauer, A.R. and Smith, O.S. 1979. Estimated genetic variability in a maize interpopulation. Journal of Heredity 70: 127-132.

Obilana, A.T. and Fakorede, M.A.B. 1981. Heritability: a Treatise. Samaru J. Agric. Res. 1:72-82.

Olonju, Dixon A.G. , Bramel-Cox, P.J. , Harvey, T.L. 1990. Diallel analysis of resistance in sorghum to green bug Biotype E:- Antibiosis and tolerance. Crop Sci. 30:1055-1059.

Omolo, E O. 1983. Screening of local and exotic maize lines for stem borer resistance with special reference to Chilo partellus (Swinhoe) in maize. Insect science and its application. 4:105-108.

Onokugu, F.A. , Guthrie, W.D. , Russell, W.A. , Reed, G.L. and Robbins, J.C. 1978. Location of genes that condition resistance in maize to sheath collar feeding by second generation European Corn Borer. J. Econ. Entomol. 71:1-4.

Opeke, B.O. 1983. Genetic variability for seedling emergence and its relationship with mature plant characteristics in maize. M.sc. Thesis, University of Ife, Ile-Ife, Nigeria. 91pp.

Ortega, A., Vassal, S.K.V. and Hershey, C. 1980. Breeding for resistance in maize. pp370-419 In maxwell, F.D. and P. R. Jennings (eds) Breeding plants resistant to insects. Wiley, New York, N Y.

Overholt, W.A. 1991, ICIPE/WAU Crop Pests Biological Control: Classical Biological Control of Chilo Partellus. ICIPE Annual Report 1991 p29-31.

Painter, R.M. 1951. Insect resistance in crop plants. Macmillan New York, 520pp.

Pathak, R.S and Othieno, S.M. 1990. Inheritance of resistance to the spotted stem borer. Chilo partellus (swinhoe) in maize. Maydica. 35:247-252.

Penny, L.H. and Dicke, F.F. 1956. Inheritance of resistance in corn to leaf feeding by European Corn Borer. Agron. J. 48:200-203.

_________ and ________ . 1957. A single gene pair controlling segregation for European Corn Borer resistance. Agron. J. 49:193-196.

Penny, L.H., Scott, G.E. and Guthrie, W.D. 1967. Recurrent selection for European Corn Borer resistance in maize. Crop Sci. 7: 407-9.

Pesek, J. and Baker, R.J. 1969a. Comparison of tandem and index selection in the modified pedigree method of breeding self-pollinated crops. Can. J. Plant Sci. 49:773-781.

Pesek, J. and R.J. Baker, 1969b. Desired improvement in relation to selection indices. Can. J. Plant Sci. 49:803-804.

Pesek, J. and Baker, R.J. 1970. An application of index selection to the improvement of self pollinated species. Can. J. Plant Sci. 50:267-276.

Rao, N.G.P., Rana, B.S. , Bala Kotaiah, K. , Tripathi, D.P. and Fayed, M.F.S. 1974. Genetics of some exotic indian crosses in Sorghum viii. F1 analysis of ovipositional non-preference underlying resistance to Sorghum Shootfly. Indian genet. Pl. Breed. 34:122-127.

Rawlings, J.O. and Thomson, D. L. 1962. Performance level as criterion for the choice of maize testers. Crop Sci. 2:217-220.

Robinson, H.F. , Comstock, R.E. and Harvey, R.H. 1949.

Estimates of heritability and the degree of dominance in corn. Agron. J. 41:353-359.

__________________________________ and ______________ . 1951. Genotypic and phenotypic correlations in corn and their implications in selection. Agron. J. 43:282-287.

Russell, W.A. , Eberhart, S.A. and Vega, U.A. 1973. Recurrent selection for specific combining ability for yield in two maize populations. Crop Sci. 13: 257-261.

Schipper, H. and Frey, K.J. 1991. Observed gains from three recurrent selection Regimes for increased Groat oil content of oat. Crop Sci. 31:1505-1510.

Scott, G.E. , Hallauer, A.R. and Dicke, F.F. 1964. Types of gene action conditioning resistance to European Corn Borer leaf feeding. Crop Sci. 4:603-604.

Scott, G.E. , Guthrie, W.D. and Pesho, G.R. 1967. Effects of second brood European Corn Borer infestation on 45 single cross corn hybrids. Crop Sci. 7:229-230.

Smith, H.F. 1936. A discriminant function for plant selection. Ann. Eugen. 7:240-256.

Silva, da W.J. and Lonnquist, J.H. 1968. Genetic variances in populations developed from Full-Sib and S_1 testcross progeny selection in an open pollinated variety of maize. Crop Sci. 8:201- 204.

Theuri, J.M. , Njuguna, J.G.M. and Ininda, J. 1988. Incidence of maize streak disease in central Kenya. A report to the Director KARI.

Visser, J.H. and Minks, A.K. 1982. Insect-plant relationships P337-346. In Proceedings of the 5th international symposium on insect-plant relationships. Wageningen,the Netherlands 1-4 March, 1982.

Velsammy, R., Heinrichs, E.A. and Khush, G.S. 1987. Genetics of field resistance of rice to Brown plant hopper. Crop Sci. 27:199-200.

Walker, P.T., 1967. A survey of losses of cereal to the pests in Kenya and Tanzania. united nations food and Agriculture Organization symposium on crop losses. Rome 2:79-88.

Walters, S.P. , Russell, W.A. and Lamkey, K.R. 1991. Performance and genetic variance among s_1 lines and test-crosses of Iowa Stiff Stalk synthetic maize. Crop Sci. 31:76-80.

Warui, C. M. and Kuria, J. N. 1983. Population incidence and the control of maize stalk borers _Chilo partellus_ (Swinhoe), _C_. _Orichalcociliellus_ strand and _Sesamia Calamistis_ Hmps in coast province, Kenya. Insect Science and its application 4:11-18.

Widstrom, N.W. , Williams, W.P., Wiseman, B.R. and Davis, F.M. 1992. Recurrent selection for resistance to leaf feeding by Fall Armyworm on maize. Crop Sci. 32:1171-1174

Williams, J.S. 1962. The evaluation of a selection index. Biometrics 18:375-393.

Williams, W.P. , Davis, F.M. 1983. Recurrent selection for resistance in corn to tunnelling by the second brood south western corn borer. Crop Sci. 23:169-170.

Williams, W.P. , Buckley, P.M. , Davis, F.M. 1989. Combining ability for resistance to fall armyworm and south western corn borer. Crop Sci. 29:913-915.

Wllson, R.L. , Wiseman, B.R. and Widstrom, N.W. 1984. Growth response of Corn Ear Worm larvae on meridic diets containing fresh and lymphilized corn silk. J. econ. ent. 77:1159-1162.

Wiseman, B.R. 1985. Types and mechanisms of host plant resistance to insect attack. Insect.Sci. and its applic. 6:239-242.

Wiseman, B.R. 1987. Technological advances for determining resistance in maize to <u>Heliothis</u> <u>zea</u>. Proceedings of the international symposium on methodologies for developing host plant resistance to maize insects p94-100. In toward insect resistant maize for the third world.

8.0 APPENDIX

1.1: Codes of the 35 sub-populations (C_1) derived from ICZ3 (C_0) maize population.

1 S_2uf leaf feeding
2 S_2uf stem tunnelling
3 S_2uf dead heart
4 S_2uf yield
5 Tchufs leaf feeding
6 Tchufs stem tunnelling
7 Tchufs dead heart
8 Tchufs ield
9 S_2 mbita leaf feeding
10 S_2 mbita stem tunnelling
11 S_2 mbita dead heart
12 S_2 mbita yield
13 Tch mbita leaf feeding
14 Tch mbita stem tunnelling
15 Tch mbita dead heart
16 Tch mbita yield
17 S_2 ufs rsi-1
18 S_2 ufs rsi-2
19 Tch ufs rsi-1
20 Tch ufs rsi-2
21 S_2 mbita rsi-1
22 S_2 mbita rsi-2
23 Tch mbita rsi-1
24 Tch mbita rsi-2
25 S_2 ufs b1
26 S_2 ufs b2
27 Tch ufs b1
28 Tch ufs b2
29 S_2 mbita b1
30 S_2 mbita b2
31 Tch mbita b1
32 Tch mbita b2
33 S_2 com yield
34 Tch com yield
35 Tch Mga yield.

Ufs = Ungoye field site, Mbita = Mbita point field station

S_2com, Tchcom = selections for yield based on two sites (UFS and Mbita)

B1, B2 = Smith -Hazel index based on parameters of resistance (leaf feeding, dead heart and stem tunnelling) and parameters of resistance and yield, respectively.

rsi-1, rsi-2 are as described in the text.