Inheritance of Weevil Resistance in Maize

By

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Declaration

I, **Ntjapa Gabriel Lebaka** hereby declare that this dessertation represents my own work and that it has not been previously submitted for a degree at this or any other university.

N. G. Lebaka

Signature

16-11-2000

Date

APPROVAL

This dissertation of **Ntjapa Gabriel Lebaka** is approved as fulfilling the requirements for the award of the degree of Master of Science in Agronomy by the University of Zambia

Signature:	Date:
Mungoma	9th August, 2000
	14th November 2000
	14/11/2000

Dedication

I dedicate this piece of work to my parents Ralehakoe Machona Paramente (deceased) and 'Matsebo Lebaka, and all my brothers and sisters for their unwavering support throughout my school life. Removed far away from home social environment of which I am part coupled with failure to adapt physically would have easily gotten me down to a point of quitting had I not a strong purpose. Every time my power runs out and I stagger to fall down, the thought of it comes back strongly and I rise again to continue. "I must make it at all odds so that we can all rejoice over it". May God bless you all.

Abstract

The study of the inheritance and gene action of weevil resistance in maize was undertaken using a 12 parent half diallel design. Seven resistant inbred lines were obtained from CIMMYT-Zimbabwe and five susceptible lines were obtained from Soils and Crop Research Branch (SCRB), Zambia. The lines were planted and crossed at Golden Valley Agricultural Research Trust (GART) in the 1998/99 growing season. The F_2 and selfed parental lines were raised at UNZA field station in winter of 1999 under irrigation. Because of the loss of some crosses and inbred lines due to unsuccessful seed production, 8 parents and 28 crosses were used in genetic analysis.

For each of these entries three replicates each of 100 grams grain was prepared and put in a clean glass jar of 0.5 litre volume. The jars were randomly arranged on three shelves in a controlled environment room at 25 ± 2^0C and 70 ± 5% relative humidity. Each entry appeared once on each shelf and each shelf was treated as a block. Twenty adult unsexed maize weevils were placed in each jar containing grain and the jars were closed with cotton cloth securely tied with the rubber bands to prevent the insects from escaping. After 21 days the jars were opened and all the insects were removed. The jars were left standing in this environment for 42 days. The jars were then opened and the insects and dust were sieved through a 5 millimeter sieve. The number of adult insects emerging were counted and recorded. The weight of the remaining grain was taken and weight loss was calculated. The grain was put back into the respective jars which were laid back on the shelves to stand for another 30 days after which the jars were removed. The same procedure was repeated and data of number of insects recovered and weight loss was recorded. These were added to the previous readings to give total number of emerged insects and total weight lost for each sample.

Three replicates each of 50 grams grain for each entry was prepared and placed in a plastic bag. This grain was for determining the grit in the grain. The grain samples were then milled at constant speed for 60 seconds in a small electric powered mill. The meal was weighed and seived through 0.5 millimeter seive to separate grit from fine meal. The remaining grit was weighed and hardness was expressed as percent grit of the total meal.

Data for percent grit was transformed using square root transformation and the data for number of insects was transformed using logarithmic transformation. Straight scale was used for weight loss. The analysis of weevil resistance involved using Griffing's diallel analysis method 2 assuming fixed effects. Heritability and relative dominance estimates were made under random effects model.

General combining ability (GCA) and specific combining ability (SCA) effects were significant for number of insects and weight loss at both infestation periods. At 63 days infestation period, GCA accounted for 49 and 71.42% of the total genetic variation for weight loss and number of insects, respectively. Relative dominance was 1.28 and 0.81 for weight loss and number of insects, respectively. Broad sense heritabilities were

76.25 for weight loss and 54.09 for number of insects. Narrow sense heritabilities were 29.01 for weight loss and 15.18 for number of insects.

However at 93 days infestation, GCA to SCA ratios changed for both weight loss and number of insects. GCA accounted for 69.28% for weight loss and 72.42% for number of insects. Relative dominance was 0.84 for weight loss and 0.80 for number of insects. Broad sense heritabilities were 46.66 for weight loss and 63.16 for number of insects. Narrow heritability was 17.37 for weight loss and 24.27 for number of insects.

Grain hardness did not appear to influence grain weevil resistance as judged by insignificant correlation coefficients between percent grit and weight loss and percent grit and number of insects. For percent grit both GCA and SCA were significant but SCA effects accounted for 87.16% of the total genetic variation. Relative dominance for this trait was in the range of overdominance (3.89).

These findings suggest that recurrent selection for general combining ability or reciprocal recurrent selection for reduced grain weight loss as a measure of weevil resistance can be an appropriate breeding method to improve weevil resistance in maize. The same cyclic selection methods would be appropriate for reducing the number of insects after infestation which is another measure of weevil resistance in maize. Results indicate that selection for weight loss would result in faster progress at 63 days infestation while number of insects would result in faster progress at 93 days infestation period.

Recurrent selection for specific combining ability would be an appropriate breeding method for grain hardness. However progress from selection would be slow and a big population would be required as narrow sense heritability was too low.

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INTRODUCTION

1.1 Background

Maize is native to Mexico and Central America (Galinat, 1976; Purseglove, 1972 and Dowswell et. al., 1996). Globally it is the most widely distributed crop, though in magnitude of production it comes third after wheat and rice among cereals (Purseglove, 1972).

There are three main purposes for which maize is used. As a staple human food maize has replaced the traditional starchy foodstuffs such as sorghum and millet in parts of Africa, particularly in South Africa, Malawi, Zimbabwe and Kenya and considerable sections of Zambia, Tanzania, Angola and Mozambique (Purseglove, 1972). It provides 25% of the people's total dietary protein. Maize is therefore an important food crop in Africa. Table 1 shows the dominance of maize as a major source of calorie intake in the Southern African Development Community (SADC) region. This indicates, in general, that the majority of people in the region derive their dietary protein from maize. Apart from its use as a major source of food, maize is a major component of feed for livestock particularly in temperate countries. In industrialized countries maize also forms an important raw material for many industrial products (Purseglove, 1972).

Table 1. Average national per capita calorie intake from maize relative to the total dietary consumption (%) for the SADC countries.

Country	Calories
Zambia	56
Malawi	54
Lesotho	46
South Africa	40
Zimbabwe	37
Swaziland	36
Namibia	30
Tanzania	36
Botswana	25

Source: Dowswell et. al.,1996 (FAO 1989 - 90 statistics)

There are several constraints facing production of maize for food in developing countries. These include inadequate financing for inputs such as fertilizer, pesticides and herbicides. Furthermore the scarcity of improved varieties and inadequate farm power which lead to late and unsatisfactory plantings as well as late harvesting have adversely affected maize production in developing countries. Further losses are also incurred in storage due to lack of improved storage facilities (Kang et. al.,1995 and Nhlane, 1989). The major sources of postharvest damage are storage pests which include maize weevil (*Sitophilus zeamais*) and the larger grain borer (*Prostephanus truncatus*) (Dowswell et. al., 1996 and Dicke, 1976).

Adoption of improved varieties such as hybrids has been hampered by their susceptibility to storage pests. Consequently this forced farmers to continue using their own traditional varieties or landraces which are resistant to storage pests but low yielding (Nhlane, 1989). Most of the hybrids are of dent type while the landraces are flint.

The flint type maize have kernels whose entire outer portion is composed of hard starch giving it a shiny surface while the dent type maize have kernels with hard starch confined to the sides of the endosperm. The amylose or soft starch forms the core and cap of the endosperm of both types of maize. The flint kernel absorbs less moisture and is less susceptible to spoilage during storage and transportation (Dowswell et. al., 1996 and Nhlane, 1989).

1.2 Justification

It is undoubted that maize is an important staple food in many developing countries. While maize production could be adequate, the realization of full value of the production is hampered by the post-harvest losses, especially those during storage. In African countries maize yield averages about 1.2 metric tons per hectare compared to an average of 6 metric tons per hectare in North and Central America (Kochhar, 1986 and Efron, 1985). In Africa further losses in storage are not desirable and should be mitigated (Nhlane, 1989).

While storage losses can be reduced by use of improved storage structures, most smallholder farmers cannot afford building such structures. As a result most of them have preferred their own varieties which, despite their low yielding ability, have better storability characteristics. Most of the landraces are of flint type and in addition to their better storability they have attributes associated with their hardness which are desirable in food preparations (Dowswell et. al., 1996 and Nhlane, 1989). According to Hill and Waller (1990) the local flint varieties may show 5 to 10% infestation within 30 days of storage while the dent varieties will show 60 to 80% infestation over the same period with the total damage realized after 6 months.

It is therefore clear that for maize productivity to be increased through use of improved varieties among smallholder farmers, maize varieties with better storability should be developed. Breeding efforts therefore must be targeted toward improving

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1.3 Objectives

The objectives of this study were:

1. To study the efficacy of three determinants of weevil resistance in maize, that is grain hardness, grain weight loss due to insect infestation and degree of infestation.
2. To study the inheritance of these traits and their application in practical plant breeding to improve weevil resistance in maize.

1.4 Hypothesis

This study was based on the premise that there exists heritable resistance to storage weevils in maize and that this trait could be selected for to develop genotypes which would have resistance to the maize weevil.

LITERATURE REVIEW

2.1 Crop Description

Maize (*Zea mays*) is an annual crop which requires warm weather with a rainfall amount of 400 to 600 mm during its growth period (Larson and Hanway, 1977). Maize requires more rain at flowering followed by three-week period after silking and then vegetative stages of growth (Larson and Hanway, 1977 and Classen and Shaw, 1970).

Maize is a monoecious plant having both male and female flower parts borne on the same plant but spatially separated. The staminate flower is borne terminally in the tassel. The pistillate flower is borne in the ear about half-way along the length of the stalk . The female and male flowers on the same plant normally mature at different times (protandrous) and this enhances outcrossing and therefore maize is normally about 95% cross-pollinated (Poehlman, 1987). The tassel normally sheds mature pollen before the silk is receptive. Repeated selfing of maize results in inbreeding depression which may be characterised by small stature, reduced pollen and seed set as well as reduced vigour and increased tenderness. But crossing of the inbreds produced by repeated artificial selfing has been effectively used by breeders to produce more vigorous hybrid plants which perform much better than either parent (Poehlman, 1987).

The maize seed develops from the ovule following a double fertilization process in which the diploid (2n) embryo is formed from paternal and maternal gamete fusion. The endosperm is formed by fusion of the two maternal nuclei and the paternal nucleus forming triploid (3n) tissue. After fertilization seed development followed by grain-filling continue normally for a period of about 60 days (physiological maturity) after which moisture loss occurs (Larson and Hanway, 1977) up to the time when harvesting is done (Russell and Hallauer, 1980).

2.2 Storage hazards

Maize is normally harvested from the field when the moisture content is about 13%. At this moisture content the grain is considered safe for storage. During storage maize is susceptible to pest damage, especially if the storage conditions are at about 25^0C and 65% relative humidity (Larson and Hanway, 1977 and Russell and Hallauer, 1980).

In the tropics the storage pests commonly encountered in stored grain are the grain weevils (*Sitophilus* spp.). This is especially so where storage facilities are not good (Dicke, 1977). A new pest known as larger grain borer (*Prostephanus trancutus*) introduced from Southern America, has become yet another important pest.

When the stored crop is heavily infested with the pests, there is loss both in terms of weight and quality. Many research workers have reported weight loss as the main form of weevil damage. However, quality reduction together with predisposition to disease has also been reported. For example, Sinha (1984) reported extensive germ and endosperm damage, significant increases in free fatty acids and fungal (*Aspergillus glaucus* group spp. and *Penicillium* spp.) as well as bacterial infections. Both pathogens are more actively destructive at the temperature of about 25^0C and humidity of about 65%. The crop is infested by the pests when it is still growing in the field though recognizable damage occurs, invariably, in storage (Floyd, 1971; Giles, 1971 and Dicke, 1977).

To date the most commonly used method of control against storage pest damage has been and continues to be chemical in nature. This involves use of chemical reagents applied in different formulations to inhibit multiplication of the insect by either directly killing it or inhibiting its fecundity. However, the chemical method has been brought into disrepute by environmental concerns since the chemical may enter the food chain. The high cost associated with this method also renders it less popular to the resource-poor farmers.

Giles and Ashman (1971) proposed three measures of prevention against the storage pest namely;

1. use of contact insecticides after harvest,
2. cleaning and spraying empty stores not later than pollination. This is so because the stores often serve as the source of infection. The insect develops in stores and the adults which are strong flyers find their way

into the fields to infest the crop after seed set and;

3. use of resistant varieties.

To be able to fully realise the potential of host resistance it is necessary to understand the biology; life cycle, the stages at which the insect becomes injurious to the crop including the time it actually infests the crop. Also important would be the characteristics of the crop that actually render it more favourable or unfavourable as feed for the pest.

2.3 The maize weevil (*Sitophilus zeamays Motsch.)*

The maize weevil is a major pest in tropical areas and lower temperate zones. It is also commonly known as larger rice weevil. The weevil is cited in most literature as one of the major insect pests causing damage to stored cereals (Dicke, 1977; Widstrom et. al., 1975; Kang et. al. 1996; Derera and Pixley, 1998 and Derera et. al., 1998).

Maize and rice weevil adults are dark reddish-brown in colour and about 3-4 millimetres long. They have light spots on each wing cover or elytra. They have well developed wings, a densely pitted thorax and prominent legs. The larvae are white, legless, thick-bodied grubs (Dicke, 1977).

The adult weevils chew small cavities in the grain in which eggs are singly deposited and protected by the 'waxy plug'. Of the 150 eggs the adult lays in its lifetime, which may span up to one year, 50% may be laid during the first 3 - 4 weeks of its life. The pest normally over-winters in grain in the form of eggs. In summer when temperature and humidity become favourable eggs hatch into larvae which feed on the germ and endosperm in the grain. At an average temperature of about 25^{0}C and relative humidity of about 70%, the eggs hatch in about six days after oviposition. The life cycle then proceeds through four larval instars taking about 25 days before pupation. Pupation takes place in the cavity chewed by the larvae. After about four days the adult weevil appears from the cocoon and chews its way out of the grain leaving the characteristic large irregular emergence hole on the grain surface. Both the adult and the larvae feed on the grain but the larva causes the greatest damage. The pest takes about 35 days to complete its life cycle at 25^{0}C and 70% relative humidity (Igbal et. al. 1992).

The adult beetles are powerful fliers and this favours easy spread and establishment of field infestation. Dicke, (1977) states that infestation in the field begins as soon as the grain has become firm. This occurs when the moisture content has dropped to below 60% (Giles and Ashman, 1971). The degree of infestation is determined by tightness and extension of the husk.

2.4 Host Resistance

2.4.1 Description of 'Resistance'

Painter (1961) describes host resistance as a phenomenon involving 3 components; that is preference or non-preference, antibiosis and tolerance. Preference or non-preference involves a group of plant characteristics and pest responses that determine the behaviour of the insect either to use or not to use the host for oviposition, food or shelter or a combination of the three. Antibiosis refers to the ability of the plant to prevent, injure or destroy insect life. Tolerance on the other hand involves the capacity of the host tissue to tolerate damage by the pest. Thus host resistance involves one or a combination of these components.

2.4.2 Characteristics associated with kernel resistance to storage pests

Most research workers concur that although storage pests cause damage to the product at storage, the actual infestation occurs in the field (Eden, 1952 a and b; Floyd and Powell, 1958; McMillian, 1968; Floyd, 1971; Giles and Ashman, 1971 and Dicke, 1977) and the amount of damage the crop will suffer at storage for a given genotype at a given environment is a function of the degree of field infestation (Floyd, 1971). Several characteristics of maize genotypes have been reported to influence resistance of maize to storage pests (Table 2). However not all attributes operate together to confer resistance for a given genotype at a given environment.

Table 2 Summary of the characteristics of maize associated with weevil resistance as reported in literature

Maize traits associated with resistance	**Traits in resistant maize genotypes**	**Authors whose findings concur**
Number of husk leaves, husk extension and tightness	Many husk leaves, well extended beyond free end of the cob and tightly wrapped around the cob	Dicke, 1977, Ramalho, 1977, Eden, 1952 a and b; Widstrom et. al., 1970,; McCain et. al., 1964, Kossou et. al.,1993, Kossou et. al.,1994 Floyd and Powell, 1958, McMillian, 1968 and Giles and Ashman, 1971
Kernel hardness	Hard endosperm and flinty kernel	Kossou et. al., 1994, Ramalho, 1977, Eden, 1952 b; Russell, 1962; Singh and McCain, 1963; McCain et. al, 1964 Russell and Rink, 1965; Dobie, 1974; Lorenzoni and Motto, 1985 and Kiregyera, 1994, Pant et. al., 1964; Purseglove,

		1972; Nhlane, 1989 and Dowswell, 1996, Urrelo et. al., 1991, Sarmiento and Ubaldo, 1978, Morales 1974
Carbohydrates composition	Lower concentration of amylopectin, glycogen and reducing sugars, higher content of maltose, polysaccharides, low sugar content and amylose	Singh and McCain, 1963, Chippendale, 1972,, McCain et.al.,1964, Rhine and Staples, 1968, Peters et. al., 1960 and Peters et. al., 1972 a and b.
Protein composition and amount	High protein content, low content of tryptophan and lysine	Dobie, 1977, Kiregyera, 1994 and Arnason et. al., 1994, Bentazos-Mentoza, 1982 and Morales, 1974
Phenolic compounds	High content of phenolic compounds particularly tannins, lignin, coumaric acid and ferulic acid	Taiz and Zeiger, 1990, Arnason et. al., 1994, Serratos et. al., 1994
Proteinase inhibitors	High content of proteinase inhibitors	Serratos, 1994
Fat content	High fat content	Peters et. al., 1972 b

Maize is partly protected from infestation by the husk in the field. Varieties with cobs tightly wrapped with well extended husks have been reported to be more resistant to infestation in the field. However, the two traits, number of husks and husk extension, are independent (McCain et. al., 1964). The degree of infestation increases with the exposure of the cob (Floyd and Powell, 1958; McMillian, 1968 and Giles and Ashman, 1971). Kossou et. al. (1993) reported husk cover as the major weevil resistance component that separated the traditional and the improved varieties in their weevil resistance. The traditional varieties had a tight, extended husk cover compared to the loose and less extended husk cover of the improved varieties. Therefore some varieties are resistant by virtue of their husk tightness and husk extension.

Apart from the husk the kernel itself has an influence on ultimate activity of the insect. The adult insect has to chew a hole on the kernel in order to oviposit the eggs. Many research workers have reported that kernel hardness has an influence on resistance to storage pests (Table 2). Flint is reported to be more resistant to storage pests than dent maize (Pant et. al., 1964; Purseglove, 1972; Nhlane, 1989 and Dowswell, 1996), floury maize (Morales, 1974 and Urrelo et. al., 1991), opaque-2 endosperm maize (Morales, 1974 and Gupta et. al., 1974) and starchy maize (Sarmiento and Ubaldo, 1978).

Shelled maize has been reported to show a higher degree of infestation than unshelled maize because on unshelled maize the preferred softer for both oviposition and emergence of adults are not easily accessible on closely packed kernels on the cob. The insect prefers the softer side opposite the embryo for oviposition emergence than the hard, horny surfaced crown (Kossou et. al., 1994 and Ramalho, 1977).

However Derera and Pixley (1998) found that some flint maize varieties were resistant while others were susceptible and some dents were equally resistant. Widstrom et. al. (1975) also established weevil resistance among test materials derived from dent inbred lines. Peters et. al. (1972 b) reported a significant negative effect of kernel hardness on the weight of male moths, but hardness did not have an effect on female moths. Schoonhoven (1972) observed that hardness did not influence resistance but undamaged pericarp did convey resistance. Eden (1952 b) also found no correlation between pericarp thickness and rice weevil damage.

The chemical composition of the kernel also plays an important role in the determination of weevil resistance in maize. Since the insect larvae inhabit and derive their nutrition from within the grain the chemical constitution of the kernel is very critical. At this level the component of resistance at play could be designated antibiosis and tolerance rather than preference which has more effect on the behaviour of the adult insects. Gomez et al., (1982) and Tipping et. al. (1988) found no relation between food suitability and attractiveness. However, Bernabe - Adalla et. al. (1978) observed that the preferred genotypes were also more suitable for development. Chippendale's (1972) study on the effect of diets with different carbohydrates composition on survival of adult rice weevil, *Sitophilus oryzae* provided important revelation about feed requirements of the weevils (Tables 3 and 4). Feed containing 40% or more of amylopectin supported the insects in a way similar to a normal feed situation (Table 3). However, when amylopectin was reduced in proportion mortality increased untill at 0% amylopectin where mortality equalled the one where no feed was given (Table 3). The study revealed that amylopectin was an essential dietary component for normal adult survival and at least 30% amylopectin was necessary for normal survival of adult weevil.

Results from the studies of the effect of various types of carbohydrates on the survival of adult rice weevils (Table 4) showed that dietary branched chain alpha (1-- 4) and alpha (1-- 6) linked polymers of glucose, Amylopectin and glycogen respectively, permit normal adult survival. Insects fed on maltose had a mortality similar to those placed on no food while those placed on its hydrolytic products, dextrin I and II had normal development. Maltose and glucose, which are hydrolytic products of starch, induced high mortality. However, it was presumed that weevils can absorb mono- and disaccharides and therefore the observed high mortalities must have resulted from unacceptable physical inconsistencies. Starch on the other hand provided a suitable physical feeding environment. High mortality among insects fed on polysaccharides was believed to have resulted due to deterrence and subsequent starvation, inability to digest polymers or a combination of both factors.

Table 3. Effect of Dietary Amylose: Amylopectin ratios on survival of Adult rice weevils

Amylose (%)	Amylopectin (%)	Mortality (%)
100	0	98
80	20	23
60	40	8
40	60	15
20	80	13
0	100	10

Source: Modified from Chippendale, 1972

Table 4. Effect of various carbohydrates on survival of adult rice weevils

Diet	Mortality
Corn	3
Glycogen	13
Cellulose	98
Inulin	100
Dextrin I or II	9
Glucose	90
Maltose	100
No food	100

Source: Chippendale, 1972

A further assessment of preference revealed starch as feeding stimulant with amylopectin being an active component, which on free-choice was more preferred than common starch. Inulin and cellulose were feeding deterrents while dextrin I and II and maize starch had equivalent feeding results on insect behaviour. Corn starch was more preferred to glucose and maltose presumably because the latter two did not meet the weevil requirements and not necessarily, that they were feed deterrents. Maize containing low content of certain carbohydrates probably has the most weevil resistance under field conditions (McCain et.al.,1964).

Rhine and Staples (1968) also found that 60% amylose reduced the number of adults that emerged and adult weight but had no appreciable effect on average time of adult emergence. However 70% amylose also reduced adult weight but increased adults emerged compared to 60% amylose and normal corn with 25% amylose. Dobie (1974) observed a positive correlation between kernel hardness and amylose content. He proposed that amylose had a small effect on susceptibility in addition to that conferred by hardness. McCain and Eden (1965) reported that susceptibility of inbreds, expressed as number of adults emerging, was positively correlated with reducing sugars and not total sugar content. Kiregyera (1994) reported that sugar content had no influence on weevil resistance. Amylose was also reported to reduce insect weight, increase development period and reduce the number of insects reaching adult stage (Peters et. al., 1960 and Peters et. al., 1972 a and b).

Some research workers have reported negative correlation between protein content and susceptibility to weevil (Table 2). Despite earlier perceptions that high-lysine maize is more susceptible to weevil some high-lysine maize hybrids have been found to have very good resistance to weevil (Derera and Pixley, 1998; Derera and Pixley 1998; Van der Schaaf et. al., 1969 and Schoonhoven, 1972). Santos et. al. (1996) also reported genotypic variations among the quality protein maize as to their resistance to maize weevil. It was concluded that the quality protein maize apart from carrying genes for enhanced protein also carries genes for resistance to maize weevil and it is the constitution at this loci that will determine the resistance status of the genotype. McCain (1963) reported that fat and protein did not affect corn susceptibility in the field. Singh et. al. (1972) also found that protein content was not related to resistance.

Bentazos - Mentoza (1982) reported that tryptophan content of maize was associated with maize weevil resistance in maize tested between 120th and 270th days of the experiment. Morales (1974) found that percent tryptophan and lysine were positively correlated with number and weight of the weevil.

Apart from primary products, plants also produce a large and diverse array of organic compounds collectively known as secondary products. These are also called secondary metabolites because they do not have any direct function in growth and development. Taiz and Zeiger (1990) indicated that the principal function of these metabolites is to defend the plant against herbivore and pathogen attack. Phenolics are a group of such metabolites. Simple phenolics such as ferulic acid and coumaric acid take part in plant - herbivore, plant - fungus and plant - plant interactions. Lignin, a complex phenolic macromolecule with both primary and secondary function, deters feeding by animals and has a chemical durability that makes it relatively indigestible to herbivores (Taiz and Zeiger, 1990). Tannins are polymeric phenolic compounds that function as feeding deterrents to herbivores. Tannins are reported to act as toxins that significantly reduce growth and survivorship of many herbivores when added to their diets. In humans, for example, tannin is reported to cause sharp, unpleasant astringent sensation due to their binding of the salivary protein (Taiz and Zeiger, 1990).

The influence of phenolic compounds on susceptibility of maize to maize weevil and larger grain borer has recently been reported (Arnason et. al., 1994 and Serratos et. al., 1994). Arnason et. al. (1994) reported the correlation of -0.93 (P = 0.002) between total phenolics and grain weight loss caused by larger grain borer. In both maize weevil and larger grain borer E-ferulic acid, the major phenolic compound in maize, had a significant negative correlation with susceptibility of the varieties. A significant negative correlation (r>-0.8, P = 0.05) between E-ferulic acid content and developmental parameters of maize weevil was observed. The correlation between E-ferulic acid content and grain weight loss caused by larger grain borer was also significant (r=-0.88, P=0.01). P-coumaric acid was only significant (r=-0.70, P=0.006) for percent damaged kernels from larger grain borer. It was also observed that the grain phenolic content was significantly and positively correlated with kernel hardness and vitreous endosperm content. It was suggested that phenolic acids contribute to mechanical hardness by cross-linking of the cell-wall hemicellulases through formation of diferulate. This strengthens the cell-wall resulting in the observed correlation between hardness and phenolic content. Phenolic amides such as diferoyl and dicoumaroyl putrescine may be antibiosis factors to maize weevil. Serratos et. al. (1994) also reported a significant negative correlation between phenolics and susceptibility of maize to maize weevil. It was suggested that phenolic fluorescence may be used as a rapid indicator of resistance by breeders who might wish to do prescreening of material for resistance to maize weevil and larger grain borer.

Proteinase inhibitors produced in response to insect infestation have also been reported to confer resistance to insect herbivores and pathogens. Proteinase inhibitors inhibit proteinase action in insect guts thus affecting their development and survivorship on resistant feed. Serratos et. al. (1994) reported that there exists an excellent negative correlation for proteinase inhibitor concentration with susceptibility of maize to maize weevil.

Gomez et al., (1982) used several indices which were correlated to see how they related to each other. Two endosperm variants; *opaque-2* and *waxy* genes were evaluated. The larvae consumed more of the hybrid than the inbreds though food utilization efficiency for hybrids was lower. It was concluded that the germ had toxic effects on the young larvae and was suitable for late instars and essential for normal development. Richards (1944) also reported that maize germ was toxic to the first instar larvae but Schoonhoven (1974) reported that addition of small germ to pellets increased the number of progeny and weight while reducing development time. However addition of larger amounts of germ tissues reduced the number of adults and their weight. Widstrom et. al. (1975) also observed that the single crosses were consistently more eaten than top-crosses. This was attributed to the possible intrakernel competition since top-cross kernels weigh more, the same weight for single crosses would have more kernels than for the top cross. *Opaque-2* gene reduced food utilization efficiency while *waxy* gene increased it. However both genes reduced time to pupation compared to normal genes. This means that the two variants are more suitable for multiplication than the normal genotypes. The *waxy* kernel fostered higher food utilization than *opaque-2.* Days to pupation was negatively correlated with fresh weight, dry weight and exponential mean live weight of the adults. Amount of food eaten, amount of faeces and consumption index were high for hybrids though food utilization was lower. Although hybrids were eaten more than the inbreds they did not support larger weight. Gomez et. al. (1983) reported that larval period was reduced and heavier pupae developed when fed on high glucose corn. Larvae reared on germless pelletized corn required longer period to pupate, produced lower pupal weights and lower food utilization efficiency than the ones reared on pelletized whole kernel. Mortality was, however, similar in both germless and whole kernel pellets indicating that while germ reduces larval period it is not essential for normal development *per se.* Homogenised distribution reduced larval development time.

Contradicting results were reported on influence of grain fat content to weevil susceptibility. Kiregyera (1994) reported that it had no influence while Peters et. al. (1972 b) observed a negative correlation between moth weight and fat content.

2.5 Genetics and heritability of maize weevil resistance

Several research workers have reported on the heritability of maize weevil resistance (Widstrom et. al., 1975; Tipping et. al., 1989; Widstrom et. al., 1983; Kang et. al., 1996; Derera and Pixley, 1998; Derera et. al., 1998 and Derera et. al., 1998). Widstrom et. al. (1975) using diallel crosses among maize inbreds derived from 80 lines found that both maternal and endosperm genotypes contributed significantly to maize weevil resistance. Both additive and dominance components were important although the larger estimates of maternal-associated intra-locus interaction effects indicated that dominant or non-additive genetic effects were more important. Cytoplasmic effects were not important. It was suggested that for a selection procedure to be efficient it must utilize both additive and dominant variation of maternal and endosperm genotypes. Recurrent selection within populations and reciprocal recurrent selection between populations was suggested. Two populations were suggested; population A consisting of crosses among inbreds common to most resistant single-crosses and population B consisting of the crosses which involved those inbreds which performed well when crossed with those in A but were not themselves in A. Kang et. al. (1996) found the estimates of general combining ability

(GCA), specific combining ability (SCA) and reciprocal effects to account for 44.5%, 20.8% and 34.6%, respectively in resistance of maize weevil (preference) among F1 seed. The combined analysis of F1 and F2 revealed that both GCA and SCA were significant in subset 1 while only GCA was significant in subset 2. For each subset a further test of SCA x years and GCA x years was performed. The results showed that maize weevil preference can well be predicted from GCA alone. GCA accounted for 60.5% for subset 1 and 55% for subset 2. The results obtained over seasons indicated lack of interaction, meaning the results for one season could fairly predict progeny performance for weevil preference. Recurrent selection among populations developed using the inbreds with significant positive GCA to incorporate the genes for nonpreference was suggested. The inbreds which had significant negative GCA were said to contribute to weevil preference. One of the inbreds (Mo17) which had significant negative GCA also had significant positive maternal effect while the other one (B17) had a significant negative maternal effect. Kang et. al. (1996) concluded that B17 should not be used as a female in commercial hybrids where weevil is a problem. The significant positive and negative SCA were also observed between some inbreds. Significant positive reciprocal effect was also observed indicating that the crosses in which it was observed could not be made in a reverse direction where maize weevil is a problem. Mo17 x B73 had significant SCA as well as reciprocal effects. GCA was more important than SCA and therefore recurrent selection was suggested as an appropriate breeding approach.

Tipping et. al. (1989) also reported that GCA and to a lesser extent SCA effects were important in the inheritance of resistance to oviposition by maize weevil. Significant maternal effects occurred in F_1 but were not expressed past the F_1 generation. Environmental effects were significant with Florida maize being more susceptible than the one in Kentucky. But resistant genotypes in one environment were among the most resistant in the other station generally.

The findings by Widstrom et. al. (1975) and Kang et. al. (1996) concur with those by other research workers (Derera and Pixley, 1998; Derera et. al., 1998 and Derera et. al., 1998). However Derera et. al. (1998) reported that both GCA and SCA were of equal importance in contrast to Kang et. al. (1996) who reported that GCA was more important than SCA in free-choice experiments. Widstrom et. al. (1975) also reported that additive effects (GCA) originating from maternal tissues were important under no-choice environment. Dominance effects (SCA) were also important for resistance among sources segregating for maternal and endosperm genotypes. Derera et. al. (1998) reported that additive, non-additive and maternal effects were important in maize weevil resistance (no-choice). Maternal effects were not important under free-choice (Derera et. al., 1998) or were of less consequence applying to just a few crosses (Kang et. al., 1998). Widstrom et. al. (1983) reported that GCA, maternal effects (through pericarp) and nuclear genotype were important and recurrent selection among the population composed of 15 best crosses was suggested for a breeding program. Serratos et. al. (1994) reported on the genetics of phenolics, proteinase inhibitors and three indices of susceptibility to maize weevil using three models of Mather and Jinks (1982) (MJ), Huidong's (1988) (HU) and

Serratos et. al. (1993) (SE) model. Significant estimated additive parameters for phenolics, proteinase inhibitors and indices of susceptibility to maize weevil infestation were observed in MJ and HU models. Rheological traits were not significant. In SE model only an estimated additive parameter for phenolics was significant. None of the dominance parameters were significant in MJ and HU. Dominance of endosperm-pericarp for phenolics in grain, and dominance of pericarp for phenolics, maximum force of compression and index of susceptibility were highly significant in the SE model.

Gomez (1983) reported that in a 6 x 6 diallel weevil resistance was controlled by the addition and / or interaction of several factors. These factors may be controlled by more than one gene locus. In his experiment one line, B37 transmitted resistance more efficiently than the other one, A632. In crossing, the susceptible loci in Mo17 were unmasked.

Li-RuMing et. al. (1998) reported that genetic variability for weevil resistance does exist in maize but they found the broad sense heritability of 0.21, suggesting a very slow progress from selection. Genotype by environment interaction was not detected but genotype by year (G x Y) was relatively large.

While it is true that considerable work has been done in this area, the existing variation observed from one place to the other points to the need for careful study of this character as it applies to a given population before a breeding approach can be selected. Inheritance of weevil-resistance is complex and it presents an intriguing challenge in the area of research (Derera and Pixley, 1998). The aspect of environment requires special attention. Russell (1962) and Russell and Rink (1965) used the same material in different localities and seasons and obtained contrasting results for both resistance and hardness. In one experiment one variety was the hardest and most resistant but in the second experiment this was the softest and most susceptible with the one that was most susceptible and softest coming up as the hardest and most resistant. Tipping et. al. (1989) also reported significant environmental effects.

MATERIALS AND METHODS

3.1 Description of the conduct of experiment

3.1.1 Phase 1

The first phase of the study involved making crosses among twelve inbred lines, seven weevil resistant from International Maize and Wheat Improvement Centre (CIMMYT) - Zimbabwe and five weevil susceptible from Soils and Crops Research Branch (SCRB) - Zambia. The lines were planted at Golden Valley Agricultural Research Trust (GART) in December, 1998 in a crossing block for diallel crossing among the inbred lines. The pedigrees of the parental lines involved in the crosses are given in Table 5. D-compound (10 N : 20 P_2O_5 : 10 K_2O) fertilizer was applied at the rate of 400 kg/ha prior to sowing. Furadan was applied at the rate of 10 l/ ha to control cut-worms. Weed control was done both by hand and a single application of 5 l/ ha of primagram herbicide. The ears of the intended female plants were covered with glycine bags before the silk was exposed and at the extrusion of the first flush of silk, the tip of the ear was carefully cut back with the pair of scissors to enhance uniform thick silk protrusion. The tassel of the intended male plant was covered one day prior to pollination. Pollination was then done by transferring pollen in the paper bag, carefully removing the bag on the ear and quantitatively shedding the pollen on exposed silk and covering the ear with the same bag used to collect pollen. Only one-way crosses were made. There were no reciprocal crosses. To raise the seed of

Table 5 Inbred lines used in the study of weevil resistance in maize

Inbred line #	Stock ID	Material pedigree	Susceptibbility	Origin
Z160585-86	1	[M605-302-3-X/ZM607#b37SR-2-3sr-6-2-X]-4-1-X-2-2-B-B	resistant (0)	CIMMYT-Zimbabwe
Z13-146	2	CML204	resistant (0)	CIMMYT-Zimbabwe
Z160510-13	3	[EBN 102/[MSR:131]-3-3-3-X]-1-X-3-B-B	resistant (3.1)	CIMMYT-Zimbabwe
Z153505/509	4	(H614/AW)-X-3063-2-2X-1-B	resistant (3.8)	CIMMYT-Zimbabwe
Z160429-30	5	8232/TZMSRW]sr-124-1-X/ZM607#bF37sr-2-3]-2-3-X-1-2-B-B	resistant (3.9)	CIMMYT-Zimbabwe
Z160356-59	6	RA 87C3108-X-5-1-1-5-X-X-B-B	resistant (3.9)	CIMMYT-Zimbabwe
Z160425-26	7	1188XF2834T-5Y-1-2W-X-2-B-B	resistant (4)	CIMMYT-Zimbabwe
L334	8		susceptible (11)	SCRB
L911	9		susceptible (11)	SCRB
L913	10		susceptible (11)	SCRB
L12	11		susceptible (11)	SCRB
LN3'	12		susceptible (11)	SCRB

Susceptibility index of 0 to 5 indicates resistant material while the index of more than 5 designates susceptible lines. Inbred lines from GART were assumed to have susceptibility index of 11 though it was not established.

the inbred lines the male plants were also selfed. The seed of the crosses and inbred lines were harvested and threshed separately for the next planting.

3.1.2 Phase 2

The second phase of the study involved planting the crosses and selfed parental inbred lines at the University of Zambia (UNZA) field station in May 1999. Only one site was used for this phase of the study because some of the crosses at GART were not successful while other crosses yielded very little quantity of seed to enable the experiment to be sited at more than one location. There were 58 F_1 crosses and 10 selfed parental inbred lines used in the second phase of the experiment to raise F_2 seed for weevil resistance evaluation instead of the expected 66 F_1 crosses and 12 selfed parental lines in the study.

The 68 entries were evaluated in a randomized complete block design with three replications. Each entry was planted in three row plots of two-meter length. The fertilizer application rate of 400 kg of D compound per hectare as basal dressing and 400 kg of urea per hectare as top dressing was applied. Phoskill was applied regularly to control the stalk-borers which were prevalent. Since the crop was raised during the dry season, irrigation was done once a week to maintain moisture content close to field capacity. At flowering, eight ears were covered with plastic bags to exclude foreign pollen. The tassels of five plants, randomly selected within each plot, were covered two days before pollination. At pollination the pollen from selected plants in the plot was bulked and used to pollinate the ears that were covered with plastic bags within the plot. Once pollinated these ears were then covered with paper bags until harvest. To avoid mixing pollen the hand was dipped in the methylated spirit before moving on to pollinate the next plot.

At harvest each plot was harvested separately and only those ears which were still covered at the time were harvested and shelled separately. The rest of the cobs in each plot were harvested, shelled and separately weighed and their weight added to that of the shelled artificially pollinated cobs to estimate plot yield. However, the artificially pollinated grain was kept separate from the open pollinated grain. It was the artificially pollinated (F_2) grain with that of the selfed parental inbred lines which was used for evaluating weevil resistance in the third and final phase of the study.

3.1.3 Phase 3

The grain was dried for five days in the fan-ventilated oven set at a temperature of 5^{0}C to bring the moisture content to an average 13%. Grain of the same genotype rom the three replications was bulked and thoroughly mixed. Three 50-grams amples of each genotype was used for the Dobie (1974) laboratory assessment of ernel hardness measure of insect resistance test. For this test the 50 gram sample f grain from each genotype was milled at the constant speed for 60 seconds. The round sample was sieved through a 0.5 mm apertures and the retained grit and he mealie-meal portions were weighed and percent grit of the combined weight for each sample was recorded.

In addition to the Dobie's (1974) hardness test, a direct test of weevil resistance in storage was carried out by subjecting the seed to insect infestation and assessing grain weight loss. For this test three samples of 100 grams of clean, undamaged grain for each genotype was placed in 500 ml disinfected glass jars. Twenty adult maize weevils previously raised on maize were placed in each jar. The lid with its top part removed and replaced with cotton cloth was firmly tied back to prevent the insects from escaping while allowing free air movement. The jars were placed in a dark constant environment room conditioned at 27 ± 2^0C and 70 ± 5% relative humidity. Each genotype appeared once on each of the three shelves. Each shelf was taken as a block. After 21 days the adult insects were removed and the lids replaced. The set-up was left under the same conditions for 42 days after which the bottles were removed and opened. The insects and debris were then removed by sieving through 5 mm aperture sieve and the number of adults recovered was recorded. The remaining grain was weighed and the weight lost derived.

The remaining grain was put back into the respective jars and laid back on the shelves and left to stand under the same condition for another 30 days. The jars were then removed, insects and debris sieved as before and the number of insects recovered counted while final weight was taken and further weight loss was calculated and recorded. The final data was added to data obtained on the first run. The data were taken as the second readings and were analysed separately from the data obtained on the first readings.

3.2 Statistical Analysis

The data collected was analysed as a randomized complete block design using Mstat C computer program. Prior to analysis, data on the number of insects recovered was transformed using the Log (x + 1) transformation. Data on residual %grit was also transformed using log transformation.

Griffing's diallel analysis method (1956) was used to study the genetics of the following three measures of weevil resistance in maize;

(a) kernel hardness as measured by % grit after milling

(b) Degree of infestation as measured by number of insects recovered after infestation

(c) grain weight loss after infestation

Combining ability analyses were done using Griffing's method 2. The data was analysed using both fixed effects model and random effects model. Random model was deemed appropriate because the inbred lines used were not chosen based on predetermined criteria but were randomly selected from a large pool of resistant and susceptible inbred lines. Random model was used to estimate genetic variance components and heritability. Heritability estimates were calculated for all weevil resistance traits. These estimates were calculated following the method proposed by Mather and Jinks (1977) using the following formulae.

$H_{bs} = (1/2D_R + 1/4H_R)/(1/2D_R + 1/4H_R + E_w + E_b)$

$H_{ns} = 1/2D_R/(1/2D_R + 1/4H_R + E_w + E_b)$

Where; H_{bs} = broad sense heritability

H_{ns} = narrow sense heritability

D_R = Additive variance

H_R = Dominance variance

$E_w + E_b$ = Error variance

The analysis using the fixed model was done for the purpose of making statements about this specific population of the inbred lines as the population of inference. This analysis was for the purpose of allowing for critical assessment of combining abilities of the inbred lines for immediate use by those researchers who may wish to use them in research. The combining abilities of the three measures of weevil resistance and their relative importance were assessed. The relative proportions of the genetic variances were also estimated thus providing the measure of the predominant gene action and the appropriate breeding approach for weevil resistance.

RESULTS

4.1 Weevil resistance parameters

Treatments were significantly (P<0.01) different for grit percentage (Tables 6 and 7). L911 and L913 were the hardest inbred lines as indicated by their high mean percent grit. They were not significantly different from each other in their mean percent grit. Z160429-30 had the lowest percent grit but it was not significantly different from Z160585-86, Z13-146 and Z160510-13 which also had low mean percent grit. Z160519-13 x L12 and Z160429-30 x L12 had the highest percent grit while Z160585-86 x Z160510-13 had the lowest percent grit in this study.

Genotypic differences were highly significant (P<0.01) for weight loss caused by weevil damage (Tables 6 and 7). Z160585-86 suffered no weight loss from insect attack while Z160510-13 suffered the greatest weight loss.

Genotypic differences were highly significant (P<0.01) for number of insects (Tables 6 and 7). L913 had the greatest degree of infestation as shown by high mean number of insects while Z160585-86 had the lowest degree of infestation. Z13-146 x Z160425-26 and Z13-146 x L911 had the least degree of infestation as indicated by low mean insect numbers. Z160425-26 x L913 had the highest degree of infestation.

Table 6 Analysis of variance of weevil resistance parameters and yield in maize

Source of variation		Variables							
		Sqrt % grit		Weight loss		Log (x+1) insects		Yield	
	Df	MS	F-value	MS	F-value	MS	F-value	MS	F-value
Replications	2	0.016	2.17	0.121	0.66	0.021	0.22	7659396.93	8.61**
Entries	67	0.040	5.55**	0.592	3.22**	0.603	6.42**	3060510.789	3.44**
Error	134	0.007		0.184		0.094		889931.474	
Total	203	3.67		64.59		53.02		35.04	
CV (%)		0.92		76.32		37.62			

*,** indicates significance at 0.05 and 0.01 probability level respectively.

Table 7 Means for weevil resistance parameters of the 36 genotypes of maize used in genetic analysis

Cross	No. of insects	Weight loss	Percent grit	Yield (kg /ha)
1selfed	0.4421 klm	0.0000 i	9.091gh	1257.26 mno
1 x 2	0.4421 klm	0.2270 hi	9.168 defg	7021.40 abc
1 x 3	3.1210 ghij	0.6430 defghi	8.802 l	8021.56 a
1 x 4	8.5280 efgh	0.5700 efghi	9.098 gh	4157.78defghij
1 x 5	1.8840 ijkl	0.3270 ghi	9.262 abcdef	4654.71 cdefgh
1 x 6	1.2909 jklm	0.0000 i	9.145 defg	3514.62 ghijklm
1 x 7	3.6452 ghij	0.9970 bcdefg	9.139 defg	5796.76 abcdefg
1 x 8	6.1450 fghi	0.1200 hi	9.113 fgh	4205.18 defghij
2selfed	1.4660 jklm	1.543 ab	9.213 cdefg	1961.66 jklmno
2 x 3	3.7643 ghij	0.6630 cdefghi	9.244 cdefg	4843.23 cdefgh
2 x 4	0.2589 lm	0.0000 i	9.186 defg	4691.20 cdefgh
2 x 5	0.0000 m	0.3470 ghi	9.152 defg	4500.13 defghi
2 x 6	0.0000 m	0.6470 defghi	9.090 gh	5936.59 abcdef
2 x 7	6.6913 fghi	1.163 adcde	9.168 defg	5089.16 bcdefgh
2 x 8	2.1769 ijkl	0.4670 fghi	9.241 cdefg	3206.27 hijklmn
3selfed	33.5144ab	1.823 a	9.248 bcdefg	1737.63 klmno
3 x 4	9.7152 cdefg	1.563 ab	9.133 efg	7376.26 ab
3 x 5	28.4442abc	1.043 bcdef	9.290 abcde	2999.34 hijklmno
3 x 6	10.3240cdefg	0.5430 efghi	9.279 abcde	6346.79 abcd
3 x 7	25.3027abcd	1.080 bcdef	9.210 cdefg	3936.44 efghijk
3 x 8	27.6418 abcd	1.267 abcd	9.414 a	5721.55 abcdefg
4selfed	4.4576 ghij	0.0400 hi	9.087 gh	2285.09 ijklmno
4 x 5	2.4754 hijk	0.5800 defghi	9.248 bcdefg	5022.44 bcdefgh

Table 6 continued

Cross	No. of insects	Weight loss	Percent grit	Yield (kg /ha)
4 x 6	3.4771 ghij	0.1900 hi	9.272 abcdef	4459.55 defghi
4 x 7	25.2422abcd	1.347 abc	9.247 bcdefg	4360.53 defghi
4 x 8	6.6033 fghi	0.7000 cdefgh	9.421a	4116.94 defghij
5selfed	9.4954defg	0.0900 hi	9.408 ab	702.16 o
5 x 6	4.0350ghij	0.6330 defghi	9.297 abcd	5200.28 bcdefgh
5 x 7	35.2243ab	1.087 bcdef	9.361 abc	5056.04 bcdefgh
5 x 8	6.3961fghi	1.070 bcdef	9.248 bcdefg	3789.86fghijkl
6selfed	16.1396 bcdef	0.6000 defghi	9.292 abcde	1503.02 lmno
6 x 8	17.4502bcdef	0.7070 cdefgh	9.241 cdefg	6182.24 abcde
7selfed	52.3335 a	0.9800 bcdefg	9.207 cdefg	991.77 no
7 x 8	0.2589 lm	0.0730 hi	9.288 abcde	5182.02 bcdefgh
8selfed	23.0436abcde	0.4930 efghi	9.095 gh	4490.27 defghi
LSD$_{(5\%)}$	0.4400	0.6890	0.1628	2683.333

Where;

1 = Z160585-86

2 = Z13-146

3 = Z160510-13

4 = Z160429-30

5 = Z160425-26

6 = L911

7 = L913

8 = L12

Means marked by the same letter are not significantly different at 5% level.

4.2 Inter-character correlations

The results obtained indicated that weight loss and number of insects were significantly correlated (r = 0.483, P<0.01). On the other hand percent grit and weight loss as well as number of insects were positively though not significantly correlated (Table 8).

4.3 Combining ability effects (fixed model) for grit%, weight loss and number of insects at 63 and 93 days after infestation

GCA and SCA effects were both significant for grit percentage. The GCA : SCA ratio was 22.84% indicating that the GCA effects were of less importance in the determination of hardness as measured by grit percentage (Table 9). SCA effects were predominant in determining grain hardness.

Both GCA and SCA effects were highly significant for weight loss at 63 days after infestation (Table 9). The GCA : SCA ratio was 49% indicating that both effects operated at almost equal strength in determination of weevil resistance as measured by the amount of damage inflicted on the grain by the weevil.

GCA and SCA effects were highly significant for number of insects at 63 days after infestation. GCA : SCA ratio was 71.42% indicating the predominance of additive effects in determining level of resistance as measured by the degree of infestation

Table 8 Inter-character correlations among the weevil resistance traits in maize.

Character	Sqrt grit	Wt loss	Log #of insects
Sqrt grit		0.054	0.234
Wt loss			0.483**
Log #			

*, ** indicates significance at 0.05 and 0.01levels of probability respectively.

Table 9 Mean squares of general and specific combining abilities and their variance components for the three measured resistance parameters in maize at 63 and 93 days after infestation

	Mean Squares		Variance components		
Trait	GCA	SCA	GCA	SCA	GCA : SCA
Sqrt % grit	0.0728**	0.0375*	0.00628	0.0275	22.84
63 days after infestation					
Weight loss	1.6690**	0.4833**	0.14897	0.3040	49.00
$\text{Log}_{(x+1)}$ insects	2.1471**	0.3634**	0.20741	0.2904	71.42
93 days after infestation					
Weight loss	13.5330**	3.2982**	1.19612	1.7264	69.28
$\text{Log}_{(x+1)}$ insects	2.3194**	0.4430**	0.21770	0.3006	72.42

*, ** indicates significance at 0.05 and 0.01levels of probability respectively.

based on the number of adult insects recovered after a period of infestation (Table 9).

GCA and SCA effects were highly significant for weight loss at 93 days after infestation (Table 9). The GCA : SCA ratio was 69.28% indicating the predominance of additive effects in genetic control of this trait.

GCA and SCA effects were highly significant for number of insects at 93 days after infestation. The GCA : SCA ratio was 72.42% which was slightly higher than that observed after 63 days infestation. The ratio still indicates the predominance of additive effects over the dominance effects in determination of weevil resistance measured by the degree of infestation (Table 9).

4.4 The general combining ability effects of parens for grit%, weight loss and number of insects at 63 and 93 days after infestation

Z160425-26 was the best general combiner for increasing grain hardness as measured by grit percentage while Z160585-86 had a highly significant negative general combining ability for this trait suggesting that it decreased grain hardness in its crosses (Table 10).

For weight loss at 63 days after infestation, Z160585-86 and L911 had significant negative general combining ability effects (-0.311 and -0.173 respectively). This

Table 10 General combining ability (GCA) effects of weevil resistance traits for the parents at 63 days after infestation

Inbred	Sqrt grit	Weight loss	Log # of insects
Z160585-86	-0.093**	-0.311*	-0.305**
Z13-146	-0.017	0.061	-0.435**
Z160510-13	0.002	0.446**	0.334**
160429-30	-0.006	-0.096	-0.038
Z160425-26	0.083**	-0.072	0.019
L911	0.004	-0.173*	0.000
L913	-0.004	0.206	0.301**
L12	0.031	-0.060	0.123*
$t_{(5\%)} \times \sqrt{g_i}$	0.035	0.144	0.091
$t_{(1\%)} \times \sqrt{g_i}$	0.091	0.381	0.242
$t_{(5\%)} \times \sqrt{(g_i-g_j)}$	0.053	0.218	0.140

*, ** indicates significance at the 0.05 and 0.01levels of probability respectively.

(suggests that they were good combiners for decreasing weight loss caused by weevil attack. On the other hand Z160510-13 had significant positive GCA effects 0.446) suggesting that it increased weight loss in its crosses (Table 10).

At 63 days after infestation period, Z13-146 (-0.435) and Z160585-86 (-0.305) were good combiners for the reduction of infestation as measured by number of insects while Z160510-13 (0.334), L913 (0.301) and L12 (0.123) had an effect of increasing degree of infestation in their crosses (Table 10).

At 93 days after infestation, Z160585-86, Z13-146, Z160429-30 and Z160425-26 had significant general combining ability effects of -2.28, -2.09, -0.97 and -0.55 respectively suggesting that they increased weevil resistance as measured by weight loss caused by insect damage. Z160510-13 had a highly significant positive general combining ability effect of 3.30 indicating that it decreased weevil resistance and genetically contributed to high weight loss in its crosses (Table 11)

For number of insects at 93 days after infestation, Z160585-86 and Z13-146 were good combiners with the general combining ability effects of -0.82 and -1.39 respectively. Z160510-13, L913 and L12 had the general combining ability effects of 1.12, 0.96 and 0.31 suggesting that they genetically contributed to high level of infestation in their crosses (Table 11).

Table 11 General Combining ability (GCA) effects of weevil resistance traits for parents at 93 days after infestation

Inbred	Weight loss	Log # of insects
Z160585-86	-2.28**	-0.82**
Z13-146	-2.09**	-1.39**
Z160510-13	3.30**	1.12**
Z160429-30	-0.97**	-0.08
Z160425-26	-0.55*	-0.11
L911	-0.24	0.02
L913	2.58**	0.96**
L12	0.25	0.31**
$t_{(5\%)} \times \sqrt{g_i}$	0.427	0.129
$t_{(1\%)} \times \sqrt{g_i}$	0.567	0.172
$t_{(5\%)} \times \sqrt{(g_i - g_j)}$	0.646	0.194

*, ** indicates significance at the 0.05 and 0.01 levels of probability respectively.

4.5 Specific combining ability effects for grit%, weight loss and number of insects at 63 and 93 days after infestation

For percentage grit, Z160510-13 x L12 and Z160429-30 x L12 had significant specific combining ability effects of 0.1750 and 0.1904 respectively suggesting that the two crosses had a greater hardness as measured by percentage grit. On the other hand Z160585-86 x Z160510-13, Z13-146 x Z160425-26 and L911 x L913 had the specific combining ability effects of -0.3103, -0.1210 and -0.2340 respectively indicating that they had much softer kernel (Table 12).

For weight loss at 63 days after infestation, Z13-146 x Z160510-13, Z13-146 x Z160429-30 and L913 x L12 had the specific combining ability effects of -0.5091, -0.6305 and -0.7558 respectively. These suggest they were resistant and suffered significantly reduced weight loss due to infestation. Z160510-13 x Z160429-30, Z160429-30 x L913 and Z160425-26 x L12 had significantly positive specific combining ability effects (0.5479, 0.5715 and 0.5369 respectively) indicating that they had high susceptibility as measured by weight loss (Table 12).

For number of insects at 63 days after infestation, Z13-146 x Z160425-26, Z13-46 x 911 and L913 x L12 had specific combining ability effects of -0.4125, -0.3942 and -1.1525 respectively. Thus these crosses were more resistant as indicated by low degree of infestation. Z160585-86 x Z160429-30, Z160429-30 x L913, Z160425-26 x L911 and L911 x L12 had significantly positive specific combining ability effects

Table 12 Specific combining ability (SCA) effects of weevil resistance parameters in maize at 63 days infestation

Cross	Sqrt %grit	Weight loss	log # of insects
Z160585-86 x Z13-146	0.0724	-0.1891	0.0708
Z160585-86 x Z160510-13	-0.3103*	-0.1575	-0.2415
Z160585-86 x Z160429-30	-0.0083	0.3112	0.4941*
Z160585-86 x Z160425-26	0.0657	0.0442	-0.0825
Z160585-86 x L911	0.0317	-0.1818	-0.1642
Z160585-86 x L913	0.0334	0.4362	-0.1579
Z160585-86 x L12	-0.0290	-0.1748	0.2061
Z13-146 x Z160510-13	0.0796	-0.5091*	-0.0515
Z13-146 x Z160429-30	0.0050	-0.6305*	-0.2559
Z13-146 x Z160425-26	-0.1210*	-0.3075	-0.4125*
Z13-146 x L911	-0.1016	0.0932	-0.3942*
Z13-146 X L913	-0.0166	0.2312	0.1921
Z13-146 x L12	0.0210	-0.1998	-0.0139
Z160510-13 x Z160429-30	-0.0676	0.5479*	-0.0949
Z160510-13 x Z160425-26	-0.0003	0.0042	0.2885
Z160510-13 x L911	0.0690	-0.3951	-0.1099
Z160510-13 x L913	0.0074	-0.2371	-0.0435

Table 12 continued

Cross	Sqrt % grit	Weight loss	Log # of insects
Z160510-13 x L12	0.1750*	0.2152	0.1705
Z160429-30 x Z160425-26	-0.0350	0.0829	-0.2692
Z160429-30 x L911	0.0710	-0.2065	-0.1409
Z160429-30 x L913	0.0527	0.5715*	0.3288*
Z160429-30 x L12	0.1904*	0.1905	-0.0339
Z160425-26 x L911	0.0050	0.2132	-0.1442
Z160425-26 x L913	0.0767	0.2879	0.4121*
Z160425-26 x L12	-0.0723	0.5369*	-0.1005
L911 x L913	-0.2340*	-0.3581	-0.1695
L911 x L12	0.0004	0.0085	0.3145*
L913 x L12	0.0554	-0.7558*	-1.1525**
$t_{(0.05)} \times g_i$	0.115	0.4880	0.311
LSD$_{(5\%)}$ for S_{ij}-S_{ik}	0.154	0.6540	0.417
LSD$_{(5\%)}$ for S_{ij}-S_{kl}	0.145	0.6170	0.393

*, ** indicates significance at the 0.05 and 0.01levels of probability respectively.

(0.4941, 0.3288, 0.4121 and 0.3145 respectively) indicating that they suffered increased infestation and therefore were more susceptible (Table 12).

There was an increase in the number of crosses with significant negative specific combining ability effects for weight loss at 93 days after infestation compared to 63 days. L913 x L 12 had the greatest negative specific combining ability effect and even other crosses also had significant negative specific combining ability effects (see Table 13). Z13-146 x L12, Z160429-30 x L913, Z160425-26 x L913 and Z160425-26 x L12 had significant positive combining ability effects (2.364, 3.675, 2.713 and 2.463, respectively) showing that they were susceptible in this study (Table13).

For number of insects at 93 days after infestation L913 x L12 had the greatest significant negative specific combining ability effect of -3.957 and eight other crosses also had significant negative combining ability effects. Five crosses had significant positive combining ability effects indicating that they were susceptible to weevil infestation. Of these, Z160429-30 x L913 had the greatest positive specific combining ability effect of 1.307 (Table 13).

4.6 Combining ability effects (random model) for grit%, weight loss and number of insets at 63 and 93 days of infestation

Percentage grit had non-significant GCA effects (0.0728). SCA effects were highly

Table 13 Specific combining ability (SCA) effects of weevil resistance parameters in maize at 93 days infestation

Cross	Weight loss	Number of insects
Z160585-86 x Z13-146	0.110	-0.476*
Z160585-86 x Z160510-13	-2.945**	-0.776**
Z160585-86 x Z160429-30	0.871	1.093**
Z160585-86 x Z160425-26	0.059	-0.335
Z160585-86 x L911	-0.628	-0.385
Z160585-86 x L913	-0.783	-0.254
Z160585-86 x L12	0.787	0.689**
Z13-146 x Z160510-13	-3.008**	-0.004
Z13-146 x Z160429-30	-0.192	-0.015
Z13-146 x Z160425-26	-0.214	-1.363**
Z13-146 x L911	-1.891**	-1.493**
Z13-146 x L913	-1.766**	0.378
Z13-146 x L12	2.364**	0.301
Z160510-13 x Z160429-30	-1.577*	-0.485*
Z160510-13 x Z160425-26	-1.519*	0.947**
Z160510-13 x L911	-3.926**	-0.483*

Table 13 continued

Crosses	Weight loss	Number of insects
Z160510-13 x L913	-4.141**	-0.362
Z160510-13 x L12	0.199	0.681*
Z160429-30 x Z160425-26	-0.023	-1.354**
Z160429-30 x L911	-0.810	-0.924**
Z160429-30 x L913	3.675**	1.307**
Z160429-30 x L12	-0.325	-0.230
Z160425-26 x L911	1.208	-0.052
Z160425-26 x L913	2.713**	1.079**
Z160425-26 x L12	2.463**	0.042
L911 x L913	-3.154**	-0.321
L911 x L12	1.256	1.052**
L913 x L12	-6.569**	-3.957**
t (0.05) x √gi	1.3089	0.3938
LSD (0.05) for √Sij - Sik	1.9364	0.5826
LSD (0.05) for √Sij - Skl	2.5715	0.5493

*, ** indicates significance at the 0.05 and 0.01levels of probability respectively.

significant. The ratio of estimate of GCA variance to estimate of SCA variance was 12.84% suggesting the predominance of SCA effects in the control of this trait (Table 14).

GCA and SCA effects were highly significant for weight loss at 63 days infestation period. The ratio of estimate of GCA variance to estimate of SCA variance was 39.00% suggesting the predominance of dominance effects (Table 14).

For number of insects at 63 days after infestation estimate of relative dominance was 0.8140 suggesting the prevalence of partial dominance (Table 14). The estimates of broad sense and narrow sense heritability were 54.09 and 15.18 respectively (Table 14).

GCA and SCA effects for number of insects at 63 after infestation were highly significant. The ratio of the estimate of GCA variance to SCA variance was 61.42% indicating that the additive effects were predominant in the determination of weevil resistance as measured by the degree of infestation (Table 14).

For weight loss at 93 days of infestation GCA and SCA effects were highly significant. The ratio of the estimate of GCA variance to estimate SCA variance was 59.28% suggesting the predominance of additive effects in determining weevil resistance as measured by weight loss caused by weevil damage (Table 14).

Table 14 General combining ability, specific combining ability, variance components estimate and the ratio of estimate of GCA variance to estimate of SCA variance for the weevil resistance traits at 63 and 93 days after infestation (random model)

	Mean Squares		Variance components		
Character	GCA	SCA	GCA	SCA	GCA / SCA
Sqrt % grit	0.0728	0.0375**	0.00353	0.0275	12.84
63 days after infestation					
Weight loss	1.6690**	0.4833**	0.11857	0.304	39
Log # of insects	2.1741**	0.3634**	0.17837	0.2904	61.42
93 days after infestation					
Weight loss	15.533**	3.2982**	1.02348	1.7264	59.28
Log # of insects	2.3194**	0.4430**	0.18764	0.3006	62.42

*, ** indicates significance at the 0.05 and 0.01 levels of probability respectively.

GCA and SCA effects were significant (P<0.01) for number of insects at 93 days after infestation. The ratio of the estimate of GCA variance to SCA variance was 62.42% suggesting that additive effects were the most important genetic effects in the control of weevil resistance as measured by number of insects (Table 14).

4.7 Estimates of relative dominance and heritability for grit%, weight loss and number of insects at 63 and 93 days after infestation

The estimate of relative dominance for percentage grit was 3.8952 indicating the prevalence of overdominance (Table 15). The estimates of broad sense and narrow sense heritability were 60.81 and 6.92 respectively (Table 16). The low narrow sense heritability estimate suggests that progress from selection will be very slow.

Weight loss at 63 days after infestation had the estimate of relative dominance of just above unit (1.282) suggesting the prevalence of complete dominance (Table 15). The estimates of broad sense and narrow sense heritability were 76.25 and 29.01, respectively (Table 16).

The estimate of relative dominance was 0.8140 for number of insects at 63 days after infestation suggesting the prevalence of partial dominance (Table 15). The estimates of broad sense and narrow sense heritability were 54.09 and 15.18 respectively (Table 16).

Table 15 Estimates of genetic variance components and relative dominance for weevil resistance parameters in maize at 63 and 93 days after infestation

Character	Additive variance (V_A)	Dominance variance (V_D)	V_D/V_A
Sqrt % grit	0.00706	0.0275	3.8952
63 days of infestation			
Wight loss	0.23714	0.3040	1.2819
Log # of insects	0.35674	0.2904	0.8140
93 days of infestation			
Weight loss	2.04696	1.7264	0.8434
Log # of insects	0.37528	0.3006	0.8010

Table 16 Broad and narrow sense heritability estimates for weevil resistance parameters in maize at 63 and 93 days after infestation

Character	Broad sense heritability	Narrow sense heritability
Sqrt % grit	60.81	6.92
63 days after infestation		
Weight loss	76.25	29.01
Log # of insects	54.09	15.18
93 days after infestation		
Weight loss	46.66	17.37
Log # of insects	63.16	24.27

For weight loss at 93 days after infestation the estimate of relative dominance was 0.8434 suggesting partial dominace gene action as opposed to 1.2819 at 63 days infestation (Table 15). There was a drop in the estimates of heritability at 93 days compared to those obtained at 63 days. The estimate of broad sense heritability was 46.66 and the narrow sense heritability estimate was 17.37 (Table 16).

For number of insects at 93 days after infestation the estimate of relative dominance for number of insects changed very slightly compared to that obtained at 63 days. At 93 days the estimate of relative dominance was 0.8010 (Table 15) suggesting the prevalence of partial dominance. The estimates of heritability increased at 93 days compared to those observed at 63 days. The broad sense heritability estimate was 63.16 while the estimate for narrow sense heritability was 24.27 (Table 16).

DISCUSSION

Weight loss and number of insects were positively, though not significantly correlated with percent grit. This finding, though not supported by statistical significance at the level set for this experiment, raises the question that requires an explanation. Many research workers have reported negative correlation between hardness and susceptibility of maize to maize weevil (Eden, 1952 b; Russell, 1962; Singh and McCain, 1963; McCain et. al, 1964 Russell and Rink, 1965; Dobie, 1974; Lorenzoni and Motto, 1985 and Kiregyera, 1994). Flint maize types have been reported to be more resistant to weevil than dent maize types (Pant et. al., 1964; Purseglove, 1972; Nhlane, 1989 and Dowswell, 1996). Urrelo et. al. (1991), Gupta et. al. (1974), Sarmiento and Ubaldo (1978) and Morales (1974) also reported hardness as a factor responsible for different responses to weevil attack between hard maize types and softer variants. Phenolic substances have been reported to be associated with kernel resistance to weevil because they are said to increase mechanical hardness and some may have antibiosis effect on the insects (Arnason et. al., 1992; Arnason et. al., 1994 and Serratos et. al., 1994). However other research workers have reported that hardness had no influence on resistance and some soft maize kernel variants like dent and high lysine maize showed resistance to the weevil (Eden, 1952b; Peters et. al., 1972; Schoonhoven, 1972 and Derera and Pixley, 1998). It appears that the hardness range observed among these genotypes was too narrow to give a good assessment of this trait as a good measure of weevil resistance. Other factors not tested here, because of limited time and lack of equipment, like sugar content, protein content and most importantly phenolic compounds could have also provided a broader assessment of weevil resistance in this study.

The SCA effects were more important for percent grit suggesting the predominance of non-additive genetic effects. GCA effects accounted for less than 30% of the variation. These results differ slightly from those reported by Serratos et. al. (1994) where the dominance effects for maximum force of compression were highly significant while the additive effects were not significant when tested by Serratos model. The method of hardness test as well as maize genotypes used here and method of analysis could have caused the observed difference in results. Selection for kernel hardness would therefore be effectively done by using reciprocal recurrent selection. The parents bearing dominant genes from two source populations would be selected and used in crosses to raise the synthetic variety from which desirable individuals carrying dominant genes would be selected and then used in production of weevil resistant varieties. In this case for example populations can be raised by using Z160425-26 in initial crosses to generate synthetic populations from which recurrent selection could be practised.

GCA and SCA effects were equally important for grain weight loss obtained after 63 days. These results concur with those observed by Derera et. al. (1998) where GCA effects and SCA effects were found to be of equal importance. However GCA accounted for 69.28% of the total variation for the data obtained after 93 days of infestation. Selection for weight loss as a parameter of resistance would therefore effectively be done by following the reciprocal recurrent selection among populations to exploit both additive and dominance effects if based on assessment over infestation period of 63 days. Recurrent selection for GCA would be appropriate for assessment over a period of 93 days. Such populations could be raised from a synthetic arising from crosses among inbred lines with significant negative GCA for weight loss. Z160585-86 and L911, for instance, could effectively be used since they had significant negative GCA effects suggesting that they reduced weight loss in their crosses. In the case of 93 days infestation period two other inbred lines, Z160429-30 and Z160425-26, also had significant negative general combining abilities for weight loss indicating that they could also be used as parents for the synthetic population.

For number of insects additive and non-additive effects were both important but GCA effects were more important than SCA effects for both infestation periods. The similar findings were reported by Kang et. al. (1996), Tipping et. al. (1989), Widstrom et. al. (1975), Derera and Pixley (1998), and Derera et. al. (1998). For this trait recurrent selection for general combining ability can be used to exploit the high level of additivity. Inbred lines with significant positive GCA were very poor combiners causing an increased insect numbers in their crosses. Z160585-86 and Z13-146 had significant negative GCA effects indicating that they reduced insect numbers in their crosses. These lines can therefore be used as the parents in making synthetic populations for recurrent selection.

The inbred lines involved in this study have shown variable responses in their ability to either increase resistance or susceptibility of maize to weevil. Since % grit did not matter in determination of resistance the combining ability of the inbreds for that trait are of less importance in this consideration. Therefore on the basis of weight loss and number of insects alone Z160585-86, Z13-146 and L911 proved to be the most preferable lines to use in a programme to breed for maize weevil resistance under both infestation periods. Z160429-30 and Z160425-26 also proved to have good resistance at 93 days infestation period. This is because they had either both significant negative general combining ability for weight loss and number of insect or the combining ability for one trait was insignificant while the other one was significant. L913 x L12 produced a good cross with the highest specific combining abilities of -0.7558 for weight loss, and -1.1525 for number of insects at 63 days and -6.569 for weight loss and -3.957 for number of insects at 93 days. There was no single cross which incorporated all the three good traits together. The crosses which performed well on resistance test did not do well on the aspect of yield and their use in production may not be justifiable unless the damage by insects offsets yield gain.

Random effects analysis revealed that percent grit had high relative degree of dominance. This further indicates that the gene action operating to determine this trait was predominantly overdominance gene action and this further suggests that SCA effects were more important than GCA effects. Number of insects and grain weight loss had the relative dominance of 0.8140 and 1.2819, respectively for the 63 days infestation and 0.8010 and 0.8434, respectively for the 93 days infestation. These show gene action of partial dominance for all but weight loss at 63 days whose relative dominance was in the range of dominance.

The broad sense heritability for the traits ranged from 41.47% for percent grit to 76.25% for weight loss. Weight loss had the narrow sense heritability of 29.01 and 17.37% for 63 and 93 days infestation, respectively. For number of insects the narrow sense heritability was 15.18 and 24.27% for 63 and 93 days of infestation respectively. These values were low showing that progress from selection would be very slow and a very large population would be required for satisfactory selection results. These results were different from those reported by Li-RuMing et. al. (1998) who observed the broad sense heritability of only 21% for weevil resistance. However the aspect of genotype by environment (Gx E) which was not estimated here could have inflated the genotypic variation thus resulting in over-estimation of heritability estimates. But the estimates obtained were also low.

Narrow sense heritability indicates the importance of additive genetic components in phenotypic expression of the character. The additive components are responsible for the parent-offspring resemblence and therefore serves as the measure to determine how much progress can be made by selecting for the trait in a breeding programme. The greater the narrow sense heritability for a character, the greater is the expected gain from selection for that character. The results indicate that weight loss would be much easier to select for than number of insects if selection is to be exercised after 63 days infestation. If selection is to be done using 93 days infestation period then number of insects would bring about a much faster progress.

CONCLUSION

In this study grain hardness did not have an effect on weevil resistance as indicated by lack of significant correlations between percentage grit and weight loss caused by weevil infestation on the one hand and percentage grit and number of insects on the other hand. It appears that the range of hardness in this material was too narrow to cause differential response to weevil attack. It is therefore concluded that grain hardness is not an important factor in determining weevil attack response among these genotypes.

Weight loss appeared to be a good index of weevil resistance and it does give an informative indication as it can directly be translated into produce and monetary losses.

Number of insects recovered gives the degree of infestation attained after the period of incubation following infestation. Degree of infestation is closely related to weight loss as indicated by significant correlation ($r = 0483$, $P<0.01$). Thus this parameter also gives a good indication of the level of resistance in maize.

Grain hardness was controlled primarily by dominance effects and gene action observed was of overdominance type. Narrow sense heritability was also very low. These suggest that recurrent selection for specific combining ability would be a proper selection method and large number of crosses would have to be tested to increase the probability of obtaining best crosses.

Weight loss was controlled by both additive and dominance effects at 63 days infestation as indicated by the GCA to SCA ratio which was close to 50%. The relative dominance was close to one suggesting preponderance of dominance. Narrow sense heritability was moderately low. Reciprocal recurrent selection would be the best selection strategy to exploit both additive and dominance effects.

At 93 days infestation GCA effects were more important than SCA effects for weight loss and partial dominance was prevalent. Narrow sense heritability dropped relative to that obtained at 63 days. Recurrent selection for general combining ability is suggested as the breeding strategy to improve weevil resistance.

Degree of infestation as measured by number of adult insects recovered was controlled primarily by additive gene effects at both infestation periods. Relative dominance was in the range of partial dominance at both periods. Narrow sense heritability estimate was larger at 93 days than at 63 days suggesting a much faster progress from selection at 93 days than at 63 days. Recurrent selection for general combining ability to exploit high level of additive effects can be used at both periods.

SUGGESTIONS FOR THE FUTURE

The results reported here were based on data obtained from one location in one season. Yield data may not be comparable to what would be obtained if the material was planted in summer. However for the comparison of the material used it does give an important information since they were all subjected to the same conditions. It is recommended that if one has interest in these crosses, they should be assessed in summer and compared with the standard varieties. Weevil resistance has been reported to vary with location and season by some researchers. Others have however reported that it did not vary with location and season in their studies. However since this environment might be different from that at other sites it is recommended that for better results multilocational and multiseasonal trials should be done to assess G x L and G x Y interactions. Significant maternal and reciprocal effects have also been reported and raising of the reciprocals alongside crosses and parents is recommended as it may furnish important information.

Finally it is recommended that biochemical tests for other components believed to influence weevil resistance be assessed in this material to find out exactly what kernel component is important in determination of resistance.

LITERATURE CITED

1. Arnason, J. T., B. Baun, J. Gale, J. D. H. Lambert, D. Bergvinson, B. J. R. Philogene, J. A. Serratos, J. Mihm, and D. C. Jewel. 1994. Variation in resistance of Mexican landraces of maize to maize weevil, *Sitophilus zeamais,* in relation to physical and biochemical parameters. Euphytica 74: 227 - 236

2. Bernable-Abdalla, C. and E. N. Bernardo. 1976. Mechanism of resistance of the maize varieties to the rice weevil complex. Philippine Agriculturist. 1976. 60 (3/4): 112 - 120

3. Betanzos-Mentoza, E. 1980. Selection of high quality protein varieties of maize for resistance to the maize weevil *Sitophilus zeamais* (Motsch.). 1. Correlation between grain characteristics and resistant indicators. Agricultura Tecnica en Mexico. 1980. 6 (1): 45 - 66.

4. Chippendale, G. M. 1972. Dietary carbohydrates: Role in survival of the adult rice weevil, *Sitophilus oryzae.* J. Insect Physiology 18: 949-957

5. Classen, M. M. and R. H. Shaw. 1970. Water deficits effects on corn. II. Grain components. Agron. J. 62 (5): 652-655

6. Derera, J., D. P. Giga, and K. V. Pixley. 1998. Combining ability among maize lines from Southern Africa, Mexico and CIMMYT-Zimbabwe for weevil (*S. zeamais*) feeding preference. Plant Breeding Symposium, 17-19 March, 1998. Golden Gate, South Africa.

7. Derera, J., Giga, D. P. and K. V. Pixley. 1998. Inheritance of maize weevil resistance in hybrids among maize lines from Southern Africa, Mexico and CYMMIT-Zimbabwe. 6th Regional Maize Conference, 21-25 Sept, 1998, Addis Ababa, Ethiopia.

8. Derera, J. and K. Pixley. 1998. Maize weevil project report: May, 1997 - April, 1998. CIMMYT, Zimbabwe.

9. Dicke, F. F. 1976. The Most important corn insects p. 553. In : G. F. Spraque (ed.) . *Corn and Corn Improvement*. Agron. Monogr. 18, ASA., Madison, WI.

10. Dobie, P. 1974. The laboratory assessment of the inherent susceptibility of maize varieties to post-harvest infestation by *Sitophilus zeamais* Motsch. (Coleoptera: Curcolionidae). J. Stored Prod. Res. 10: 183-197

11. Dobie, P. 1977. The contribution of the Tropical Stored Products Centre to the study of insect resistance in stored maize. Tropical Stored Products

Information 34: 7-12

12. Dowswell, R. C., R. L. Paliwal, and R. P. Candul. 1996. *Maize in the Third world*. Westview Press, U.K.

13. Eden, W. G. 1952 a. Effect of husk cover on rice weevil damage in Alabama. J. Econ. Entomol. 45: 543 - 544.

14. Eden, W. G. 1952 b. Effect of kernel characteristics and components of husk cover on rice weevil damage to corn. J. Econ. Entomol. 45: 1084 - 1085.

15. Efron, Y. 1985. Use of temperate and tropical germplasm for maize breeding in tropical area of Africa. In: A. Blandolini and F. Salamini (Eds.) *Breeding Strategies for Maize Production improvement in the Tropics.* FAO

16. Floyd, E. H. 1971. Relationship between maize weevil infestation in corn at harvest and progressive infestation during storage. J. Econ. Entomol. 64 (2): 408 - 411.

17. Floyd, E. H. and J. D. Powell. 1958. Some factors influencing the infestation in corn in the field by the rice weevil. J. Econ. Entomol. 51: 23 -

26.

18. Galinat, W. C. 1976. Origin of Corn. In: G. F. Spraque (ed) *Corn and Corn Improvement*. Agron. Monogr. 18, ASA., Madison, WI.

19. Giles, P. H. and F. Ashman. 1971. A study of preharvest infestation of maize by *Sitophilus zeamais* Motsch. (Coleoptera: Curculionidae) in the Kenya Highlands. J. Stored Prod. Res. 7: 69 - 83.

20. Gomez, L. A. 1983. Mechanism and inheritance of resistance of selected maize genotypes, *Zea mays L.*, to the rice weevil, *Sitophilus oryzae* (L.). CAB - Plant Breeding Abstracts (1983).

21. Gomez, L. A., G. J. Rodriques, and D. F. Blake. 1982. Preference and utilization of maize endosperm variants by the rice weevil. J. Econ. Entomol. 75: 363-367.

22. Gomez, L. A., G. J. Rodriquez, C. G. Poneleit, D. F. Blake, and C. R. Smith. 1983. Influence of nutritional characteristics of selected corn genotypes of food utilization by the rice weevil (Coleoptera, Curculionidae). J. Econ. Entomol. 76: 728-732.

23. Gupta, S. C., V. L. Asnani, and B. P. Khare. 1974. Effect of the opague-2

gene in maize (*Zea mays* l.) on the extent of infestation by *Sitophilus oryzae* l. CAB: Plant breeding abstracts.

24. Hill, D. S. and J. M. Waller. 1990. *Pests and Diseases of Tropical Crops.* Field Handbook. Longman Scientific and Technical, Essex CM 20 2JE, England.

25. Igbal, J., M. Irshad, and U. K. Baloch. 1994. Insects of stored cereals and their ecology. In; Integrated Pest Management in Food grain. U. K. Baloch (ed.). FAO and Pakistan Agricultural Research Council. Islamabad, Pakistan.

26. Kang, M. S., Y. Zhang, and R. Magari. 1996. Combining ability for maize weevil preference of grain maize. Crop Sci. 35: 1556-1559.

27. Kocchar, S. L. 1986. *Tropical Crops, a textbook of economic botany.* Macmillan Publishers, India.

28. Kossou, D. K., N. A. Bosque-Perez, and J. H. Mareck. 1993. Effects of shelling maize cobs on the oviposition and development of the maize weevil. IITA Research (Jan) 6: 7 - 10.

29. Kossou, D. K., J. H. Mareck, and N. A. Bosque-Perez. 1994. Comparison

of maize varieties for susceptibility to the maize weevil. IITA (Sept) 9: 11 - 16.

30. Larson, W. E. and J. J. Hanway. 1977. Corn production. In: G. F. Spraque (ed) *Corn and Corn Improvement*. Agron. Monogr. 18, ASA., Madison, WI.

31. Li-RuMing, M. S. Kang, O. J. Moreno, L. M. Pollak, and R. M. Li. 1998. Genetic variability in exotic x adapted maize (*Zea mays L.*) germplasm for resistance to maize weevil. Plant Genetic Resources Newsletter. (114): 22 - 25.

32. Lorenzoni, C. and M. Motto. 1985. Breeding Methodologies for Maize Quality Improvement. In: A. Blandolini, and F. Salamini (Eds.) *Breeding Strategies for Maize Production improvement in the Tropics*. FAO.

33. McCain, F. S., W. G. Eden, and D. N. Singh. 1964. A technique for selecting for rice weevil resistance in corn in the laboratory. Crop Sci. *4(1):109 - 110.*

34. McCain, F. S. and W. G. Eden. 1965. Corn hybrids sought with built-in insect resistance. Crops and Soils. 17(8): 27 - 28.

35. McMillian, W. W., N. W. Widstrom, and K. J. Starks. 1968. Rice weevil

damage as affected by husk treatment within methods of artificially infesting field corn plots. J. Econ. Entomol. 61: 918 - 921.

36. Morales, A. C. 1974. Nutritive value and susceptibility of opaque-2 composite K and different types of corn to the larger rice weevil *Sitophilus zeamais* Mots. Philippine Agriculturist. 1974. 58 (7/8):280 - 286.

37. Nhlane, W. G. 1989. Breeding flint maize hybrids (hard endosperm grain) in Malawi in response to small holder processing needs. In: *Maize improvement, Production and Protection in Eastern and Southern Africa*. Proceedings of the third Eastern and Southern Africa regional Maize workshop. Nairobi and Kitale, Kenya, Sept 18-22. 1989.

38. Pant, J. C., S. Kapoor, and N. C. Pant. 1964. Studies on the relative resistance of some maize varieties to *Sitophilus oryzae* (L). Indian J. Entomol. 26: 434 - 437.

39. Painter, R. H. 1951. *Insect Resistance in Crop Plants*. The Macmillan Co., New York. 521 pp.

40. Peters, D. C., M. S. Zuber, and V. Fergason. 1960. Preliminary evidence of resistance of high amylose corn to the angoumois grain moth. J. Econ. Entomol. 53 (4): 573 - 574.

41. Peters, L. L., M. L. Fairchild, and M. Z. Zuber. 1972 a. Effect of corn endosperm containing different levels of amylose on angoumois grain moth biology 1: life-cycle, certain physiological responses and infestation rates. J. Econ. Entomol. 65: 576 -581.

42. Peters, L. L., M. L. Fairchild, and M. Z. Zuber. 1972 b. Effect of corn endosperm containing different levels of amylose on angoumois grain moth biology 2: Physical and chemical properties of experimental corn. J. Econ. Entomol. 65: 581 - 584.

43. Purseglove, J. W. 1972. *Tropical crops- Monocotyledons.* Longman Scientific and Technical. John Wiley and Sons, Inc. New York.

44. Ramalho, F-de-S. 1976. Resistance of races, hybrids and varieties of corn in the shuck and as grain to *Sitophilus zeamais* Motschulsky, 1855. CAB-Plant Breeding Abstracts (1977)

45. Rhine, J. J. and R. Staples. 1968. Effect of high-amylose field corn on larval growth and survival of five stored grain insects. J. Econ. Entomol. 67:280-282.

46. Richards, O. W. 1944. The two strains of rice weevil, Calandra oryzae (L.) (Coleoptera: Curculionidae). Trans. R. Entomol. Soc. London 94Russell, M. P. 1962. Effects of sorghum hybrids on the development of the lesser rice weevil, *Sitophilus oryzae* (L.). Ann. Entomol. Soc. Amer. 55 (6): 678-85.

47. Russell, W. A. and A. R. Haullauer. 1980. Corn. In: R. W. Fehr, and H. H. Hadley (eds.) *Hybridization of Crop Plants.* Am. Soc. Agr. and Crop Sci. Soc. Am. Madison, Wisconsin, USA. 299 - 312.

48. Russell, M. P., and M. M. Rink. 1965. Some effects of sorghum varieties on the development of a rice weevil, *Sitophilus zeamais* (Coleoptera, Curculionidae). Ann. Entomol. Soc. Amer. 58 (5): 763.

49. Santos, J. P., P. E. O. Guimaraes, J. M. Waquil, and J. E. Foster. 1996. Resistance in maize weevil in quality protein maize lines and commercial corn hybrids. Resistant Pest Management 8 (1): 52 - 54.

50. Schoonhoven, A. V., C. E. Wassom, and E. Hober. 1972. Development of maize weevil on kernels of opaque-2 and floury-2, near isogenic corn inbred lines. Crop Sci. 12: 862 - 863.

51. Schoonhoven, A. V., R. B. Mills, and E. Hober. 1974. Development of

Sitophilus zeamais Motschulsky, in maize kernels and pellets made from maize kernel fractions. J. Stored Prod. Res. 10: 73 - 80.

52. Serratos, J. A., A. Blanco-Labra , J. T. Arnason and J. A. Mihm. 1994. Genetics of maize grain resistance to maize weevil . In: J. A. Mihm (Ed.) Insect resistant maize, Recent Advances and Utilization. Proceedings of International Symposium - CIMMYT, UNDP: 132 - 137

53. Signh, D. N. and F. S. McCain. 1963. Relationships of some nutritional properties of the corn kernel to weevil infestation. Crop Sci. 3: 259 - 261.

54. Sinha, R. N. 1984. Effects of weevil (Coleoptera: Curculionidae) infestation on abiotic and biotic quality of stored wheat. J. Econ. Entomol. 77: 1483 - 1488.

55. Tipping, R. W., P. L. Cornellius, D. E. Legg, C. G. Poneleit, and J. G. Rodriquez. 1989. Inheritance of resistance in whole kernel maize to oviposition by the maize weevil (Coleoptera: Curculionidae). J. Econ. Entomol. 82 (5): 1464 - 1466.

56. Tipping, P. W., K. L. Mikolajczak, J. G. Rodriquez, C. G. Poneleit, and D. E. Legg. 1987. Effects of whole corn kernels and extracts on behaviour of maize weevil (Coleoptera: Curculionidae). J. Econ. Entomol. 80 (5): 1010 - 1013.

57. Urrelo, R., V. V. Wright, R.B. Mills, and C. E. Wassom. 1989. Screening for resistance against the maize weevil *Sitophilus zeamaiz* (Coleoptera: Curculionidae) in Peruvian maize accessions. CAB - Plant Breeding Abstracts 1991

58. Van der Schaaf, P, D. A. Wilbur, and R. H. Painter. 1969. Resistance of corn to laboratory infestation of the larger rice weevil, *Sitophilus zeamais.* J. Econ. Entomol. 62: 352-355.

59. Widstrom, N. W., W. W. McMillian, L. M. Redlinger, and W. J. Wiser. 1983. Dent corn inbred sources of resistance to the maize weevil (Coleoptera: Curculionidae). J. Econ. Entomol. 76: 31 - 33.

60. Widstrom, N. W., W. D. Hanson, and L. M. Redlinger. 1975. Inheritance of maize weevil resistance. Crop Sci. 15: 467-470.

61. Wiseman, B. R., W. W. McMillian, and N. W. Widstrom. 1970. Husk and kernel resistance among maize hybrids to an insect complex. J. Econ. Entomol. 63:1,260-1262.